CENTRAL OREGON LANDWATCH

2843 NW Lolo Drive., Ste. 200 | Bend, OR 97703
Phone (541) 647-2930
www.colw.org

March 14, 2025

Filed via online comment system: https://cara.fs2c.usda.gov/Public/CommentInput?Project=64745

Jacqueline Buchanan, Pacific Northwest Regional Forester
Jennifer Eberlien, Pacific Southwest Regional Forester
United States Forest Service
1220 SW 3rd Avenue, Ste. G015
Portland, OR 97204

Re: Comments on Northwest Forest Plan Amendment Draft Environmental Impact Statement

Regional Forester Buchanan and Regional Forester Eberlien,

Central Oregon LandWatch submits these comments in response to the Draft Environmental Impact Statement ("DEIS") for the Northwest Forest Plan Amendment ("Amendment"), which was published in the Federal Register on November 15, 2024.

Central Oregon LandWatch ("LandWatch") is a conservation organization which has advocated for preservation of natural resources in Central Oregon for over 35 years. With over 950 members in Central Oregon, LandWatch has a long history of protecting the forests and streams in and around the Deschutes National Forest and other lands managed under the Northwest Forest Plan ("NWFP"). LandWatch's members and supporters live in Central Oregon, including on lands adjoining the Deschutes National Forest, and recreate in the Crescent, Fort Rock and Sisters Ranger Districts. They hunt, fish, take photographs, view wildlife, hike, drive, and engage in other recreational activities on National Forest lands, generally, and on lands within the boundary of the NWFP area specifically.

LandWatch's comments are focused on the NWFP area east of the Cascade Crest and primarily within the Deschutes National Forest, an extremely varied Central Oregon landscape ranging in elevation from 10,358 feet to 2,900 feet, and encompassing a broad spectrum of wildlife, plant groups, forest composition types, and fire regimes. Notably, it contains areas considered "dry forest," as well as areas of "moist forest" or mixed moisture composition.

Recent forest management projects on the Deschutes National Forest are often framed in terms of "forest restoration," with a narrow purpose and need centered reducing fuels and mitigating the perceived threat of extreme wildfire behavior.[1] The over-reliance on fuels-centric projects, however, is leading to an artificial ceiling on forest restoration efforts, the misapplication of treatments in the context of place, and increasing controversy in the Central Oregon region related to the management of National Forest lands.

[1] Examples include: Green Ridge Landscape Restoration; Cougar Rock Restoration Project; West Bend Vegetation Management Project.

While there is broad consensus that some ponderosa pine and dry-mixed coniferous forests under the NWFP are in a degraded state, defining the purpose and need for restoration is not without controversy; the when, where, why, and how to restore forest ecosystems east of the Cascades continues to be highly debated in scientific, public, and policy forums. The Forest Service's often narrow focus on reducing fuels to restore forest condition fails to address the full suite of factors that have fundamentally changed disturbance regimes and degraded forests. Further, a fuels-centric approach has significant tradeoffs for fish and wildlife, plant community pattern and composition, and is unlikely to meaningfully influence the 2 percent of fires that burn most forested acres.

In updating the NWFP, LandWatch continues to urge the Forest Service to consider establishing forest plan standards and other sideboards that help re-calibrate forest management and restoration projects east of the Cascades—especially where projects propose to address large-scale risks such as wildfire—and embrace a more balanced forest management framework that centers on ecological restoration and drivers of degradation. This framework should limit large tree logging, grazing, and road networks, reintroduce keystone species such as beaver, and balance the benefits of fire against its continued exclusion.

The United Nations Convention on Biodiversity has defined ecological restoration as:

> the process of managing or assisting the recovery of an ecosystem that has been degraded, damaged or destroyed as a means of sustaining ecosystem resilience and conserving biodiversity. Degradation is characterized by a decline or loss of biodiversity or ecosystem functions. Degradation and restoration are context-specific and refer to both the state of ecosystems and to ecosystem processes.[2]

Similarly, Stine et al. (2014) defined ecological restoration as:

> the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed. Ecological restoration focuses on re-establishing the composition, structure, pattern, and ecological processes necessary to facilitate terrestrial and aquatic ecosystem sustainability, resilience, and health under current and future conditions.

Recalibrating forest management to lead with ecological restoration is necessary to facilitate terrestrial and aquatic ecosystem resilience and health under current and future conditions. Further, by taking a more balanced approach to fuels management, restoration efforts can better address ecological concerns related to forest ecosystem structure, process, pattern, and composition, improve forest resiliency in the face of climate change, and decrease the level of controversy around federally managed public forests.

LandWatch appreciates the Forest Service's stated goal of implementing NWFP updates that reflect evolving social and ecological realities. However, the alternatives presented in the DEIS ultimately fail to lead with ecological integrity and resilience and largely propose to perpetuate a counter-productive fuels-

[2] UN Conference of the Parties to the Convention on Biological Diversity (2016). Ecosystem restoration: short-term action plan. https://www.cbd.int/doc/decisions/cop-13/cop-13-dec-05-en.pdf.

centric approach to forest management east of the Cascades.

In amending the NWFP, LandWatch urges the Forest Service to consider a more balanced approach to forest management and restoration that builds upon the core tenets and purpose of the 1994 plan, while beginning to rectify the exclusion of Tribes in the original NWFP. To that end, our comments focus on strengthening key management standards and sideboards around four themes: 1) ensuring that fuels-reduction efforts and timber harvest do not further degrade ecological integrity, wildlife habitats, and other key forest values; 2) meaningfully including Tribes, establishing co-stewardship, and respecting sovereignty; and 3) safeguarding mature and old-growth forests while improving our understanding of forest treatment outcomes in a changing climate.

The DEIS fails to offer a suite of updates that would cohesively solve any of these key social-ecological concerns, and fails to uphold the 1994 NWFP's original purpose, need, and spirit, which is a disservice to the communities and wildlife habitats in and around the NWFP planning area.

I. AMENDMENT PURPOSE AND NEED

The DEIS states that the purpose of the Amendment is:

> to amend, all or part of 17 national forest land management plans, as amended, within the NWFP area to establish new or modify existing plan components to better enable the Forest Service to meet the original intent of the 1994 NWFP to conserve mature and old-growth ecosystems and habitat for the conservation of northern spotted owl and other Endangered Species Act (ESA) listed and non-listed species, protect riparian areas and waters, and provide a sustainable supply of timber and non-timber forest products. (DEIS at 1-4)

The DEIS describes the need for the NWFP Amendment process as "driven by evolving ecological understandings and the need for the Forest Service to adapt their management strategies to current and future challenges" (DEIS at 1-5). This need comprises five key focus areas: (1) wildfire resistance and resilience; (2) climate change adaptation; (3) conserving and recruiting mature and old-growth ("MOG") forests, ensuring habitat for species dependent on MOG systems, and supporting biodiversity; (4) Tribal inclusion and incorporating Indigenous Knowledge into project planning and implementation; and (5) supporting the economic sustainability of communities near the NWFP planning area through a "predictable supply" of timber and non-timber products (DEIS at 1-5).

The purpose and need ostensibly align with the intent of the 1994 NWFP while acknowledging the need to adapt to shifting climatic, ecological, and social conditions and to include Tribes in NWFP development and implementation. However, the analysis contained within the DEIS fails to demonstrate that any of the Alternatives—including and especially the Proposed Action Alternative—would meet all of these needs. Instead, the DEIS continues to focus largely on logging to achieve unfounded fuels treatment targets, with no compelling evidence of the co-benefits to long-term wildfire resilience, climate change adaptation, mature and old-growth stands, threatened and endangered ("T&E") species, biodiversity, or local

economies. In fact, the DEIS repeatedly acknowledges the potential for the Alternatives to result in habitat degradation and fails to make the case that forest and non-forest products from the NWFP area will be a vital part of sustaining local communities. The DEIS also presents alternatives that would fail to uphold Tribal treaty rights, meaningfully include Indigenous knowledge, or guarantee Tribal co-management.

Ultimately, the proposed approaches in each of the Alternatives are inadequate to meet the Amendment's stated purpose and need. In other words, the DEIS fails to articulate a rational connection between the facts found and the conclusion made.[3]

II. INADEQUATE RANGE OF AMENDMENT ALTERNATIVES

Despite a vast, interconnected set of issues and goals identified in the purpose and need, the DEIS fails to evaluate a reasonable range of alternatives to fulfill the intent of this complex Amendment in accordance with the National Environmental Policy Act ("NEPA").[4]

In the DEIS, the Forest Service only analyzes four alternatives, including a No Action Alternative ("Alternative A"), a Proposed Action ("Alternative B"), and two action alternatives. By contrast, the 1994 NWFP considered and analyzed ten alternatives that covered a broad range of possible approaches to achieving the NWFP's original purpose and need. Even within the four alternatives, with regard to key issues such as age thresholds for logging late-successional and old-growth ("LSOG") stands, there are functionally only two alternatives. Of the four alternatives presented in the Amendment DEIS, the key proposed management thresholds and objectives for LSOG in dry forest Late-Successional Reserves ("LSR") and Matrix are the exact same in Alternatives A and C; the proposed thresholds in Alternatives B and D are also identical to one another. Effectively, this means that the Forest Service only analyzed two alternatives connected to one of the NWFP's core issues: conservation of mature and old-growth trees.

Courts have previously determined that where the Forest Service considered only a no-action alternative (in this DEIS, Alternative A and the identical Alternative C), and "two virtually identical alternatives" the agency "failed to consider an adequate range of alternatives."[5] Although there is no NEPA requirement for the minimum number of considered alternatives, an EIS that considers only two reasonable alternatives will rarely satisfy the statute's "hard look" standard.[6]

NEPA requires federal agencies to include a detailed statement on "a reasonable range of alternatives to the proposed agency action," and Forest Service regulations require an EIS to "document the examination of reasonable alternatives to the proposed action," which "should meet the purpose and need and address one

[3] *Mtr. Vehicle Mfrs. Ass'n v. State Farm Mut. Auto. Ins. Co*., 463 U.S. 29, 43 (1983) (The agency must "articulate a satisfactory explanation for its action including a rational connection between the facts found and the choice made.")
[4] 42 U.S.C. § 4332(2)(H)
[5] *Muckleshoot Indian Tribe v. U.S. Forest Serv.*, 177 F.3d 813 (9th Cir. 1999)
[6] *Native Ecosystems Council v. U.S. Forest Serv.*, 428 F.3d 1233 (9th Cir. 2005)

or more significant issues related to the proposed action.[7] To amend the NWFP in line with the DEIS's purpose and need, and comply with federal law, the Forest Service must analyze alternatives encompassing a range of additional potential activities, standards, guidelines, and desired conditions. For example, the Forest Service did not consider any alternatives that would eliminate commercial logging, eliminate salvage logging, emphasize managed wildfire, or holistically prioritize habitat conservation and restoration for the suite of important forest species beyond northern spotted owl. The Forest Service also did not consider a set of alternatives that would equally uphold Tribal treaty rights, ensure Tribal inclusion, establish durable co-stewardship, and elevate Indigenous Knowledge. Instead, the three action alternatives manufacture a trade-off between actively managing forests and fulfilling the agency's trust responsibilities.

At minimum, the Forest Service should have included at least one alternative considering and analyzing the following for the treatment of dry forests and/or forests east of the Cascades:

- Maximizing recruitment and retention of mature and old-growth trees and forests by only harvesting trees younger than 80 years.
- Mechanical treatment methods that only use thinning from below.
- Retaining all trees greater than or equal to 20 inches diameter at breast height ("DBH").
- Eliminating post-fire salvage logging.
- Prioritizing gappy-patchy-clumpy forest composition outcomes to support wildlife habitat needs, and in alignment with site-specific local information about best ecological practices.
- Retention of known migration corridors for terrestrial wildlife species, such as mule deer and elk. This would include considering an alternative to retain 20-40% cover in all known corridors as indicated by GPS collar data, mapped Oregon Department of Fish and Wildlife ("ODFW") Priority Wildlife Connectivity Areas ("PWCA"), or equivalent data-driven information.
- An alternative that does not contain arbitrary targets for the number of acres treated per decade. Treatment acreages should be site-specific, project-level decisions.

III. MEANINGFUL PUBLIC REVIEW AND INFORMED AGENCY DECISION-MAKING

a. Incomplete and Inaccurate Environmental Baseline

The Forest Service did not provide sufficient data regarding the baseline conditions in the NWFP area to support its conclusions. NEPA's primary purposes are to ensure fully informed decision-making by the agency and to provide for public participation in the environmental analysis and decision-making process.[8] To achieve these purposes, NEPA requires every federal agency to prepare an EIS for "all major Federal actions significantly affecting the quality of the human environment."[9] An EIS shall "provide full and fair discussion of significant environmental impacts and shall inform decisionmakers and the public of the

[7] 42 U.S.C. § 4332(2)(H); 36 C.F.R. § 220.5(e)
[8] 36 C.F.R. § 220.5(e)
[9] 42 U.S.C. § 4332(2)(C)

reasonable alternatives which would avoid or minimize adverse impacts or enhance the quality of the human environment."[10]

To comply with NEPA's "hard look" mandate, an agency must maintain inventories or otherwise collect and disclose information about the resources it manages so that an adequate baseline exists to evaluate the environmental impacts of a proposed action.[11] Without establishing the baseline conditions in the Project area before the action begins, "there is simply no way to determine what effect the [action] will have on the environment and, consequently, no way to comply with NEPA."[12]

Among other missing, incomplete, or inaccurate elements of the DEIS baseline, the Forest Service failed to adequately include or consider:

- **Barriers to Tribal stewardship, including cultural burning**. Despite the centrality of Tribal inclusion to this Amendment process, with cultural burning and beneficial fire at its core, the DEIS does not account for the existing bureaucratic and structural barriers to Indigenous fire use. The DEIS also does not disclose how and where beneficial fire use and other Indigenous stewardship practices will be applied, nor how these will supplant the existing fire suppression paradigm.
- **Methodological and spatial information on forest and forest treatment types.** The definitions of "dry" and "moist" forest provided in Appendix F and the guidelines for distinguishing between these forest types under FORSTW-ALL-GDL provide only the vaguest level of insight into the potential treatment approaches that might be employed under the Amendment (DEIS at A1-15). The process for determining dry or moist forest classifications remains unclear, which makes the coarse-resolution interactive map of dry and moist forest types nearly meaningless in assessing potential impacts of each alternative. The DEIS also lacks any mapping of past burn and vegetation removal areas, which would necessarily inform any analysis of potential impacts to dry and moist forest types.
- **Baseline in formation on eastside forest vegetation treatments and effectiveness monitoring.** The Forest Service failed to disclose and analyze data on vegetation treatment implementation and outcomes over the first 30 years of the NWFP. This data is critical to inform management in the future, and should necessarily inform priority actions for achieving desired ecological conditions.
- **Species distributions and statuses.** While the DEIS extensively lists various Threatened and Endangered Species that may occur within the NWFP area (DEIS at 3-52 to 3-55), it does not include baseline information on how the first 30 years of the NWFP has impacted these species in terms of population, distribution, or habitat. Instead, Section 3.5 only offers descriptions of habitat types and vegetation associations and incorporates by reference more detailed accounts of only a handful of species. Appendix C, the Draft Biological Evaluation ("BE"), lists 776 species that may

[10] Id.
[11] See *Neighbors of Cuddy Mountain v. U.S. Forest Serv.*, 137 F.3d 1372, 1379-80 (9th Cir. 1998).
[12] *Half Moon Bay Fishermans' Marketing Ass'n v. Carlucci,* 857 F.2d 505, 508 (9th Cir. 1988); see also *Am. Rivers v. FERC,* 201 F.3d 1186, 1195 & n.15 (9th Cir. 2000) (noting that an accurate and complete baseline against which to compare potential effects of reasonable alternatives is "critical" to the NEPA process).

be in the NWFP area, along with their associated habitat types, but does not provide any spatial information on their likely habitat distributions to compare to proposed treatments (DEIS at C-12 to C-57). For all but 9 of these species, the BE determines that the action alternatives will have "No Impact" or "May Impact Individuals or Habitats" (DEIS at C-8). However, without any spatial data or underlying analysis to reach those conclusions, this offers no meaningful information to decision-makers or the public.

- **Baseline conditions for Northern Spotted Owl habitat.** Given the NWFP's intent to protect and increase habitat for Northern Spotted Owl ("NSO"), it is imperative that the Forest Service disclose and analyze baseline conditions for NSO dispersal, nesting, roosting, and foraging habitats, all of which are central to determining suitable forest management approaches. This is particularly crucial in light of the emerging impacts of climate change and barred owl population expansion on NSO.
- **The NWFP's contributions or impediments to climate adaptation.** The DEIS lists carbon stocks by National Forest (DEIS at 3-87) and lists treatment acreages (DEIS at 3-93),[13] but does not attempt to analyze or quantify how existing or proposed management would influence any part of the NWFP area's capacity to adapt to climate change.
- **Wildfire, fuels treatment, and suppression history within the NWFP area.** The DEIS centers wildfire as a threat to communities and timber resources and especially highlights the need for fuels treatments in dry forests, yet does not analyze the specific histories of wildfires, logging, restoration work, or suppression activities that might influence shifting fire regimes or management decisions.
- **Impacts to aquatic and riparian ecosystems.** Although the DEIS does not propose changes to the Aquatic Conservation Strategy ("ACS"), it also contains no information on past or potential impacts to riparian and aquatic systems within the NWFP area. The proposed increases in logging, including in Riparian Reserves, will inherently affect aquatic ecosystems above and beyond the status quo. It is incumbent upon the Forest Service to fully study and disclose how the various alternatives could impact riparian and aquatic habitats.
- **Roads, routes, and trails.** The DEIS does not disclose or consider temporary and system road networks, ML 1-5 road densities, user created roads, trail networks, and other relevant data on existing roads and trails.

b. Failure to Disclose, Analyze, and Consider the Reasonably Foreseeable and Cumulative Effects of the Proposed Amendment

The agency must disclose, analyze, and consider the reasonably foreseeable[14] and cumulative effects[15] of a proposed action. NEPA's "action-forcing" procedures also require that an agency takes a "hard look" at the

[13] Without more information on forest composition or geography, acreage is a relatively meaningless proxy for carbon stores (M.E. Harmon, Deschutes Collaborative Forest Project presentation, February 13, 2025).
[14] 42 USC § 433(2)(C)
[15] 36 C.F.R. § 220.4(f)

environmental consequences of its proposed action in advance of a final decision.[16]

The DEIS fails to provide adequate information, evidence, and analysis for the public to assess the potential outcomes of the proposed alternatives. Instead, it relies on simply listing potential actions and biological resources, physically describing geographic areas, and summarizing research without connecting findings to the impacts of the NWFP itself. From these lists and descriptions, the DEIS then offers subjective assessments of potential effects without any data or evidence, nor any information about past and present project implementation within the NWFP area (See relevant discussion in DEIS Chapter 3, at 3-1 to -164). The DEIS also fails to consider the cumulative effects of other land management agency actions, such as the secession of 2.6 million acres of Bureau of Land Management ("BLM") land from the NWFP, which has resulted in increased logging of key resources formerly within the NWFP planning area. The Forest Service must consider and disclose the cumulative and reasonably foreseeable effects of increased logging on all federal ownerships as part of the FEIS. Similarly, the Forest Service must account for changes in the federal forest management policy landscape. The DEIS consistently defers to the National Old-Growth Amendment ("NOGA")—which was withdrawn in the final days of the Biden Administration—for meaningful protections of mature and old-growth trees. The FEIS must account for the reasonably foreseeable effects of NOGA's withdrawal and must adequately protect mature and old-growth trees and forests in the NWFP area in the absence of NOGA.

Concerningly, and as discussed further in sections below, the DEIS also fails to consider the direct, indirect, and cumulative impact of new roads. Roads are necessary to implement any of the alternatives, and to achieve the proposed dramatic increases in treatment acreages. Road construction, therefore, is a connected action that must be considered as part of the NWFP Amendment NEPA review.[17]

The Forest Service's failure to sufficiently disclose, analyze, and consider the direct, indirect, and cumulative effects of the Amendment violates NEPA and is arbitrary, capricious, an abuse of discretion, not in accordance with, and without observance of procedure required by law.[18] Additionally, the Forest Service has failed to demonstrate compliance with the 2012 Planning Rule and the National Forest Management Act.[19]

i. Simply Listing All Relevant Actions is Not the Same as Cumulative Effects Analysis

The DEIS particularly lacks adequate information on cumulative effects to allow for meaningful public review and an informed decision. The cumulative impact or effect from an action means "effects on the environment that result from the incremental effects of the action when added to the effects of other past, present, and reasonably foreseeable actions…Cumulative effects can result from actions with individually minor but collectively significant effects taking place over a period of time.[20] Accordingly, "[i]n a

[16] *Robertson v. Methow Valley Citizens Council*, 490 U.S. 332, 350–51 (1989).
[17] 40 C.F.R. § 1501.3(b)
[18] 5 U.S.C. § 706(2).
[19] 36 C.F.R. Part 219; 16 U.S.C. § 1600 *et seq.*
[20] 36 C.F.R § 220.4(f)

cumulative impact analysis, an agency must take a 'hard look' at *all* actions" that may combine with the action under consideration to affect the environment.[21]

"Simply listing all relevant actions is not sufficient."[22] Rather, "some quantified or detailed information is required. Without such information, neither the courts nor the public . . . can be assured that the [agency] provided the hard look that it is required to provide."[23] To be useful to decision makers and the public, a cumulative impact analysis must include "some quantified or detailed information; . . . general statements about possible effects and some risk do not constitute a hard look absent a justification regarding why more definitive information could not be provided."[24]

Except for minimal considerations of cumulative effects in Section 3.8 (See DEIS at 3-99, "Issue 7 – Sustainability of Regional Communities"), which extends its analysis into 72 "NWFP-socioeconomic region counties" (despite the NWFP area only intersecting 54 counties across Washington, Oregon, and California), the DEIS fails to address cumulative effects. For the other six key issue areas, the DEIS merely offers the types of "general statements about possible effects and some risk" that courts have deemed insufficient to constitute a "hard look." Section 3.9, "Cumulative Effects" (DEIS at 3-156) spends four pages listing other land management agencies and types, then simply enumerates some actions connected to each of the seven key issue areas. For each issue area, the DEIS presents no "quantified or detailed information" before drawing conclusions about action alternatives respective unspecified cumulative effects. For example, Section 3.9.2.2, "Issue 2 – Forest Stewardship," lists potential activities that other agencies could carry out, suggests that agencies may work together cooperatively, and then concludes "[t]he cumulative effects of the proposed action alternatives as they relate to forest stewardship would be expected to be overall beneficial when combined with other reasonably foreseeable future actions" (DEIS at 3-162). This does not constitute any analysis of the cumulative effects of forest stewardship activities and is so vague that it offers no insight to agency decision-makers or the public.

The Forest Service must revise and add to the DEIS's cumulative effects summaries to include detailed descriptions of past and present project activities that have altered the planning area (*i.e.*, the time, type, place, and scale). For example, the cumulative effects analysis should include consideration of:

- Past thinning and forest restoration projects;
- Past maintenance, construction, and temporary construction of roads, routes, and trails;
- Past wildfires and suppression activities;
- Recreation impacts;
- The combined effects of past thinning projects and recreation opening up the forest to higher levels of disturbance that impact wildlife habitats.

[21] *Te-Moak Tribe of W. Shoshone of Nev. v. U.S. Dep't of Interior*, 608 F.3d 592, 603 (9th Cir. 2010) (emphasis added).
[22] *Great Basin Res. Watch v. Bureau of Land Mgmt.*, 844 F.3d 1095, 1104 (9th Cir. 2016)
[23] *Neighbors of Cuddy Mountain v. U.S. Forest Serv.*, 137 F.3d 1372, 1379 (9th Cir. 1998).
[24] *Ocean Advocates v. U.S. Army Corps of Eng'rs*, 402 F.3d 846, 868 (9th Cir. 2005) (quoting *Neighbors of Cuddy Mountain*, 137 F.3d at 1379–80).

Only after analyzing these additional cumulative effects can the Forest Service fully understand and disclose the reasonably foreseeable effects of each alternative on each resource type n the NWFP.

IV. ECOLOGICAL AND CULTURAL ISSUES

a. Incorporation of Indigenous Knowledge and Increased Tribal Engagement

Central Oregon, including those lands managed by the Forest Service, are the original homelands of the Wasq'u (Wasco) and Tana'ma (Warm Springs) Tribes. The Klamath and Molalla tribes—among others—have also traditionally frequented this area, as have the Nama (Paiute), who were eventually forcibly relocated to the Warm Springs Reservation by the United States government. What we now know as Central Oregon are the ceded lands of the Confederated Tribes of Warm Springs (Wasco, Warm Springs, and Northern Paiute), where they reserve the right to hunt, fish and gather.

LandWatch supports amending the NWFP in a way that recognizes the role Indigenous peoples have played in stewarding forest landscapes, including those east of the Cascades, since time immemorial (Kimmerer & Lake, 2001; Steen-Adams et al., 2019). The final decision must ensure that Tribal inclusion, Tribal sovereignty, and Indigenous knowledge remain central to National Forest management, which should be conducted in co-stewardship with Tribal nations.

Here, LandWatch reiterates some of the key requests by the NWFP Federal Advisory Committee ("FAC") and the Northwest Forest Plan Just Futures Collaborative to ensure Tribal sovereignty. We recognize that these groups represent a subset of Tribal views, and we defer locally to the goals, approaches, ideas, and understandings of the Tribes whose lands are now considered part of the Deschutes National Forest.

i. Tribal Consultation is Required

Irrespective of the selected Amendment alternative or final Record of Decision, the Forest Service is legally obligated to consult early and often with Tribal governments to ensure that Indigenous people's interests and knowledge are brought forward in the planning process and that land use allocations do not conflict with landscapes of cultural significance or Tribal treaty rights. Given this, the No Action Alternative (Alternative A) is not a legitimate option, since it would continue to represent a NWFP devoid of Tribal input and would not rectify the Forest Service's long-term exclusion of Tribes, rejection of Indigenous Knowledge, and dereliction of its trust responsibilities.

ii. Strengthen and Retain All Tribal Inclusion Plan Components

The alternatives in the DEIS arbitrarily partition Tribal inclusion plan components and force a manufactured decision between upholding Tribal sovereignty and advocating for approaches that prioritize ecological landscape function over commercial logging. Given the primary of Tribal inclusion, Indigenous knowledge, co-stewardship, and trust responsibilities in this Amendment, the Tribal inclusion plan components warrant

consideration and adoption irrespective of the timber and restoration targets set in the updated NWFP.

We urge the Forest Service to retain all Tribal inclusion plan components present in Alternative B. Similarly, we urge the Forest Service to adopt Tribal inclusion measures only present in Alternative D—which particularly focus on first foods—into the Record of Decision. The Forest Service should also change all Forest Stewardship Potential Management Approaches (TRIBAL-FORSTW-ALL-PMA) to be standards so that they become enforceable, meaningful sideboards for Tribal inclusion.

iii. Address the Impacts of Tribal Exclusion

The DEIS does not fully confront the causes or consequences of Tribal exclusion—and by extension, fire exclusion—within the NWFP area. Echoing a request by the NWFP Just Futures Collaborative, we ask that the final Record of Decision better account for the role the Forest Service and the 1994 NWFP have played in perpetuating this exclusion by including the FAC's full Tribal Inclusion recommendations (NWFP Just Futures Collaborative at 2).

iv. Indigenous Knowledge Must be Central to the Amendment and Its Implementation

Although the DEIS presents alternatives that would substantially improve tribal inclusion and incorporation of Indigenous knowledge in the NWFP, its underpinning analyses include relatively little Indigenous science and knowledge. The alternatives also lack sideboards for ensuring that Indigenous knowledge will be a core part of any project-level assessment within the NWFP area. The FAC, which included members and representatives from a wide geographic range of Tribes in the NWFP area, offered extensive recommendations for objectives, standards, and guidelines that would better protect Indigenous sovereignty by consistently incorporating Indigenous knowledge in project planning and implementation. The proposed action (Alternative B) includes standards that protect Indigenous knowledge and require closer collaboration with Tribes (e.g., TRIBAL-COSTW-STD-01 and TRIBAL-IK-STD), but the final standards should go further to recognize Indigenous knowledge as a key basis for the development of any project.

For example, FAC recommendation 1-50, which is a Potential Management Approach for Tribal Forest Stewardship (see TRIBAL-FORSTW-ALL-PMA), should be an enforceable standard or guideline in the Final Decision: "Management activities shall consider Indigenous and western scientific research and ethnographic research related to relevant Tribal cultural land-use activities and interests when analyzing project effects. Ensure that no adverse effects are caused to any Treaty and other Tribal Rights, sacred places, practices, or elements of the landscape identified as culturally important to relevant Tribes" (FAC Recommendations at 15; DEIS at A1-8).

v. Remove Structural Barriers to Cultural Fire and Other Reserved Treaty Rights

While including cultural burning, prescribed fire, and managed wildfire to the DEIS alternatives represents an important shift in the NWFP's approach to wildfire and forest management, the DEIS does not account for the structural and bureaucratic barriers that currently limit cultural burning and Tribal-led prescribed

fire. Nor does the DEIS adequately include Tribal cultural objectives—rather than western silvicultural objectives—of forest stewardship. Rather than simply acknowledging beneficial fire, the Forest Service must analyze and disclose how it will ensure that beneficial fire use will be a meaningful part of implementing the amended NWFP. Similarly, the Forest Service must analyze and disclose spatial information indicating where beneficial fire may be used within the NWFP area and must also adopt policies that further clarify how and when prescribed fire and cultural burning will be employed. These additional analyses will provide necessary sideboards to ensure that fire inclusion—a critical part of Tribal inclusion—will occur in practice.

b. Forest Stewardship

The alternatives presented in the DEIS all substantially decrease protections for mature and old-growth trees in all forest types, while also proposing silvicultural treatment approaches that would prove counter to forest resilience, habitat, and climate goals and may also inhibit Tribal sovereignty.

i. Standards and Guidelines in Dry Forest Types

1. Decreased Protections for Mature and Old-Growth Trees

LandWatch is concerned by the proposal for reduced protections for mature and old-growth trees in both Late-Successional Reserves ("LSR") and Matrix in all alternatives. In Alternatives B and C, this change would allow harvest of trees up to 150 years old in dry LSR and trees established after 1850 in dry matrix (DEIS at 3-25). In Alternative D, trees and stands established after 1850 could be harvested in both dry LSR and dry matrix. For trees in the matrix under Alternatives B and C, the arbitrary proposed age thresholds contain significant exceptions for undefined "restoration" and to "reduce wildfire risks," while also substantially reducing protections for 936,000 acres within the NWFP area (DEIS at 3-29). Alternative D, meanwhile, guarantees that trees established after 1850 can never age into protection, which directly contradicts the NWFP's intent to conserve mature and old-growth forests and habitat. In dry forest LSR, this amounts to an estimated additional 1.23 million acres of potential treatment. Adding to the concern, these increased age thresholds would also apply to riparian forests in LSR (DEIS at 3-37). The DEIS does not offer any evidence or analysis to support these age threshold changes in any forest types, beyond vague assertions that the thresholds will help "address the need…for mature and old-growth forest conservation, while balancing for other priorities" (DEIS at 3-24).

The Forest Service has also precluded any meaningful public analysis of the impacts of these proposed changes, since the DEIS does not adequately define or quantify "dry forest" or "moist forest," so it is not clear exactly how or where these revised standards and guidelines ("S&Gs") would apply. It is important to note that forests east of the Cascades are dynamic and encompass a continuum of moist and dry forest types. For example, on the Deschutes National Forest, Sisters Ranger District, some of the best owl habitat is within the wet mixed conifer (referred to as "PST") Plant Association Group (PAG).[25] These areas are

[25] Green Ridge Landscape Restoration Project, Wildlife Report, EA, p. 38

not dry forests, but the lack of clarity around forest type definitions raises concerns that forest types like the PST PAG may be inappropriately managed.

The DEIS further prevents clear assessment by presenting a table summary of "Current and proposed LSOG management thresholds for conservation by alternative" (Table 3-2, DEIS at 3-25) that contains different information about age thresholds for harvest in various LUAs than the narrative descriptions of "Effects on late-successional and old-growth in dry forests in LSR and MLSA" (DEIS at 3-28 and 3-29) and "Effects on late-successional and old-growth in dry forests in Matrix" (DEIS at 3-30). Whereas Table 3-2 describes the age threshold for dry forest LSR and Matrix in Alternative C as being the same as Alternative A (80 year threshold), the narrative descriptions of Alternative C treatments in dry forest Matrix and LSR describe the threshold as 150 years, or identical to Alternative B. This type of confusing discrepancy renders it impossible to understand the intended goals or likely outcomes of the various Amendment alternatives.

Beyond the confusion and uncertainty introduced by the proposed decrease in protections for mature and old-growth forests, each of the alternatives would pose substantial threats to wildlife that depend on mature and old-growth habitat, as well as on the broader ecosystem integrity of forests east of the Cascades, which already have a deficit of large, old trees (Buotte et al., 2020; Mildrexler et al., 2020). The Forest Service has failed to disclose and consider the cascading impacts to threatened, endangered, and sensitive species that would result from its proposed actions in all dry forest LUAs. Relatedly, there is a significant contradiction between the Forest Service saying, on the one hand, that the Amendment will not cause "substantial adverse impacts" to any species (DEIS at 1-7), while allowing considerably more logging of mature and old-growth forests, and by extension eliminating suitable ecological conditions for multiple listed species and species of conservation concern.

2. Standards to Protect Large, Mature, and Old-Growth Trees and Forest Types

Instead of allowing increased logging of mature and old-growth forests and trees, the Amendment should include a standard that meaningfully protects all large, mature, and old-growth trees across the entire NWFP area, including in areas the Forest Service has determined to be at risk of large-scale disturbance. This type of standard would require managing NWFP area forests, and particularly dry forests, to maximize the recruitment and retention of mature and old-growth trees and stands. Such a standard is critical for forests and surrounding communities to receive the full benefits of healthy mature and old-growth forests.[26]

The best available science is clear that protecting mature and old growth forest conditions is essential to mitigating the impacts of climate change (Hudiburg et al., 2009; Law et al., 2018, 2022; Mildrexler et al., 2020), providing clean and cool water for fish, wildlife, and growing communities, and providing refuge for wildlife and people alike (Brandt et al., 2014). In fact, two of the architects of the original NWFP have called for an end to all logging of mature and old growth trees within the NWFP planning area.[27] As the

[26] 36 C.F.R. § 219.13(b)(6); 36 C.F.R. § 219.9(b)
[27] Guest Column: Protect older natural forests in the western Cascades (2021). *The Register-Guard*. Accessed February 14, 2025.

Federal Register Notice ("FRN") for the NWFP Amendment states, "[p]rotecting and enhancing biodiversity of mature and old growth ecosystems is a central tenet of the NWFP, and the 2012 Planning Rule's focus on ecosystem integrity emphasizes this priority. Mature and old growth ecosystems are critical components of biodiversity and provide carbon storage" (88 FR 87396). In considering management east of the Cascades, this central tenet must lead the development of all management actions, and the retention of all large trees should be part of all projects, which none of the DEIS alternatives guarantee.

Protecting mature and old growth trees on forests east of the Cascades does not prevent the Forest Service from implementing projects to address fuel concerns in forests where frequent fire was historically common. Large trees are not driving concerns related to fuel loading or the risk of large-scale disturbance. Removing small trees, including via methods such as thinning from below, can achieve fuels management objectives without logging large trees.

3. Removal of Risk Reduction Guideline in LSR

The shift from a guideline based on reducing risk of major disturbances in LSR east of the Cascades to a set of geographically undefined age thresholds is especially antithetical to the original intent of the NWFP. The 1994 NWFP defines LSR as forests containing mature and old-growth age classes of trees, and describes creating LSR with "an objective to protect and enhance conditions of late-successional and old-growth forest ecosystems, which serve as habitat for late-successional and old-growth forest related species including the northern spotted owl."[28] LSR, as such, is intended to mature into our future old-growth forests and treatments are only allowed in very specific, very limited circumstances. This is further emphasized by another 1994 NWFP LSR description: "these reserves represent a network of existing old-growth forests that are retained in their natural condition with natural processes, such as fire, allowed to function to the extent possible" (NWFP at B-4). Further, the Forest Service concedes "[LSR] forest communities are the result of a unique interaction of disturbance, regeneration, succession, and climate *that can never be recreated in their entirety through management*. The structure, species composition, and function of these forests are, in their entirety, not fully understood" (NWFP at B-5; emphasis added).

As such, the 1994 NWFP set guidelines that focused on young and plantation stand management to reduce the risk of catastrophic fire, with narrow exceptions for treatments in older LSR:

> While risk-reduction efforts should generally be focused on young stands, activities in older stands may be appropriate if: (1) the proposed management activities will clearly result in greater assurance of long-term maintenance of habitat, (2) the activities are clearly needed to reduce risks, and (3) the activities will not prevent the Late-Successional Reserves from playing an effective role in the objectives for which they were established. (NWFP at C-13)

[28] NWFP- *Standards and Guidelines for Management of Habitat for Late-Successional and Old-Growth Forest Related Species Within the Range of the Northern Spotted Owl- Attachment A to the ROD for Amendments to Forest Service and Bureau of Land Management Planning Documents Within the Range of the Northern Spotted Owl,* https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprd3843203.pdf, p A-1, B-1

Although this guideline may have ultimately placed too much emphasis on fire suppression, it also supported a management direction more focused on disturbance regimes and successional processes that could have been further enhanced in this DEIS through Tribal inclusion and beneficial fire use. Instead, the DEIS seemingly abandons the understanding of LSR as communities that cannot result purely from silvicultural prescriptions. Simultaneously, it fails to correct the 1994 NWFP's omission that Indigenous cultural burning was central to the development of the late-seral, mature, and old-growth conditions that provide for habitat, ecological function, and cultural needs.

Further, removing the three exception factors outlined in the 1994 guideline for risk-reduction treatments in older LSR threatens to undermine the purpose of the NWFP and its ability to protect the ecological integrity of east side forests. The three factors are important sideboards for guiding informed project development, and the DEIS fails to demonstrate how the removal of mature trees (up to 150 years in dry LSR) will reduce risks and support long-term habitat maintenance for NSO and other species. Logging large trees conflicts with the purpose of the original NWFP, exacerbates large tree structure scarcity problems, and provides little if any benefit to reducing the risk of large-scale disturbance events.

ii. End All Salvage Logging

The science has long been clear that there is no ecological reason to conduct salvage logging operations (Brown et al., 2004; Noss et al., 2006). The Forest Service should end salvage logging in all LUAs, including on both dry and moist forest types east of the Cascades. In not including a DEIS alternative without salvage logging, the Forest Service failed to consider reasonable Amendment alternatives.

Research has found that the detrimental effects of salvage logging can include increased fine fuels, decreased tree regeneration (Donato et al., 2006), soil compaction (Jennings et al., 2012), impaired water quality (Emelko et al., 2011), increased fuel loading (Donato et al., 2013), and altered bird nesting (Hutto & Gallo, 2006; Kronland & Restani, 2012), among other impacts. Salvage logging also has negative climate consequences: standing dead trees that remain post-fire continue to store substantial carbon (Harmon et al., 2011; Powers et al., 2013). The USFS literature review by Nemens et al. (2019) that the DEIS relies on to substantiate its commitment to salvage harvest specifically highlights each of these impacts. Yet, the DEIS insists there remains an open "public and scientific debate on the economic and accelerated forest development benefits of postfire harvest of fire-killed trees," despite not seriously analyzing any benefits beyond timber outputs (DEIS at 3-32). If any debate exists, it is around the tradeoffs between selling post-fire logged trees and ecologically degrading burned areas. The Forest Service uses this idea of a "debate" to justify including salvage logging in all alternatives, with no quantified analysis of the specific impacts to the NWFP area, nor any consideration of a no-salvage alternative.

Alternative C places the greatest restrictions on salvage logging, prohibiting its use in moist LSRs and limiting dry forest salvage for "protection of critical infrastructure, and along existing system roads" (FORSTW-ALL-DRY-STD-03-C; see DEIS at 2-20). We contend that this type of "salvage" would be better classified as hazard tree felling, and that this standard should be strengthened to only allow hazard tree felling within a specified narrow distance of roads or other infrastructure, which would retain

significant habitat benefits while removing hazards to humans and infrastructure.

iii. Setting Unsubstantiated Treatment Targets is Arbitrary and Capricious

Under the proposed action, the DEIS sets a target of logging one third of all dry forests in the NWFP area within 15 years of Amendment approval—790,000 to 964,000 acres every 15 years, not including acres of salvage logging (DEIS at 3-33). From an ecological, cultural, and climatic perspective, this is a completely arbitrary target that will also fail to meet fire resilience objectives. The DEIS lacks a rationale for why logging as much as four times more per decade than the current NWFP would achieve any of the DEIS's intended outcomes beyond potentially—though by no means certainly, given the depressed state of eastside timber markets—increasing decadal MMBF sales.

For all "dry forest" LUAs, the Forest Service proposes to conduct all logging projects and achieve timber production objectives using "ecological forestry methods," which the DEIS defines in Appendix F:

> Ecological forestry utilizes ecological models from natural forest systems as a basis for managing forests. It incorporates principles of natural forest development, including the role of natural disturbances, in the initiation, development, and maintenance of forests and forest landscape mosaics. Most importantly, ecological forestry recognizes that forests are ecosystems with diverse biota, complex structure, and multipole functions, and not simply collections of trees valuable primarily for the production of wood. In doing so it seeks to maintain the fundamental capacities (integrity) of the forest ecosystems to which it is applied (DEIS at F-2, citing Franklin et al., 2018).[29]

The stated structural complexity and biodiversity outcomes of "ecological forestry methods" are promising in a vacuum, but this definition offers no clarity as to how, where, or over what time scales the Forest Service might employ these methods. The vague concept of ecological forestry is especially concerning considering the arbitrary logging treatment acreage targets set by the DEIS. To truly achieve ecological outcomes and support natural disturbances as described the above definition, the Forest Service should lead with ecological forestry methods, which in turn should dictate the number of acres requiring treatment. As it stands, the DEIS has the order of operations reversed by starting with decadal treatment acreage targets, which will inevitably result in conflicts between timber production and the conditions dictated by ecological forestry modeling outputs. Without clearer methodology sideboards, this conflict will likely prioritize timber over any commitment to forest ecosystem diversity or structural complexity.

c. Fire Resistance and Resilience

Fire is a key ecological driver in Central Oregon forests, having shaped forest structure, process, pattern, and composition for millennia. There is little controversy over whether a lack of fire in forest communities that historically experienced frequent, low to mixed severity fires—such as lower elevation ponderosa pine

[29] This reference lacks a bibliographic entry in the DEIS, which makes it difficult to determine what, precisely, the Forest Service intends to cite. Presumably, the reference is to the 2018 textbook "Ecological Forest Management" by Jerry F. Franklin, K. Norman Johnson, and Debora L. Johnson.

and dry-mixed coniferous forests—has fundamentally transformed and contributed to the degradation of many of these forest ecosystems (Brown et al., 2004; Haugo et al., 2015; Noss et al., 2006). While public perception is often that too much of our forests are burning in the modern era, western forests continue to be in a fire deficit (Hessburg et al., 2021; Parks et al., 2015) and modern fire suppression efforts effectively put out 97-98 percent of all fire starts (Dombeck et al., 2004; Hessburg et al., 2021; North et al., 2015). The two percent of fires that escape suppression efforts are most often driven by extreme fire weather and account for 97 percent of all firefighting costs and area burned (Calkin et al., 2005; Hessburg et al., 2021).

The past century and a half of fire exclusion and suppression is also a direct result of Tribal exclusion from public lands. Indigenous peoples in the Pacific Northwest have practiced cultural burning since time immemorial, including east of the Cascades in what is now the NWFP area (Kimmerer & Lake, 2001; Steen-Adams et al., 2019). These practices were eliminated and criminalized as settler colonists began occupying the West and the Federal government dispossessed Tribes of land and culture (Long et al., 2021).

Changes in fire frequency and extent are just one of a suite of factors that have profoundly influenced forest ecosystems east of the Cascades. The transformation and degradation of lower elevation pine dominated forests and watersheds has primarily been driven by logging of large fire-resistant trees,[30] extensive road building, fire exclusion, and livestock grazing (Brown et al., 2004; Stine et al., 2014). The combination of these "drivers of degradation" have culminated in dramatic impacts to forest ecosystems, playing a leading role in the biodiversity crisis and the loss or near loss of multiple keystone species. Though the challenges related to addressing these drivers of degradation are large, each is fundamentally a resource management decision that can be changed, mitigated, or prohibited all together through this amendment

i. Fire inclusion is a necessary cultural and ecological practice

Mature and old-growth forests and trees have historically been an outcome—though not necessarily a direct objective—of Indigenous fire use, which helped maintain overall forest structure and biodiversity and eliminated smaller fine fuels on many forested landscapes (Long et al., 2021). By extension, the NWFP Amendment must include Indigenous cultural and prescribed burning as a critical management approach for supporting holistic forest function, particularly in fire-dependent forests east of the Cascade Crest. Cultural burning may support forest biodiversity and specialized habitat needs at a finer scale than is possible merely through frequent, low-severity wildfire (Long et al., 2021). Cultural burning—in combination with wildfire regimes—also supports the availability of First Foods, browse and forage for game species, and basketry materials (Anderson & Lake, 2016; Marks-Block et al., 2019, 2021; Steen-Adams et al., 2019).

The FEIS must retain cultural burning and other Indigenous stewardship elements to ensure that Indigenous fire practices are recognized as both vital and distinct from Western prescribed burning. Fuels reduction must not be the sole purpose of beneficial fire use in the Amendment. Protecting and prioritizing Indigenous

[30] Despite the ecological impacts, large tree logging continues to occur on the Deschutes National Forest: Group sounds alarm over plan to cut big, old trees near Bend - OPB (2022).

fire practices will help restore not only an ecological fire regime, but also a cultural fire regime across the NWFP area.

ii. Standards and Guidelines for Community and Infrastructure Protection

Despite the ostensible goal of enhancing community wildfire protection, the DEIS fails to take a hard look at the robust science around home hardening, defensible space, and human ignition prevention as the most effective ways to protect built infrastructure and people from wildfire damage (Cohen, 2000; Syphard et al., 2014). Rather, the Forest Service continues to rely on a wildfire management approach that "inverts" the wildfire problem by basing prevention strategies on the misguided idea that forests encroach on communities, rather than recognizing the reality that communities encroach on forests (Calkin et al., 2023).

Insofar as the DEIS devotes attention to community protection, the Guidelines for Fire Resilience under the proposed action specifically give primacy to fuels treatments (*i.e.*, vegetation removal) over the goals of other important ecological S&Gs. Guideline FIRE-ALL-GDL-03, for example, deprioritizes riparian reserve S&Gs in service of near-community vegetation removal: "In community protection areas, fuels treatments should take precedence over riparian reserve standards and guidelines when necessary to meet fire behavior objectives consistent with sustaining long-term aquatic ecosystem function (see DC-01; 1994 NWFP Standards and Guidelines page C-35, FM-01)" (DEIS at A1-26). Similarly, FIRE-ALL-GDL-04 supersedes *all other* S&Gs across all other LUAs in service of vegetation removal: "In community protection areas, fuels treatments should take precedence over other standards and guidelines across the LUAs when necessary to meet fire behavior objectives while meeting the long-term purposes of these LUAs (see DC-01)" (DEIS at A1-26). Meanwhile, "community protection area" is loosely defined as "locations where wildfire risks affect communities, tribal values, and infrastructure. There is significant risk of potential economic loss and public safety concerns posed by a wildfire occurring within this area" (DEIS at F-1). In other words, the Forest Service could determine that a community protection area exists almost anywhere, and accordingly remove vegetation deemed to be "hazardous fuels" at the expense of other important forest values.

Community protection is clearly an important and worthwhile aim of the Amendment, but these "community protection" S&Gs continue to rely on mechanical fuels reduction in wildlands as the primary solution to what is fundamentally a built infrastructure problem (Calkin et al., 2023). While fuels removal will undoubtedly play a role in enabling fire suppression tactics in and near communities, the Forest Service must do more to realistically face this problem by developing S&Gs that elevate the importance of home hardening and defensible space, and that use specific definitions of community risk that incorporate social vulnerability and adaptive capacity in addition to proximity to forests (Lacey et al., 2025).

iii. Standards and Guidelines for Prescribed and Cultural Burning

In amending the NWFP, new S&Gs should require understory burning to be the primary focus of projects proposing to remove small trees. Whether it is the only treatment, or implemented shortly after science-based thinning, carefully applied understory burning provides important ecological benefits, creating

landscape heterogeneity, reducing surface and ladder fuels, lowering stand densities, improving drought resistance of surviving trees, and may be the most appropriate treatment in riparian areas that historically experienced frequent fire (Brown et al., 2004; Kauffman et al., 1997; Knapp & Keeley, 2006; Mildrexler et al., 2023; van Mantgem et al., 2016). These S&Gs should support the use of both prescribed burning and cultural burning as forms of beneficial fire.

iv. Standards and Guidelines for Suppression Activities

Neither the existing NWFP nor the proposed Amendment alternatives include S&Gs for management during fire suppression. Given the DEIS's focus on refining and updating management guidance to address wildfire concerns—especially east of the Cascades—the Amendment should provide additional clarity around what actions are allowed during suppression activities, particularly in mature and old-growth forests.

For example, additional clarity is needed around how, when, and whether the Forest Service builds fuel breaks as part of suppression activities. The Forest Service should consider S&Gs that clearly define when and where fuel breaks are appropriate. Where fuel breaks are deemed necessary to suppression efforts, new S&Gs that provide clarity around how they are implemented will greatly reduce negative outcomes. For example, S&Gs around the development of gappy, patchy, clumpy fuel breaks and shaded fuel breaks where all large trees are retained would mitigate the potential ecological impacts of suppression activities.

The Forest Service should also develop S&Gs that account for emerging research indicating that wildfire management decisions—including using managed wildfire for resource benefit—are likely to result in better ecological outcomes and reduced high-severity fire when compared to mechanical management approaches (Furniss et al., 2024). Relatedly, the Forest Service should consider and adopt an alternative that includes S&Gs to more cautiously employ suppression tactics, given the evidence that intensive suppression leads to an increased proportion of high-severity, uncontrollable, and dangerous wildfires on forest landscapes, a phenomenon termed "suppression bias" (Kreider et al., 2024). Concerningly, the DEIS ties itself explicitly to the Wildfire Crisis Strategy, which implies continued primacy of fuels removal and fire suppression that will further entrench suppression bias without thoughtful S&Gs in place.

S&Gs for suppression activities will assist the Forest Service in fully meeting the original purpose of the NWFP, including conserving and mitigating impacts to mature and old-growth ecosystems, NSO and other species habitats, and riparian areas.

d. Biological Resources – Ecological Integrity and Habitat Protection

i. Standards and Guidelines to Protect the Ecological Integrity of Forests

The Forest Service should establish new forest plan S&Gs that protect the ecological integrity of the forest, including key wildlife habitat, under all management scenarios.[31] For example, the Forest Service should

[31] 36 C.F.R. § 219.9(a)(1)

develop and adopt a standard that protects all large (≥20 inches DBH), mature, and old growth trees. Large trees, regardless of species and age, provide critical wildlife habitat (both alive and dead), store the majority of forest carbon, are in a deficit east of the Cascades, and are generally the most fire-resistant trees on the landscape. Logging large trees as part of risk reduction efforts conflicts with the purpose of the original NWFP, exacerbates large tree structure scarcity problems, and provides little if any benefit to reducing the risk of large-scale disturbance events. Further, protecting large trees will reduce the controversy and contentious tradeoffs that surround large tree logging, thus streamlining silviculture prescriptions for LSR stands and improving the public's trust in the Forest Service.

Protecting large trees, landscape heterogeneity, and broader ecosystem integrity will require S&Gs that support the total ecological and cultural function of a landscape, rather than simply its silvicultural composition. While certain place-specific assessments and management approaches are appropriately left to the project level, landscape-scale analysis is still critical to guiding decisions at the National Forest or Ranger District level.

ii. Failure to Assess Aquatic and Riparian Impacts

LandWatch supports leaving the Aquatic Conservation Strategy ("ACS") intact as part of this Amendment process, and the Forest Service should ensure the ACS remains unchanged in the FEIS. However, a lack of change to the ACS direction and approach does not mean that the DEIS alternatives will not have impacts on aquatic and riparian ecosystems. The DEIS improperly dismisses impacts to aquatic and riparian resources from consideration under the premise that "impacts to water resources would not be expected to change under the Proposed Action and action alternatives because the proposed amendment does not modify the framework of the ACS" (DEIS at 1-12). This is flawed, unsubstantiated, and circular reasoning; effectively, the Forest Service claims that because the ACS Standards and Guidelines will remain in place, there cannot be meaningful effects on aquatic and riparian areas. Yet, the proposed action will explicitly increase logging in riparian reserves ("RRs"), and the proposed one million additional annual acres of logging activity will require road construction and maintenance likely to contribute to increased erosion, sedimentation, and other riparian impacts. Furthermore, the DEIS explicitly admits the possibility of impacts to aquatic species in its inclusion of 11 federally listed fish species "potentially affected by the Proposed Amendment Action or Action Alternatives," including multiple culturally important anadromous fish and sucker species (DEIS at 3-54 to 3-55). In relying on faulty logic and neglecting to disclose and consider the impacts of heavier logging in RRs, the Forest Service has failed to take a hard look at the reasonably foreseeable effects of the proposed actions on aquatic and riparian habitats and resources.

Although the DEIS fails to analyze potential impacts to listed fish and other aquatic species, the likely effects of management approaches such as removing large, old trees in RRs are distinct and well-understood. Large trees are integral to a variety of crucial aquatic and riparian ecosystem functions and processes—both as standing trees and downed wood (large woody debris)—such as helping to store sediments and nutrients, shaping channel morphology and instream habitats, supporting groundwater flows, and shading streams (Beschta et al., 1987; Bilby & Ward, 1991; Frissell et al., 2014; Pollock & Beechie, 2014). Removal of large riparian trees under the Amendment will trigger foreseeable adverse effects—both

direct and indirect—to threatened and endangered aquatic species and their habitat, including (but not limited to): Deficits of large woody debris and pool frequency; increases in stream temperature, peak flows, and sediment delivery; decreases in base flows; and reductions in habitat complexity. See the attached expert reports from fisheries biologist Amy Stuart and hydrologist Jonathan Rhodes for additional documentation of the importance of protecting aquatic and riparian systems in forests east of the Cascades.

The Forest Service must disclose and consider riparian and aquatic impacts of the proposed action and alternatives and must adopt an alternative that prevents further degradation of ESA-listed species habitats.

iii. Northern Spotted Owl Dispersal, Nesting, Roosting, and Foraging Habitat

Protecting NSO dispersal habitat is an essential management consideration east of the Cascades, especially as climate change and drought place additional stressors on wildlife species, shifting habitats and forcing species to adapt to survive (Buchanan, 2004). As of 2025, the plight of the NSO is urgent: forest losses and barred owl invasions have caused NSO populations to continue declining, prompting the US Fish and Wildlife Service ("USFWS") to recommend that NSO ESA listing status be changed from "threatened" to "endangered" (Davis et al., 2022).

NSO dispersal habitat is essential in supporting the transience and colonization phases of dispersal, which includes nesting, roosting, and foraging habitat ("NRF"). As research has found, "juveniles strongly select for old forest with closed canopy (>70 percent canopy cover) and large-diameter trees (>20 inch DBH), which are similar forest conditions selected by adult spotted owls for nesting and roosting" (Lesmeister et al., 2018). The same study found that canopy cover of 40% or less is "unlikely to be sufficient to facilitate juvenile movements on the landscape…Stands managed for dispersing spotted owls should be at least 80 percent canopy cover and have large average tree diameter" (Lesmeister et al., 2018). USFWS data collected to complete the 2011 NSO recovery plan further supports these statements, finding that "availability of suitable forest cover was critical for territory acquisition and sustained occupancy by spotted owls," and essential to NSO dispersal and survival (Lesmeister et al., 2018).

Logging one third of all dry forests in the NWFP area within 15 years of Amendment approval would have significant impacts on NSO habitats and raise concerns for dispersing wildlife in the face of climate change. While the acreage targets are framed as measures to improve forest resistance and resilience to fire, and to retain old trees, those outcomes are uncertain, whereas the scale of proposed treatments will directly impact the resilience of NSO by substantially changing habitat conditions.

Despite likely devastating NSO habitat, the proposed large-scale logging in the DEIS is also unlikely to prevent or mitigate fire severity and impacts during the period where fuels on the landscape remain reduced. Research by Baker and Rhodes (2008) demonstrated that the probability of high severity and high-moderate severity fires affecting treated areas in their window of effectiveness was very low, concluding that in "92-98% of treated areas, fuel treatment impacts on watershed processes are not likely to be counterbalanced by a reduction in higher-severity fire" (Baker & Rhodes, 2008). A 28-year study on NSO dispersal also found that while nesting habitat has been lost due to wildfire, very little loss of forest due to wildfire has

actually occurred in the dispersal areas studied (Jenkins et al., 2019).

Dispersal habitat on federal lands has seen a 1% increase since the NWFP was adopted (DEIS at 3-74), but the Forest Service fails to take a hard look at how fuels treatments in dry forests would impact dispersal habitat. The DEIS cites no studies or monitoring reports from projects east of the Cascades—where fuels treatments have specifically been implemented to address the perceived threat of fire—that could provide insights into the implications of the proposed actions on dispersal habitat and, by extension, the ability of species to move and adapt to changing climatic conditions. The DEIS also fails to consider that NSO may be using dry forests more frequently than previously understood, largely due to the threat of barred owls, which are less likely to use dry forests. The level of uncertainty and lack of supporting information on NSO habitat in the DEIS fails to support an informed process, and the Forest Service must account for the best available science on trends in NSO dispersal in the FEIS.

The DEIS states that the Amendment process is "driven by evolving ecological understanding and the need for the Forest Service to adapt their management strategies to current and future challenges" (DEIS at ES-2). To meet future challenges, including changing habitat conditions, wildlife must be able to move and disperse. Yet, the Forest Service fails to analyze any alternative that substantially increases dispersal habitat for NSO or other wildlife species.

iv. Failure to Analyze the Impact of Roads

The DEIS includes roads on the list of "Other Resources Considered or Dismissed," despite acknowledging:

> It is possible that the forest road networks could be affected by project/treatment-specific actions authorized by the proposed amendment. Potential effects to this resource may include the creation of new roads for logging, impacts to existing roads due to management activities, or construction or alteration of forest roads due to forest thinning or prescribed burns. (DEIS at 1-12)

The DEIS then dismisses this as an issue for consideration because "the scope, extent, and location of these effects cannot be determined at this time, and a project/treatment specific evaluation would be required for impacts to individual roads or road networks" (DEIS at 1-12).

The DEIS further goes on to say that:

> [t]he proposed NWFP amendment does not authorize or make any project-level decisions; therefore, the extent and location of project-specific ground-based disturbances (e.g., restoration treatments, prescribed burning, cultural burning, timber harvest, and road construction/reconstruction activities) are not known, nor is it possible to obtain this information at this time. (DEIS at 1-14)

Despite this explanation about why such information cannot be obtained, the DEIS repeatedly discusses restoration treatments, prescribed burning, cultural burning, and timber harvest within the scope of its proposed activities and Alternatives—all of which it acknowledges would require road construction—but

roads themselves remain absent from the analysis.

Extending the logic of excluding roads from the DEIS analysis, any projected timber targets or analyses of resource impacts in the NWFP planning area should have been dropped from consideration due to inability to determine "scope, extent, and location." If treatment acreage targets can be set in the NWFP amendment, there should be some ability to estimate additional road needs, associated potential habitat impacts, and long-term roadway restoration and decommissioning processes.

Road construction and maintenance are connected actions and must be analyzed in the EIS. As discussed previously in this comment, the Forest Service has failed to adequately address connected actions. Here, in order for the Forest Service to proceed with projects to meet the proposed dry forest logging targets outlined under the preferred alternative—logging 790,000 to 964,000 acres every 15 years, not including acres of salvage logging—the Forest Service will first need to conduct road maintenance and construction activities to facilitate logging access. Since increased logging targets and increased road construction and maintenance are necessarily connected, the Forest Service must analyze and disclose the extent, density, and impacts of anticipated road construction under the various alternatives. In particular, the new age thresholds and treatment acreage targets indicate substantially more roads would be necessary in LSR—a reasonably foreseeable effect which the Forest Service fails to address.

The biological impacts of roads are well documented. For example, additional sediment loads in streams over extended periods of time from timber harvest and roads have been known for decades. Bjornn and Reiser (1991) summarized that:

> Sedimentation affects fish habitat quality by increasing fines which embed gravels and substrates. Embedded gravels reduce spawning habitat by making gravel difficult to lift, reduces dissolved oxygen to incubating eggs, and covers rearing fish. Turbidity affects fish production by reducing production of aquatic insects and plankton, and foraging efficiency of fish. Sediment fills interstitial spaces between rocks in the substrate, reduces habitable area in streams, and when it exceeds 20 percent of the total area on the substrate, can smother fish and frog eggs and increase mortality.

May and Lee (2004) found that "increases in coarse sediment supply can be associated with sharp reductions in salmonid habitat and productivity" and reported that streams with discontinuous flow caused by sediment increases reduced survival by crowding fish into smaller areas with reduced food availability. The additional bedload of both fine sediments and coarser sediment delivered to streams fills in the channel, decreasing pool depth, channel complexity, and changing the channel profile to a shallow, wide profile.

Recent research by Kampf et al. (2021) on intermittent and ephemeral streams indicates that these nonperennial streams drain almost 60% of forested lands and are the primary connectors with aquatic systems. The authors stated that "land uses that modify flow regimes in these streams can affect sediment and organic matter transport and distribution, stream temperature dynamics, and biogeochemical processing" (Kampf et al., 2021). Even selective logging increases fine sediments along with increased water temperatures and these changes in habitat quality are found decades after logging activities have

ceased (Guenther et al., 2014; Kreutzweiser et al., 2005; Miserendino & Masi, 2010).

Upland impacts of roads are well known, too. For example, negative effects of motor vehicle use and roads on wildlife include wildlife mortality, decreased reproductive success, direct and indirect loss of habitat, displacement, and reduced habitat connectivity. These negative impacts are the result of a series of factors, including access for predators and people, fragmentation of habitat patches, behavioral changes in response to human use, increased noise, and physical alteration of habitat. Further, motorized use of roads and routes substantially increases movement rates of wildlife, causing a series of cascading effects including higher stress levels, increased energetic costs, and reduced productivity.

The Forest Service must analyze the impacts of road construction activities as part of the same NEPA, including establishing an accurate baseline of the existing road network within the NWFP area.

v. Exemptions from Survey and Manage Requirements in Alternative D

Eliminating Survey and Manage requirements for "hazardous fuel reduction treatments" within 0.25 miles of communities, as proposed in Alternative D, is arbitrary and antithetical to the purposes of the NWFP (DEIS at 3-81 to 3-82). The DEIS fails to clarify what constitutes a "community" for purposes of hazardous fuels reduction treatments and does not justify the selection of a 0.25-mile buffer. The only reasoning for this set of exemptions seems to be fast-tracking fuels removal, but with no justification as to why this would require an exemption from Survey and Manage requirements, nor how such an exemption would improve community wildfire safety. Under no circumstances should the Forest Service adopt an alternative that would decrease species protection, particularly with no evidence that this approach would increase community safety.

e. Climate Change and Carbon Storage

A need to incorporate considerations around climate change, ecological integrity, and carbon purportedly drove this Amendment process. However, the DEIS neither meaningfully analyzes how the proposed action would impact climate adaptation and carbon storage, nor how the proposed Amendment alternatives would interact with current and anticipated social, ecological, cultural, and economic impacts of climate change. NEPA calls on agencies to "fulfill the responsibilities of each generation as trustee of the environment for succeeding generations,"[32] and the Forest Service has blatantly failed to do so in this DEIS.

i. Climate Adaptation

It is incumbent upon the Forest Service to disclose and consider the climate implications of its management decisions within the Amendment, yet the DEIS contains almost no information on climate change adaptation in NWFP forests. To support an informed process, the DEIS should have incorporated the best available, regionally relevant research, such as the biannually-updated Oregon Climate Assessments[33] and

[32] 42 U.S.C. § 4331(b)(1)
[33] Oregon Climate Change Research Institute released the 7th Oregon Climate Assessment on January 8, 2025.

equivalents from Washington and California as baseline data on climate impacts and adaptation.

Climate change projections—and their implications for adaptation and adaptive management—should be central to any adopted alternative. Only Alternative D explicitly calls for analysis of projected climate impacts on vegetation, but this type of consideration should be present in any adopted alternative in conjunction with the best available science on ecological forest stewardship (DEIS at 2-12). Further, to ensure Tribal inclusion and co-stewardship, the Forest Service must incorporate components from Tribal climate adaptation plans into its FEIS.[34]

ii. Carbon Storage

To the extent that carbon stocks matter to the NWFP Amendment *per se* in the context of climate change, it is as a form of mitigation, with National Forests providing substantial aboveground and belowground carbon sinks. Instead of emphasizing the important role of forest carbon—particularly in mature and old-growth forests—as a climate mitigation strategy, the DEIS offers a faulty and cherry-picked analysis of carbon stocks and storage that over-emphasizes the role of wildfire in forest carbon emissions and uses the concept of "carbon stability" in confusing and irrelevant ways (see DEIS at 3-86 to 3-93).

The over-emphasis on wildfire-induced carbon emissions also omits any comparative analysis between fire-based emissions and carbon storage losses from logging large, old trees. This is a critical omission; since before the development of the 1994 NWFP, research has demonstrated that harvesting old-growth trees and converting forests to be younger and faster-growing will *not* result in decreased atmospheric CO2. Instead, post-logging forest carbon storage is greatly reduced and does not return to old-growth capacity for at least 200 years. This is true even when accounting for ongoing storage in timber products (Harmon et al., 1990). In eastside forests, retention of the largest, oldest trees is especially critical for carbon storage. East of the Cascades, only 3% of remaining trees are considered large (≥21" DBH), but these trees store 42% of aboveground forest carbon (Mildrexler et al., 2020). Larger, older trees in dry forests are also the most fire resistant and resilient.

Given the body of research on fire resilience and carbon storage in dry forests and forests east of the Cascades, it is particularly imperative to protect mature and old-growth trees in both dry forest matrix and LSR. The replacement of the risk-reduction guideline and the increase in harvest age thresholds are in direct conflict with the Amendment's stated goals of enhancing fire and climate resilience. Alternative proposals, such as creating reserves to protect forest carbon and reduce biodiversity loss, should have been considered alongside other carbon factors in the DEIS (Law et al., 2022). Without improved analysis and a more expansive view of forests' roles in both climate adaptation and mitigation, the Amendment will fail to meaningfully incorporate climate change considerations.

[34] The Tribal Climate Change Project maintains a Tribal Climate Change Guide that includes Tribal Climate Adaptation Plans from across the United States, including the Northwest.

V. EFFECTIVENESS MONITORING

Effectiveness monitoring has been part of the NWFP since its inception, under the premise that "[i]nformation gained through monitoring, research, and other sources of information provide a basis for adaptive management and decision-making based on best available scientific information (DEIS at 2-25). This Amendment should therefore update monitoring systems to better reflect the best available science on climate change, fire, habitat connectivity, and old growth forests. Updating these monitoring systems must also incorporate Indigenous knowledge and perspectives to fully inform both ecological and cultural outcomes of management decisions. Fundamentally, quality monitoring is key to adaptive management, which should be central to forest management in the context of climate change.

The Forest Service should consider and adopt new forest plan standards that require effectiveness monitoring for a percentage of all treated stands within a watershed to better understand the outcomes of management. For example, the Forest Service should adopt a standard that requires 15-20% of all treated stands within a watershed to be monitored for the duration of the plan, which could in turn inform adaptive management strategies for future treatment approaches. In addition, effectiveness monitoring should be triggered when a fire occurs within a watershed. Effectiveness monitoring is paramount to assessing whether treatments are attaining project goals, especially as it relates to wildlife habitat and risk reduction. An effectiveness monitoring program must be carefully developed and include a defined framework, with clear process for establishing a monitoring plan, implementation, and inter-disciplinary team review.

As part of an effectiveness monitoring program, the Forest Service must consider and specify how it will sustain monitoring efforts through time, including how efforts will be staffed and funded. The Forest Service should also consider what role local groups can play in assisting in effectiveness monitoring efforts. Harnessing Indigenous and local knowledge based on long-term observations and experiences, including community-based monitoring, can assist the Forest Service in achieving monitoring and adaptive management goals (Keenan, 2015). Tapping local knowledge can also improve agency relationships with the public and provide sustained institutional knowledge for an agency that sees high staff turnover at the forest level. This is especially important now, as the Forest Service is conducting mass firings and significantly impacting the ability of the agency to meet is Forest Plan obligations. The original NWFP was heavy on the promise of monitoring but often failed to deliver in practice. In amending the NWFP, the agency is obligated to recalibrate its monitoring goals and provide the necessary support to follow through.

VI. CONCLUSION

Amending the 1994 NWFP is necessary for the Forest Service to demonstrate its commitment to Tribal inclusion, ecologically sound wildfire management, and adaptive management practices in the context of a rapidly warming climate. We urge the Forest Service to use this opportunity to elevate non-timber interests to holistically manage the 17 NWFP National Forests for the benefit of present and future generations.

Further, Amending the NWFP provides the Forest Service an opportunity to improve public trust and transparency in how our National Forests are managed. The recent trend of transitioning from standards to

guidelines has caused significant concern and increased uncertainty around forest management outcomes, eroding public trust in the Forest Service as an institution. The DEIS largely continues this trend away from standards—and even, in several alternatives, from guidelines—toward ever-greater forest-level discretion. Maintaining and building upon standards, especially for wildlife and ecological integrity, is vital for ensuring transparency around intended project outcomes and management actions. Forest plan standards are a cornerstone to public trust with the Forest Service; further eroding standards will only lead to more conflict and increased public mistrust of the agency.

Thirty years after the NWFP's initial adoption, and in a time of great ecological and social uncertainty, it is time for the Forest Service to update its management approach in the Pacific Northwest to fulfill its responsibilities to the people and species of the region. We urge the Forest Service to adopt a NWFP Amendment that prioritizes Tribal inclusion, supports ecological integrity, protects habitat quality and connectivity, and integrates beneficial fire use at scale.

Thank you for considering these comments. Please retain Central Oregon LandWatch on your list of interested public for this project.

Sincerely,

Fiona Noonan
Wild Lands & Water Program Manager
Central Oregon LandWatch
fiona@colw.org

CC:

Ben Gordon
Executive Director
Central Oregon LandWatch
ben@colw.org

Jeremy Austin
Wild Lands & Water Program Director
Central Oregon LandWatch
jeremy@colw.org

References

Anderson, M. K., & Lake, F. K. (2016). Beauty, Bounty, and Biodiversity: The Story of California Indian's Relationship with Edible Native Geophytes. *Fremontia, 44*(3), 44–51.

Baker, W. L., & Rhodes, J. J. (2008). Fire Probability, Fuel Treatment Effectiveness and Ecological Tradeoffs in Western U.S. Public Forests. *The Open Forest Science Journal, 1*(1), 1–7. https://doi.org/10.2174/1874398600801010001

Beschta, R. L., Bilby, R. E., Brown, G. W., Holtby, L. B., & Hofstra, T. D. (1987). Stream Temperature and Aquatic Habitat: Fisheries and Forestry Interactions. In E. O. Salo & T. W. Cundy (Eds.), *Streamside Management: Forestry and Fishery Interactions* (pp. 191–232).

Bilby, R. E., & Ward, J. W. (1991). Characteristics and Function of Large Woody Debris in Streams Draining Old-Growth, Clear-Cut, and Second-Growth Forests in Southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(12), 2499–2508. https://doi.org/10.1139/f91-291

Bjornn, T.C. and Reiser, D.W. (1991). Habitat requirements of salmonids in streams. In Meehan, W. (Ed) Influences of forest and rangeland management on salmonid fishes and their habitats. *American Fisheries Society Special Publication, 19*, 83-138.

Brandt, P., Abson, D. J., DellaSala, D. A., Feller, R., & von Wehrden, H. (2014). Multifunctionality and biodiversity: Ecosystem services in temperate rainforests of the Pacific Northwest, USA. *Biological Conservation*, *169*, 362–371. https://doi.org/10.1016/j.biocon.2013.12.003

Brown, R. T., Agee, J. K., & Franklin, J. F. (2004). Forest Restoration and Fire: Principles in the Context of Place. *Conservation Biology*, *18*(4), 903–912. https://doi.org/10.1111/j.1523-1739.2004.521_1.x

Buchanan, J. B. (2004). In My Opinion: Managing habitat for dispersing northern spotted owls—Are the current management strategies adequate? *Wildlife Society Bulletin*, *32*(4), 1333–1345.

Buotte, P. C., Law, B. E., Ripple, W. J., & Berner, L. T. (2020). Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States. *Ecological Applications*, *30*(2), e02039. https://doi.org/10.1002/eap.2039

Calkin, D. E., Barrett, K., Cohen, J. D., Finney, M. A., Pyne, S. J., & Quarles, S. L. (2023). Wildland-urban fire disasters aren't actually a wildfire problem. *Proceedings of the National Academy of Sciences*, *120*(51), e2315797120. https://doi.org/10.1073/pnas.2315797120

Calkin, D. E., Gebert, K. M., Jones, J. G., & Neilson, R. P. (2005). Forest service large fire area burned and suppression expenditure trends, 1970-2002. *Journal of Forestry. 103(4): 179-183.* https://research.fs.usda.gov/treesearch/24526

Cohen, J. D. (2000). Preventing Disaster: Home Ignitability in the Wildland-Urban Interface. *Journal of Forestry*, *98*(3), 15–21. https://doi.org/10.1093/jof/98.3.15

Davis, R. J., Lesmeister, D. B., Yang, Z., Hollen, B., Tuerler, B., Hobson, J., Guetterman, J., & Stratton, A. (2022). *Northwest Forest Plan—The First 25 Years (1994–2018): Status and Trends of Northern Spotted Owl Habitats* (General Technical Report No. PNW-GTR-1003). U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Dombeck, M. P., Williams, J. E., & Wood, C. A. (2004). Wildfire Policy and Public Lands: Integrating Scientific Understanding with Social Concerns across Landscapes. *Conservation Biology*, *18*(4), 883–889. https://doi.org/10.1111/j.1523-1739.2004.00491.x

Donato, D. C., Fontaine, J. B., Campbell, J. L., Robinson, W. D., Kauffman, J. B., & Law, B. E. (2006). Post-Wildfire Logging Hinders Regeneration and Increases Fire Risk. *Science*, *311*(5759), 352–352. https://doi.org/10.1126/science.1122855

Donato, D. C., Fontaine, J. B., Kauffman, J. B., Robinson, W. D., & Law, B. E. (2013). Fuel mass and forest structure following stand-replacement fire and post-fire logging in a mixed-evergreen forest. *International Journal of Wildland Fire*, *22*(5), 652. https://doi.org/10.1071/WF12109

Emelko, M. B., Silins, U., Bladon, K. D., & Stone, M. (2011). Implications of land disturbance on drinking water treatability in a changing climate: Demonstrating the need for "source water supply and protection" strategies. *Water Research*, *45*(2), 461–472. https://doi.org/10.1016/j.watres.2010.08.051

Frissell, C. A., Baker, R. J., DellaSala, D. A., Hughes, R. M., Karr, J. R., McCullough, D. A., Nawa, R. K., Rhodes, J., Scurlock, M. C., & Wissmar, R. C. (2014). *Conservation of Aquatic and Fishery Resources in the Pacific Northwest: Implications of New Science for the Aquatic Conservation Strategy of the Northwest Forest Plan*. Coast Range Association.

Furniss, T. J., Povak, N., Hessburg, P. F., Salter, R. B., Duan, Z., & Wigmosta, M. (2024). Wildfire management decisions outweigh mechanical treatment as the keystone to forest landscape adaptation. *Fire Ecology*, *20*(1), 105. https://doi.org/10.1186/s42408-024-00339-y

Guenther, S. M., Gomi, T., & Moore, R. D. (2014). Stream and bed temperature variability in a coastal headwater catchment: Influences of surface-subsurface interactions and partial-retention forest harvesting. *Hydrological Processes*, *28*(3), 1238–1249. https://doi.org/10.1002/hyp.9673

Harmon, M. E., Ferrell, W. K., & Franklin, J. F. (1990). Effects on Carbon Storage of Conversion of Old-Growth Forests to Young Forests. *Science*, *247*(4943), 699–702. https://doi.org/10.1126/science.247.4943.699

Harmon, M. E., Woodall, C. W., Fasth, B., Sexton, J., & Yatkov, Misha. (2011). *Differences between standing and downed dead tree wood density reduction factors: A comparison across decay classes and tree species* (No. NRS-RP-15; p. NRS-RP-15). U.S. Department of Agriculture, Forest Service, Northern Research Station. https://doi.org/10.2737/NRS-RP-15

Haugo, R., Zanger, C., DeMeo, T., Ringo, C., Shlisky, A., Blankenship, K., Simpson, M., Mellen-McLean, K., Kertis, J., & Stern, M. (2015). A new approach to evaluate forest structure

restoration needs across Oregon and Washington, USA. *Forest Ecology and Management*, *335*, 37–50. https://doi.org/10.1016/j.foreco.2014.09.014

Hessburg, P. F., Prichard, S. J., Hagmann, R. K., Povak, N. A., & Lake, F. K. (2021). Wildfire and climate change adaptation of western North American forests: A case for intentional management. *Ecological Applications*, *31*(8), e02432. https://doi.org/10.1002/eap.2432

Hudiburg, T., Law, B., Turner, D. P., Campbell, J., Donato, D., & Duane, M. (2009). Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. *Ecological Applications*, *19*(1), 163–180. https://doi.org/10.1890/07-2006.1

Hutto, R. L., & Gallo, S. M. (2006). The Effects of Postfire Salvage Logging on Cavity-Nesting Birds. *The Condor*, *108*(4), 817–831. https://doi.org/10.1093/condor/108.4.817

Jenkins, J. M. A., Lesmeister, D. B., Forsman, E. D., Dugger, K. M., Ackers, S. H., Andrews, L. S., McCafferty, C. E., Pruett, M. S., Reid, J. A., Sovern, S. G., Horn, R. B., Gremel, S. A., Wiens, J. D., & Yang, Z. (2019). Social status, forest disturbance, and Barred Owls shape long-term trends in breeding dispersal distance of Northern Spotted Owls. *The Condor*, *121*(4), duz055. https://doi.org/10.1093/condor/duz055

Jennings, T. N., Smith, J. E., Cromack, K., Sulzman, E. W., McKay, D., Caldwell, B. A., & Beldin, S. I. (2012). Impact of postfire logging on soil bacterial and fungal communities and soil biogeochemistry in a mixed-conifer forest in central Oregon. *Plant and Soil*, *350*(1–2), 393–411. https://doi.org/10.1007/s11104-011-0925-5

Kampf, S. K., Dwire, K. A., Fairchild, M. P., Dunham, J., Snyder, C. D., Jaeger, K. L., Luce, C. H., Hammond, J. C., Wilson, C., Zimmer, M. A., & Sidell, M. (2021). Managing nonperennial headwater streams in temperate forests of the United States. *Forest Ecology and Management*, *497*, 119523. https://doi.org/10.1016/j.foreco.2021.119523

Kauffman, J. B., Beschta, R. L., Otting, N., & Lytjen, D. (1997). An Ecological Perspective of Riparian and Stream Restoration in the Western United States. *Fisheries*, *22*(5), 12–24. https://doi.org/10.1577/1548-8446(1997)022<0012:AEPORA>2.0.CO;2

Keenan, R. J. (2015). Climate change impacts and adaptation in forest management: A review. *Annals of Forest Science*, *72*(2), 145–167. https://doi.org/10.1007/s13595-014-0446-5

Kimmerer, R. W., & Lake, F. K. (2001). The Role of Indigenous Burning in Land Management. *Journal of Forestry*, *99*(11), 36–41. https://doi.org/10.1093/jof/99.11.36

Knapp, E. E., & Keeley, J. E. (2006). Heterogeneity in fire severity with early season and late season prescribed burns in a mixed conifer forest. *International Journal of Wildland Fire. 15:37-45*, *15*, 37–45. https://doi.org/10.1071/wf04068

Kreider, M. R., Higuera, P. E., Parks, S. A., Rice, W. L., White, N., & Larson, A. J. (2024). Fire suppression makes wildfires more severe and accentuates impacts of climate change and fuel accumulation. *Nature Communications*, *15*(1), 2412. https://doi.org/10.1038/s41467-024-46702-0

Kreutzweiser, D. P., Capell, S. S., & Good, K. P. (2005). Effects of fine sediment inputs from a logging road on stream insect communities:a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology*, *39*(1), 55–66. https://doi.org/10.1007/s10452-004-5066-y

Kronland, W. J., & Restani, M. (2012). Effects of Post-Fire Salvage Logging on Cavity-Nesting Birds and Small Mammals in Southeastern Montana. *The Canadian Field-Naturalist*, *125*(4), 316. https://doi.org/10.22621/cfn.v125i4.1260

Lacey, L. M., Suraci, J. P., Littlefield, C. E., Busse, B. S., & Dickson, B. G. (2025). Informing proactive wildfire management that benefits vulnerable communities and ecological values. *People and Nature*, *7*(1), 52–66. https://doi.org/10.1002/pan3.10733

Law, B. E., Hudiburg, T. W., Berner, L. T., Kent, J. J., Buotte, P. C., & Harmon, M. E. (2018). Land use strategies to mitigate climate change in carbon dense temperate forests. *Proceedings of the National Academy of Sciences*, *115*(14), 3663–3668. https://doi.org/10.1073/pnas.1720064115

Law, B. E., Moomaw, W. R., Hudiburg, T. W., Schlesinger, W. H., Sterman, J. D., & Woodwell, G. M. (2022). Creating Strategic Reserves to Protect Forest Carbon and Reduce Biodiversity Losses in the United States. *Land*, *11*(5), 721. https://doi.org/10.3390/land11050721

Lesmeister, D. B., Davis, R. J., Singleton, P. H., & Wiens, J. D. (2018). *Chapter 4: Northern Spotted Owl Habitat and Populations: Status and Threats* (General Technical Report No. PNW-GTR-966; Synthesis of Science to Inform Land Management Within the Northwest Forest Plan Area, pp. 245–300). U.S. Department of Agriculture, Forest Service Pacific Northwest Research Station.

Long, J. W., Lake, F. K., & Goode, R. W. (2021). The importance of Indigenous cultural burning in forested regions of the Pacific West, USA. *Forest Ecology and Management*, *500*, 119597. https://doi.org/10.1016/j.foreco.2021.119597

Marks-Block, T., Lake, F. K., Bliege Bird, R., & Curran, L. M. (2021). Revitalized Karuk and Yurok cultural burning to enhance California hazelnut for basketweaving in northwestern California, USA. *Fire Ecology*, *17*(1), 6. https://doi.org/10.1186/s42408-021-00092-6

Marks-Block, T., Lake, F. K., & Curran, L. M. (2019). Effects of understory fire management treatments on California Hazelnut, an ecocultural resource of the Karuk and Yurok Indians in the Pacific Northwest. *Forest Ecology and Management*, *450*, 117517. https://doi.org/10.1016/j.foreco.2019.117517

May, C. L., & Lee, D. C. (2004). The Relationships among In-Channel Sediment Storage, Pool Depth, and Summer Survival of Juvenile Salmonids in Oregon Coast Range Streams. *North American Journal of Fisheries Management*, *24*(3), 761–774. https://doi.org/10.1577/M03-073.1

Mildrexler, D. J., Berner, L. T., Law, B. E., Birdsey, R. A., & Moomaw, W. R. (2020). Large Trees Dominate Carbon Storage in Forests East of the Cascade Crest in the United States Pacific Northwest. *Frontiers in Forests and Global Change*, *3*, 594274. https://doi.org/10.3389/ffgc.2020.594274

Mildrexler, D. J., Berner, L. T., Law, B. E., Birdsey, R. A., & Moomaw, W. R. (2023). Protect large trees for climate mitigation, biodiversity, and forest resilience. *Conservation Science and Practice*, *5*(7), e12944. https://doi.org/10.1111/csp2.12944

Miserendino, M. L., & Masi, C. I. (2010). The effects of land use on environmental features and functional organization of macroinvertebrate communities in Patagonian low order streams. *Ecological Indicators*, *10*(2), 311–319. https://doi.org/10.1016/j.ecolind.2009.06.008

Nemens, D. G., Varner, J. M., & Johnson, M. C. (2019). *Environmental effects of postfire logging: An updated literature review and annotated bibliography* (No. PNW-GTR-975; p. PNW-GTR-975). U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/PNW-GTR-975

North, M. P., Stephens, S. L., Collins, B. M., Agee, J. K., Aplet, G., Franklin, J. F., & Fulé, P. Z. (2015). Reform forest fire management. *Science*, *349*(6254), 1280–1281. https://doi.org/10.1126/science.aab2356

Northwest Forest Plan Federal Advisory Committee (2024). *Northwest Forest Plan Amendment: Federal Advisory Committee Recommendations to the U.S. Forest Service*. 1-89.

Northwest Forest Plan Just Futures Collaborative (2025). Recommendations for Tribal Sovereignty and Environmental Justice in the Northwest Forest Plan Amendment Draft Environmental Impact Statement. Northwest Forest Plan Just Futures Symposium, Eugene, OR. https://blogs.uoregon.edu/nwfpjustfutures/resource-guide-for-making-public-comment/. Last accessed March 13, 2025.

Noss, R. F., Franklin, J. F., Baker, W. L., Schoennagel, T., & Moyle, P. B. (2006). Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment*, *4*(9), 481–487. https://doi.org/10.1890/1540-9295(2006)4[481:MFFITW]2.0.CO;2

Parks, S. A., Miller, C., Parisien, M.-A., Holsinger, L. M., Dobrowski, S. Z., & Abatzoglou, J. (2015). Wildland fire deficit and surplus in the western United States, 1984–2012. *Ecosphere*, *6*(12), 1–13. https://doi.org/10.1890/ES15-00294.1

Pollock, M. M., & Beechie, T. (2014). Does Riparian Forest Restoration Thinning Enhance Biodiversity? The Ecological Importance of Large Wood. *Journal of the American Water Resources Association*, *50*(3), 543–559.

Powers, E. M., Marshall, J. D., Zhang, J., & Wei, L. (2013). Post-fire management regimes affect carbon sequestration and storage in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management*, *291*, 268–277. https://doi.org/10.1016/j.foreco.2012.07.038

Spies, T.A., Stine, P.A., Gravenmier, R., Long, J.W., & Reilly, M.J. (eds). (2018). *Synthesis of Science to Inform Land Management Within the Northwest Forest Plan Area* (General Technical Report No. PNW-GTR-966). U.S. Department of Agriculture, Forest Service Pacific Northwest Research Station.

Steen-Adams, M. M., Charnley, S., McLain, R. J., Adams, M. D. O., & Wendel, K. L. (2019). Traditional knowledge of fire use by the Confederated Tribes of Warm Springs in the eastside Cascades of Oregon. *Forest Ecology and Management*, *450*, 117405. https://doi.org/10.1016/j.foreco.2019.06.002

Stine, P., Hessburg, P., Spies, T., Kramer, M., Fettig, C. J., Hansen, A., Lehmkuhl, J., O'Hara, K., Polivka, K., Singleton, P., Charnley, S., Merschel, A., & White, Rachel. (2014). *The ecology and management of moist mixed-conifer forests in eastern Oregon and Washington: A synthesis of the relevant biophysical science and implications for future land management* (No. PNW-GTR-897; p. PNW-GTR-897). U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/PNW-GTR-897

Syphard, A. D., Brennan, T. J., & Keeley, J. E. (2014). The role of defensible space for residential structure protection during wildfires. *International Journal of Wildland Fire*, *23*(8), 1165. https://doi.org/10.1071/WF13158

U.S. Department of Agriculture and U.S. Department of Interior. (1994). *1994 Record of Decision for Amendments to Forest Service and Bureau of Land Management Planning Documents within the Range of the Northern Spotted Owl*.

U.S. Department of Agriculture. (2024). *Northwest Forest Plan Amendment Draft Environmental Impact Statement, Vols. 1 & 2.* U.S. Forest Service Pacific Southwest and Pacific Northwest Regions.

van Mantgem, P. J., Caprio, A. C., Stephenson, N. L., & Das, A. J. (2016). Does Prescribed Fire Promote Resistance to Drought in Low Elevation Forests of the Sierra Nevada, California, USA? *Fire Ecology*, *12*(1), Article 1. https://doi.org/10.4996/fireecology.1201013

CENTRAL OREGON LANDWATCH

2843 NW Lolo Drive., Ste. 200 | Bend, OR 97703
Phone (541) 647-2930
www.colw.org

Attachment 1

Cited Literature Copies – Journal Articles and Professional Reports

BEAUTY, BOUNTY, AND BIODIVERSITY: THE STORY OF CALIFORNIA INDIANS' RELATIONSHIP WITH EDIBLE NATIVE GEOPHYTES

by M. Kat Anderson and Frank K. Lake

California supported a great diversity of plants with edible underground storage organs available to Indian tribes. Together, plant foods, fish and meat made up an indigenous diet that was well-rounded, diverse, and relatively secure. The edible underground parts possessed by these plants are classified as bulbs, corms, taproots, tubers and rhizomes, and when conditions turn unfavorable (too cold or too dry), the above-ground stems die back and the underground organs remain alive. Botanists and ecologists call the plants that employ this strategy *geophytes*. Indians often call them Indian potatoes or "root foods" because they are hidden under the ground. Geophytes were an important source of food for indigenous people throughout California.

STAPLE FOOD CROP

In pre-contact California there were dozens of species of geophytes gathered for their edible underground storage organs in multiple plant communities from the salt marshes, to the deserts, to chaparral, to the open understories of coniferous forests and oak woodlands. For example: the Ohlone dug the bulbs of harebell (*Campanula prenanthoides*) in winter and early spring for food in the vicinity of tan oaks; the Wailaki and Pomo harvested the bulbs of the fawn lily (*Erythronium oregonum*) in the openings amongst interior live oaks; and the Kashaya Pomo unearthed the tubers of elegant piperia (*Piperia elegans*) in dry areas between California black oaks. Some of the most important genera gathered by many







TOP: Raw camas (*Camassia* sp.) bulbs and brodiaea (*Brodiaea* and *Triteleia* spp.) corms on a bed of Pacific big leaf maple leaves prior to baking them in an earth oven. Photograph by Frank K. Lake, 2005. • BOTTOM LEFT: A bounty of camas (*Camassia quamash* subsp. *breviflora*) for food. Photograph by Heron Brae, 2012. The camas bulb, found several inches below the earth's surface, is about the size of a large hazelnut, but can grow as large as a walnut. Camas (*C. leichtlinii* subsp. *suksdorfii* and *C. quamash* subsp. *breviflora*) produces few offsets, but Native people note that when dug repeatedly and encouraged, they tend to divide. • BOTTOM RIGHT: Cooked camas (*Camassia* sp.) bulbs and brodiaea (*Brodiaea* and *Triteleia* spp.) corms wrapped in a bed of Pacific big leaf maple leaves after baking them in an earth oven. Photograph by Frank K. Lake, 2005.

tribes include *Allium*, *Brodiaea, Camassia, Chlorogalum, Calochortus, Dichelostemma, Lilium, Lomatium, Perideridia, Sanicula,* and *Triteleia.*

Indian potatoes were not only diverse, but also provided a variety of tastes to please the palate from slightly bitter, to mildly nutty, to sweet. They were eaten raw, boiled, baked, or steamed and then mashed, made into cakes similar to a frittata, bread or biscuits. Many of these geophytes were stored in their raw state in great quantities for later cooking and consumption or stored after baking, roasting and/or drying them.

The use of geophytes as part of the regular human diet in California





ABOVE RIGHT: Alferetta and Grapevine Tom, Achomawi, digging the edible, medicinal, and ceremonial tubers of *búlidum'*, (*Lomatium californicum*). A hardwood digging stick was the most common digging implement used up and down California to pry millions of plump, juicy bulbs, corms and tubers from the earth. Photograph by J.P. Harrington, Catalog number JPH-CA-AC-18. Courtesy of the Santa Barbara Museum of Natural History, circa 1931-32. • ABOVE LEFT: A close-up of the tubers of *búlidum'* (*L. californicum*), one of eight lomatiums with edible tubers eaten by California Indian tribes. Others include Wasatch desertparsley (*L. bicolor* var. *leptocarpum*), Canby's lomatium (*L. canbyi*), Gray's lomatium (*L. grayi*), bigseed biscuitroot (*L. macrocarpum*), Nevada biscuitroot (*L. nevadense*), Indian biscuitroot (*L. piperi*), and nineleaf biscuitroot (*L. triternatum*). Photograph by J.P. Harrington, Catalog number JPH-CA-AC-19. Courtesy of the Santa Barbara Museum of Natural History, circa 1931-32. • RIGHT: Edible, dried, peeled taproots of bigseed biscuitroot (*L. macrocarpum*), some of which have been ground into flour. They will be combined with dried huckleberries and pine nut flour to make pinch cakes. Photograph by Heron Brae, 2013.







TOP: Columbia lily (*Lilium columbianum*) and other lilies have bulb scales which readily separate and scatter in the digging process. The bulbs of this species and at least three other lilies were eaten by California Indian tribes including leopard lily (*L. pardalinum*), alpine lily (*L. parvum*), and Washington lily (*L. washingtonianum*). • BOTTOM: The larger bulbs of checker lily (*Fritillaria affinis*) were roasted in ashes or baked in earth ovens, and mashed and made into cakes by various tribes. It has numerous rice-grain bulblets that scatter when dug. At least three other fritillarias were gathered for food: brown bells (*F. micrantha*), yellow fritillary (*F. pudica*), and scarlet fritillary (*F. recurva*). Photographs by Fred Sharpe, 2007.

is very old. The archeological record shows that geophyte harvesting is at least 10,000 years old on the Channel Islands and that bulbs, corms, and tubers were more or less harvested in most if not all regions of the state during the last several thousand years. This storage organ had its own month in many tribal calendars, denoting a predictable, renewable food source. For example, one of the 12 moons of the Central Pomo year *Putitcda* (our May) meant "edible bulbs ripening." These storage organs also have high nutritional value, containing significant amounts of fiber, and complex carbohydrates.

Before the substantial ecological changes brought by European settlement, many of the geophytes of California had all of the attributes of a staple food crop: they were abundant, widespread, storable, intensifiable, and nourishing. As little as 200 years ago, many areas in California were clothed in geophyte flowers during the spring and summer—purple patches of blue dicks, orange swaths of tiger lily, yellow carpets of common goldenstars, and snowy areas of wild carrots. Early reports suggest that wildflowers with storage organs were much more prevalent historically and gathered in prodigious amounts. As will be discussed, the abundance of edible geophyte populations observed in certain areas around the time of contact (circa AD 1840–1850s) may have been due, in part, to human management of the plants and their habitats.

THE HARVEST

Gathering the edible parts of geophytes, hidden below the surface of the soil, required extraction with a digging stick sharpened to a point. While digging time spanned the whole year, May to late October was the peak season. Harvesting different genera of geophytes differed by tribe and area. For example, among the Karuk, of northwestern California, *Brodiaea*, *Calochortus*, *Dichelostemma*, and *Triteleia* were dug in the spring to summer and *Lilium* species in the fall. Traditional gathering sites were visited annually, and areas were specifically owned and maintained by particular families and passed down intergenerationally.

Despite relatively intensive, annual gathering, populations of geophytes remained robust. This was due in part to the gatherers' awareness of harvesting methods and how they affected the plant's regeneration and the overall health of the habitat. Always thinking about the harvest into the future, tribes made sure that the harvest would help increase future yields.

When indigenous people harvested geophytes, they did more than just retrieve the largest storage organs for consumption. They replanted the smaller bulblets, cormlets, tuber fragments, and bulb scales; they tilled the soil to facilitate the growth of the new plants; weeded non-desired plants; and they scattered the seeds contained within the dried seed pods to enhance reproduction. A grassland or coastal prairie subject to this kind of management might not show overt signs of human manipulation, but the valued foods would likely have broader distributions and higher population numbers than would be the case in the absence of any tribal manage-







UPPER LEFT: Blue dicks has dozens of different names in Indian languages and was probably the most widely eaten geophyte in California. The corms are eaten raw, boiled, or roasted in ashes. Photograph by M. Kat Anderson, 1988. • LOWER LEFT: A single blue dicks plant can produce a large number of both corms and cormlets. This and other underground swollen stems were eaten in great quantity and gathered at the same sites year after year by employing harvesting and management strategies designed to benefit populations and ensure their continuation. One of these techniques was to replant the cormlets after digging, while another is described by Mono elder Melba Beecher to ensure re-seeding: "The bulb [*Dichelostemma capitatum*] is harvested in late summer or early fall when the blooms are gone." Photograph by Kat Anderson, 1992. • RIGHT: Ross Stone, Big Pine Paiute, gathering *nahavita*, also known as blue dicks (*D. capitatum*) corms, a favorite traditional Paiute food on the east side of the Sierra Nevada. Photograph by Bill Helmer, 2005. All of the four other *Dichelostemma* spp. were also dug and eaten by California Indian tribes including fork-toothed ookow (*D. congestum*), firecracker flower (*D. ida-maia*), wild hyacinth (*D. multiflorum*), and twining brodiaea (*D. volubile*).

ment. Many tribal harvesters learned from, or emulated the digging-related disturbances of wildlife, such as gophers or bears.

The harvest of geophytes could be coupled closely with propagation because of the nature of their reproductive adaptations. Evolving in environments in which drought, fire, and herbivory were common, geophytes all developed clonal structures—offsets or propagules in the form of scales, bulbils, bulblets, or cormlets—which if severed or otherwise separated from the parent structure could grow into genetically identical plants. With these adaptations, disturbances, especially herbivory, that might threaten the existence of the parent plant were also likely to separate and disperse

the propagules—thus ensuring the continuation of the genome. In feasting upon these highly nutritious foods, gophers, voles, moles, bears, deer, or elk would simultaneously be acting as predators and dispersers. Native people who exploited geophytes as food were taking advantage of the pre-existing adaptations that made most geophytes excellent subjects for food intensification strategies.

Aerated and loosened with digging sticks, the soil had a higher moisture-holding capacity and became a better environment for seed germination and propagule growth. Native people also managed plant density, preferentially harvesting the densest patches to keep the plants from getting too clumped and thus maximizing production. Perhaps, most importantly, indigenous people made conscious decisions about what to harvest and what to leave behind, based on accumulated knowledge about the plants' reproduction and adaptive traits. In the case of blue dicks, for example, Leah Harper, Nor-Rel-Muk (pers. comm. 2003) explained how she harvested the largest organs and left in the soil the immature ones: "Grandma told us how to take the big bulb and leave the babies. And put them back in."



Ruby Pomona, North Fork Mono, with the edible *tana* or turkey pea (*Sanicula tuberosa*) dug in open black oak and ponderosa pine stands in Sierra National Forest. According to Ruby (pers. comm. 1989), *tana*, as well as a brodiaea with a purple flower, and wild carrot (*Perideridia* spp.), "came up better after a burn." The small tuber was gathered widely by the Mono, Nisenan, Pomo, Salinan, Sierra Miwuk, and Wailaki and it is still relished today and generally eaten raw. Already by 1932, Salinan consultants, Maria and David Mora, relayed to interviewer John P. Harrington that *tr'ôtêmák* (*Sanicula tuberosa*) is "scarce now." Photograph by M. Kat Anderson, 2006. At least two other sanicles were dug for their edible tubers, sharptooth blacksnakeroot (*S. arguta*) and poison sanicle (*S. bipinnata*).

Human geophyte harvesters could also benefit the plants' sexual reproduction by properly timing the harvest. When dug after seeds had matured, this process could facilitate dispersal of the seeds, which were more likely to find safe germination sites in tilled soil. It was a common practice to take this facilitation a step further by placing broken stems with seed pods into the holes before covering them. Undesirable plants were also weeded out to favor geophytes at many gathering sites—thus reducing competition and increasing site productivity.

Through observation and experimentation, Native Americans in California learned a great deal about the ecological requirements of the edible geophytes. The most important conclusion they came to was that fire was good for many of the "root foods," which included checker lilies, leopard lilies, sanicles, and wild carrots, among others. By burning geophyte habitats, Indians could maintain the sunny environments that most required, eliminate competition, reduce accumulated leaf litter and duff, that could block or hinder their emergence each year, and thus enhance reproduction. The results were manifested at both the individual and population levels: individual plants grew more vigorously, producing larger or more numerous underground storage organs, and populations were enlarged rela-



tive to what would have been the case without fire.

In the historical and ethnographic record there are accounts of Indians burning to enhance the geophyte harvest. For example, anthropologist J.W. Duncan equated the Maidu burning of oak areas with motive of fostering more bulbs and greens. Linguist Alice Shepherd (1989:411) recorded for the Wintu: "Where the ground has been burned, wild potatoes grow in bunches and ripen big...They go to find things there." Today Native elders equate productive bulb collection areas with deliberate burning or wildfires.

Because of their underground storage organs, geophytes are well adapted to withstand the effects of fire. Growing deep in soil, the bulbs, corms, and rhizomes are protected and insulated from the heat. Fire benefits geophytes in a number of ways, and are actually dependent on its regular occurrence.

One hypothesis is that for some geophyte species, fire confers its beneficial effects directly to the plants through heat. Their underground storage organs have contractile roots, and thus can pull themselves down deeper in the soil when stimulated by the heat of a fire. When this happens, the scales, bulblets, or cormlets attached to the main "mother" organ are stripped off. While attached, the growth of these clones is suppressed; when separated, they grow into new plants. In this direct way, therefore, fire promotes asexual reproduction and enlargement of population sizes. Geophytes receive



ABOVE: **Lois Conner Bohna (North Fork Mono/Chukchansi) sustainably harvesting wavyleaf soap plant (*Chlorogalum pomeridianum*) bulbs, another traditional food, by breaking them off at the root crowns and leaving them behind to grow into new plants. This was also a common practice among various Sierra Miwuk and Yokuts cultural groups. Photograph by M. Kat Anderson, North Fork, 2008. At least three other soap plants were harvested for food including narrowleaf soap plant (*C. angustifolium*), smallflower soap plant (*C. parviflorum*), and Santa Lucia purple amole (*C. purpureum* var. *purpureum*).** • RIGHT: **Lois Conner Bohna (North Fork Mono/Chukchansi) taking two additional conservation-minded steps. She scattered the seeds into the hole and covered them and the remaining root crowns with additional soil. This North Fork site had been burned the year before. She remarked: "Where it has been burned I find plants that are doubles, triples, and bigger clusters, and the bulbs are huge." Photograph by M. Kat Anderson, 2008.**



Tanya Spoonhunter, Dorothy Stewart, Jannah Terrazas, and Margaret Romero of the Big Pine Paiute tribe, displaying *nahavita* (*Dichelostemma capitatum*) corms that they will plant on their reservation in a large community garden plot and for a conservation field trial, October 2005. This effort is an example of diverse tribes bringing back traditional stewardship practices in various parts of California. Photograph by M. Kat Anderson.

most of the benefits of fire indirectly, however, through fire's effects on the environment or habitat in which they live. Thick layers of leaf litter and duff can inhibit or even prevent geophyte growth. The bulbs remain alive in the soil, but the accumulated dead biomass blocks the heat and light that would stimulate growth, and may even act as a physical barrier for sprouting. In overgrown areas, bulbs can sit in the soil bank for decades without growing. After the leaf litter and other biomass covering the soil are eliminated by fire, however, the plants are able to push through the blackened earth.

When fire reduces duff and litter, the sun can warm the soil thoroughly where the warming effect may increase by the light-absorbing black color of the carbon that results from burning. Such warming is necessary for both vegetative growth and flower bud differentiation, and it also provides the sequence of cold–warm–cold temperatures that most edible geophytes in California need for good bulb development. Warmer soil temperatures in the spring promote more flower buds, and this means more dry fruits with seeds that can grow into new plants. Fire's cleansing properties, are therefore, a mechanism which promotes larger and denser geophyte patches.

Fire also impacts geophytes through its effects on the soil. Burning releases a flush of nutrients, but Indian burning may also have changed the soil's texture or physical properties in ways that benefited geophyte growth and/or facilitated harvest by humans. The bi-product of burning woody material results in the production of charcoal or "biochar" that serves to increase soil porosity, nutrient retention and moisture holding capacity in addition to increasing soil texture complexity. Today, the traditional beneficial uses of biochar are being investigated and technologically developed for modern garden and agricultural uses.

Probably the most important effect of fire on geophytes is to maintain (or increase) the size of the areas in which the environmental conditions are suitable for geophyte

growth. To a great extent, this means simply eliminating or suppressing the growth of plants that compete with geophytes for light. Most edible geophytes require full or partial exposure to the sun to grow and reproduce properly. The flowering and bulbing of wild onions (*Allium* spp.) and wild lilies (*Lilium* spp.), for example, are greatly affected by how much light they receive. In the lily family, low light intensities usually result in flower abortion. The high light requirements of most geophytes are a primary reason for their occurrence in open habitats. When trees or brush encroach on open lands and create unfavorable shaded conditions, camas (*Camassia* spp.), leopard lily (*Lilium pardalinum*), wild onions, and other geophytes remain as a corm and bulb bank in the soil, their growth suppressed. With fire, plants are released from the shaded environments, and grow and flower vigorously. Flowering greatly benefited insects and other pollinators. Botanist Mark Skinner (pers. comm. 2007) said: "Burning definitely encourages (the growth of) many North American *Lilium* taxa. Some are adapted to frequent fires (*L. pyrophilum, L. iridollae, L. catesbaei*), some proliferate after fires (*L. washingtonianum*). I'm sure it's nutrient availability to some degree, but mostly it's light availability that drives that phenomenon."

CONCLUSIONS

Tribal gathering secured huge quantities of subterranean plant parts by revisiting the same traditional gathering sites. Tribal harvesting and management strategies were designed to benefit populations and ensure their continuation with ecological consequences for species, populations, and plant communities. The Native gathering and management systems have been in place long enough to influence what constituted fitness for evolving geophyte species. Over the last two centuries, there has been a general decline in geophyte populations, and today there are numerous rare and endangered geophyte taxa in California; this decline may be tied not only to habitat loss and fragmentation, but also to the termination of the former indigenous disturbance and management regimes under which the geophytes most recently evolved.

While few indigenous people gather or manage root foods today, this is changing. Tribes are renewing their gathering rights and practices, forming new collaborations with land management entities, setting up ethnobotanical gardens, creating their own land trusts, restoring digging, and returning fire to their reservations, rancherias, and other traditional lands. Many tribes are incorporating food security interests with landscape restoration strategies. An example is thinning of dense trees and shrubs and prescribed burning to meet the dual objectives of hazardous fuels reduction and the re-establishment of edible geophytes aligned with broader tribal resource objectives. These efforts are helping to restore the beauty, bounty, and biodiversity of California landscapes.

REFERENCES

Anderson, M.K. 1997. From tillage to table: The indigenous cultivation of geophytes for food in California. *Journal of Ethnobiology* 17(2):149-169.

Anderson, M.K. and D.L. Rowney. 1998. California geophytes: Ecology, ethnobotany, and conservation. *Fremontia* 26(1):12-18.

_____. 1999. The edible plant *Dichelostemma capitatum:* its vegetative reproduction response to different indigenous harvesting regimes in California. *Restoration Ecology* 7(3):231-240.

Clarke, P.J., M.J. Lawes, J.J. Midgley, B.B. Lamont, F. Ojeda, G.E. Burrows, N.J. Enright, and K.J.E. Knox. 2013. Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. *New Phytologist* 197(1): 19-35.

Coomes, O.T. and B.C. Miltner. 2016. Indigenous charcoal and biochar production: Potential for soil improvement under shifting cultivation systems. *Land Degradation & Development* 00:1-11. DOI: 10.1002/ldr.2500

Einert, A.E. and C.O. Box. 1967. Effects of light intensity on flower bud abortion and plant growth of *Lilium longiflorum*. *Proceedings of the American Society for Horticultural Science* 90:427-432.

Gill, K. 2014. Seasons of change: using seasonal morphological changes in *Brodiaea* corms to determine season of harvest from archaeobotanical remains. *American Antiquity* 79(4): 638-654.

Harrington, J.P. 1932. Tobacco among the Karok Indians of California. *Bureau of American Ethnology Bulletin* No. 94. Smithsonian Institution, Washington, D.C.

Le Nard, M. and A.A. De Hertogh. 1993. Bulb growth and development and flowering. In: *The Physiology of Flower Bulbs*. A. De Hertogh and M. Le Nard (eds.), pp. 29-43. Elsevier Science Publishers, Amsterdam, The Netherlands.

Major, J. 2013. Biochar: A new soil management tool for farmers and gardeners. *International Biochar Initiative and Appalachian Sustainable Development Bulletin*. 12 p.

Nabhan, G.P., D. Walker, and A.M. Moreno 2010. Biocultural and ecogastronomic restoration: The renewing America's Food Traditions Alliance. *Ecological Restoration* 28 (3): 266-279.

Shepherd, A. 1989. Wintu texts. *University of California Publications in Linguistics* Vol. 117. University of California Press, Berkeley, CA.

Stone, E.C. 1951. The stimulative effect of fire on the flowering of the golden brodiaea (*Brodiaea ixioides* Wats. var. *lugens* Jeps.). *Ecology* 32(3):534-537.

M. Kat Anderson, USDA NRCS, California State Office, 430 G. St., Davis, CA 95616; mkanderson@ucdavis.edu; Frank K. Lake, USFS Orleans Ranger Station, P.O. Box 410, Orleans, CA 95556; franklake@fs.fed.us

Fire Probability, Fuel Treatment Effectiveness and Ecological Tradeoffs in Western U.S. Public Forests

Jonathan J. Rhodes[1] and William L. Baker[*,2]

[1]*Planeto Azul Hydrology, PO Box 15286, Portland, Oregon 97293, USA*

[2]*Ecology Program and Department of Geography, Dept. 3371, 1000 E. University Ave., University of Wyoming, Laramie, Wyoming 82071, USA*

Abstract: Fuel treatment effectiveness and non-treatment risks can be estimated from the probability of fire occurrence. Using extensive fire records for western US Forest Service lands, we estimate fuel treatments have a mean probability of 2.0-7.9% of encountering moderate- or high-severity fire during an assumed 20-year period of reduced fuels.

INTRODUCTION

Fuel treatments to reduce fire impacts have been promoted as a public forest restoration priority by policy [1] and the Healthy Forests Restoration Act of 2003. It is difficult to generalize about the effectiveness of fuel treatments under all conditions [2, 3], but treatments are not universally effective when fire affects treated areas [4]. Factors influencing effectiveness include forest type, fire weather [4], and treatment method [5].

However, treatments cannot reduce fire severity and consequent impacts, if fire does not affect treated areas while fuels are reduced. Fuels rebound after treatment, eventually negating treatment effects [3, 6]. Therefore, the necessary, but not sufficient, condition for fuel treatment effectiveness is that a fire affects a treated area while the fuels that contribute to high-severity fire have been reduced. Thus, fire occurrence within the window of effective fuel reduction exerts an overarching control on the probability of fuel treatment effectiveness. The probability of this confluence of events can be estimated from fire records. Although this probability has not been rigorously analyzed, it has often been assumed to be high [7].

The probability of future fire occurrence also abets assessing the ecological risks incurred if fuels are not treated. Therefore, analysis of the likelihood of fire is central to estimating likely risks, costs and benefits incurred with the treatment or non-treatment of fuels.

Assessing fire occurrence and its effect on fuel treatment effectiveness also has merit because treatments can incur ecological costs, including negative impacts on aquatic systems [8], soils [7], and invasion by non-native plants [9, 10]. Here, we use watershed and aquatic systems as a specific context for evaluating tradeoffs involved with treatment and non-treatment of fuels on western public lands. However, the analysis applies to upland ecosystems as well.

The effects of fire on watersheds and native fish vary with several biophysical factors, including watershed and habitat conditions, the condition of affected populations, and fire severity and extent [11]. If treatments reduce the watershed impacts of severe fire, they may provide benefits that outweigh treatment impacts because high-severity fire can sometimes trigger short-term, severe erosion and runoff [12] that can negatively affect soils, water quality, and aquatic populations. However, fuel treatments can also have impacts on aquatic systems. The magnitude and persistence of these treatment impacts vary with treatment methods, location, extent and frequency.

Although some fuel-treatment methods could have lower impacts, ground-based mechanical treatments are often employed because other methods generate activity fuels [7] and are more costly. Ground-based methods and associated machine piling, burning of activity fuels, construction and increased use of roads and landings can increase soil erosion, compact soils, and elevate surface runoff [8, 13, 14]. Although the effects of prescribed fire on watersheds are typically limited and fleeting, it can increase soil erosion and sediment delivery, sometimes significantly and persistently [15], especially if fires escape and burn larger and more severely than planned.

When impacts are extensive, proximate to streams, or in terrain with erosion hazards, treatments can increase runoff and sediment delivery to streams. Road activities that increase sediment production, such as elevated road traffic, often affect stream crossings where sediment delivery is typically efficient and difficult to control [16]. Elevated sediment delivery to streams contributes to water quality degradation that impairs aquatic ecosystems [17].

The extent and frequency of treatments may be significant. Stephens and Ruth [18] suggested treating fuels on 9.4 million ha, or ~53% of USFS lands in the Pacific Northwest and California. Agee and Skinner [7] suggested repeating treatments every 10-20 years, due to transient effects on fuels.

Repeated treatments increase the potential for cumulative effects on aquatic ecosystems due to the persistence and additive nature of watershed impacts over time [19] and may increase the establishment of non-native plants [9]. The chronic watershed impacts from repeated treatments may be more deleterious to native fish than pulsed disturbances from wildfires [8].

*Address correspondence to this author at the Ecology Program and Department of Geography, Dept. 3371, 1000 E. University Ave., University of Wyoming, Laramie, Wyoming 82071, USA; E-mail: bakerwl@uwyo.edu

1874-4208/08 2008 Bentham Science Publishers Ltd.

Additional degradation of aquatic habitats on public lands may hamper efforts to protect and restore aquatic biodiversity. These habitats are increasingly important as cornerstones for restoring aquatic ecosystems and native fish [14].

Where fuel treatments might incur soil and watershed impacts, the risks from treatment and non-treatment should be assessed [7]. Although the respective impacts of treatments and fire are influenced by numerous factors, the occurrence of fire strongly affects the net balance between costs and benefits. If fire does not affect treated areas while fuels are reduced, treatment impacts on watersheds are not counterbalanced by benefits from reduction in fire impacts.

We provide a framework for quantitatively bounding the potential effectiveness of fuel treatments and the likelihood of fire affecting untreated watersheds, based on the probability of fire and the duration of treatment effects on fuels. This can be used to help statistically estimate the expected value associated with treatments or non-treatment based on the probability of possible outcomes and their associated costs and benefits [20]. Previous assessments of watershed tradeoffs from treatment and non-treatment [21, 22] did not include these in quantifying risk to aquatic systems associated with treatment versus non-treatment of fuels.

We use geographically-explicit data on fire on public lands in the western US to estimate, at a broad-scale, the probability that fuel treatments will be affected by fire during the period when fuels have been reduced. We also estimate the risk of higher severity fire occurring in watersheds if fuel treatments are foregone. These estimates provide a broad-scale bounding of treatment effectiveness and potential return from the fiscal and environmental costs of fuel treatments.

METHODS

The Analytical Model

Our analysis is based on the simple conceptual framework that unless fire occurs while fuels are reduced, fuel treatments cannot affect fire severity. We examine the probability of discrete classes of fire severity because fire impacts on watersheds vary with severity [11]. For instance, lower-severity fire has minimal, transient watershed impacts [11].

Future fire occurrence in specific locations cannot be predicted with certainty, but its probability can be estimated from empirical data. The probability of fire of a particular severity affecting treated areas can be estimated using the standard formula for the probability of an event occurring during a specific time frame:

$$q = 1 - (1 - p)^n \quad (1)$$

where q is the probability that a fire that would be of a specific severity in the absence of treatment occurs within n years, p is the annual probability of fire of a specific severity at the treatment location, and n is the duration, in years, that treatments decrease fuels and can reduce fire severity. In Equation 1, q provides an estimate of the mean fraction of an analysis area likely to burn at a specific severity within a given time frame in the absence of fuel treatments, which also represents the upper bound of potential effectiveness of treatments in reducing fire, since treatments cannot lower fire severity unless a fire occurs.

Both n and p can be estimated from available data. The duration of post-treatment fuel reduction, n, likely varies regionally with factors affecting vegetation re-growth rates, but fuels in western U.S. forests generally return to pre-treatment levels in 10-20 years [3, 7]. To estimate the upper limit of treatment effectiveness, we assume $n = 20$ years. We estimated the annual probability of fire of various severities, p, for each analysis area based on standard methods [23]:

$$p = (F*r)/(A*D) \quad (2)$$

where p is the annual probability of fire of a specific severity, F is total area burned at any severity within the analysis area over the duration of the data record, r is the estimated fraction of F that burned at the specified severity over the analysis area, A is the total analysis area, and D is the total duration of the data record, in years.

We based our estimates of the annual probability of fire on post-1960 fire records rather than reported natural fire return intervals for two primary reasons. First, evidence indicates that natural fire regimes no longer operate in many forests, because of direct fire suppression and indirect changes in fuels from livestock grazing, logging and fire exclusion [24]. Annual burned area has also increased in some forest types, likely due to climatic warming [25]. Recent fire data ostensibly integrate these alterations, reflecting how fires are likely to burn in the near future under current conditions and management. Natural fire return intervals do not capture these alterations. Second, there is considerable uncertainty regarding the accuracy of reported natural fire intervals [23, 24]. However, we stress that our approach can easily accommodate alternate estimates of annual fire probability using more geographically-refined data or where management changes might alter future fire probability.

We confined analysis to USFS lands in 11 western states, the focus for most proposed fuel treatments on public lands. The probability of fire varies geographically with several factors, including weather, ignition, fuels, and forest types. To bracket this effect, we estimated the annual probability of high-severity fire, p, for (*i*) all landcover types and (*ii*) more frequently burning ponderosa pine (*Pinus ponderosa*) forests at the scale of U.S. Forest Service (USFS) administrative regions that are the finest scale at which extensive data allow estimation of fire severity. We focus on high-severity fire, but also analyze fires of broader severity, including (1) either high- or moderate severity and (2) any severity.

Our estimates represent an initial, broad-scale first approximation of the potential of fire to affect areas within a given time frame, based on the assumption that fire and treatments are random. Although fire is not random, data are insufficient to accurately quantify more local patterns. Our approach provides a valid mean result at our scale of analysis, based on data from more than 40,000 fires across the western U.S. Site-specific data could be used in future, local studies where the probability of fire is known to depart considerably from the regional mean. Ideally, fuel treatments may not be randomly located, but instead focused in areas where fire is most likely. However, this is not assured by current policy [26]. Widely used methods for assessing the risk of high-severity fire may have limited accuracy [27].

Therefore, our analysis assumes random treatment location, as a first approximation.

West-Wide Analysis

To provide a broad-scale perspective of potential fuel treatment efficacy, we estimated mean annual probability, *p,* of fire for all USFS lands in the 11 western U.S. states, excluding Alaska, for the entire duration that data on total annual fire area are available (1960-2006). Data on fire area from 1993-2003, reported by agency ownership [28], were used to estimate mean annual fraction of total fire area on USFS lands, which was extrapolated to estimate mean annual fire area on USFS lands from 1960-1993 and 2004-2006, for which fire area data were reported [29], but not by agency ownership. Annual fire area on USFS lands in the 11 western states was assumed proportional to the fraction of total USFS area in these states. Total number of fires on western USFS lands from 1960-2006 is not reported, but based on the foregoing areal partitioning, the fire area data are from several hundred thousand fires on western USFS lands. The estimated annual fire area on these western USFS lands from 1960-2006 was summed to yield *F* in Equation 2.

The fraction of total fire area, *r*, that burned at high severity and high-moderate severity was estimated from data in USFS burned area emergency rehabilitation reports (BAER) for 470 fires in the 11 western states from 1973-1998 in six western USFS regions [30].

Regional Analysis of Fire in Ponderosa Pine

Because ponderosa pine forests are a key forest with more frequent fire, we estimated the mean annual probability of fire by severity in these forests on USFS lands: 1) on a regional basis, in six western USFS regions; and 2) West-wide. We used geographical information system (GIS) data for 40,389 fires in these forests for the entire period of data availability, 1980-2003 (Fig. **1**). Data were in a GIS point dataset, containing burned area for each fire, maintained by the Bureau of Land Management [31] and derived from a systematic National database [32]. We quality controlled these data for our study area, removing a few duplicate records.

A GIS map of ponderosa pine forests was obtained by selecting codes 5-7 (ponderosa pine) in the Westgap map from the GAP program, which includes national vegetation mapping from satellite imagery [33]. A GIS map of U.S. Forest Service regions is from the agency [34]. We converted all maps to Albers projection, Clarke 1866 datum, then used these to extract all fire records (n = 40,389) for ponderosa pine forests on USFS land in the 11 western states. We used USFS maps to subset fires by region, and then: (*i*) areas of individual fires were summed to yield *F* in Equation 2; (*ii*) the GIS was used to obtain *A*, and (*iii*) fire severity data by USFS region from 1973-1998 [30] were used to estimate *r* by severity.

RESULTS AND DISCUSSION

West-Wide Analysis

For the period 1960-2006, an estimated mean of ~220,000 ha, or a decimal fraction of 0.0037 of USFS western lands burned annually at any severity. Despite the approximations involved, our estimate of the mean annual fraction of areas burning at any severity compares reasonably with independent estimates by falling between them. Fire of any severity annually burned a mean fraction of ~0.0014 of the Deschutes National Forest in Oregon, from 1910-2001 [35], and ~0.0046 of 11 national forests in the Sierra Nevada, California, based on data from 1970-2003 [36].

Together with fire severity data [30], our West-wide estimate yields an estimated mean annual probability, *p*, of 0.001 and 0.002 for high- and high-moderate severity fire, respectively (Table **1**). Based on these estimates of *p*, Equation 1 yields a probability, *q*, of 0.020 and 0.042, respectively, for high- and high-moderate-severity fire. Substituting space for time, our results indicate that, on average, approximately 2.0 to 4.2% of areas treated to reduce fuels are likely to encounter fires that would otherwise be high or high-moderate severity without treatment. In the remaining 95.8-98.0% of treated areas, potentially adverse treatment effects on watersheds are not counterbalanced by benefits from reduced fire severity. These results also provide an estimate of the likelihood of high-severity fire affecting forests, if fuels are untreated. On average, over a 20-year period, about 2.0-4.2% of untreated areas would be expected to burn at high or high-moderate severity, respectively.

Using Equation 1, our results indicate that if treatments were repeated every 20 years across all USFS lands in the West, it would take about 720 years (36 cycles of treatments), on average, before it is expected that high-severity fire affects slightly more than 50% of treated areas while fuels are reduced. Treatments would have to be repeated at 20-year intervals for 340 years (17 cycles of treatments) before high-moderate severity fire is expected to encounter more than 50% of treated areas. Even after this duration of repeated treatments, it is likely that almost 50% of treated areas will be cumulatively affected by repeated treatments without compensatory benefits from reduced fire severity.

These West-wide estimates provide perspective, but include forest types, such as subalpine forests, typified by low-frequency, high-severity fire, where fuel treatments are unlikely to encounter fire [4]. Other forests, such as ponderosa pine, burn more often.

Regional Analysis of Ponderosa Pine

For ponderosa pine forests, the probability, *q*, of treated areas being affected within their window of effectiveness varies regionally from 0.020 to 0.040 for high-severity fires and from 0.042 to 0.079 for high-moderate severity fires (Table **1**). As expected, *q* in these forests is higher than for the West-wide analysis of all cover types. The highest probabilities, as expected, are in the Southwest and in the Northern Rockies, with its dry summers (Table **1**).

In these forests with more frequent fire, it is likely that fuel treatments can potentially reduce fire severity on a small fraction of treated areas. The results (Table **1**) indicate that in 92.1-98.0% of treated areas, fuel treatment impacts on watershed processes are not likely to be counterbalanced by a reduction in higher-severity fire.

Across the six regions, treatments would have to be repeated every 20 years for 340 to 700 years (17 to 35 times), on average, before it is expected that high-severity fire affects more than 50% of treated areas during periods of treat-

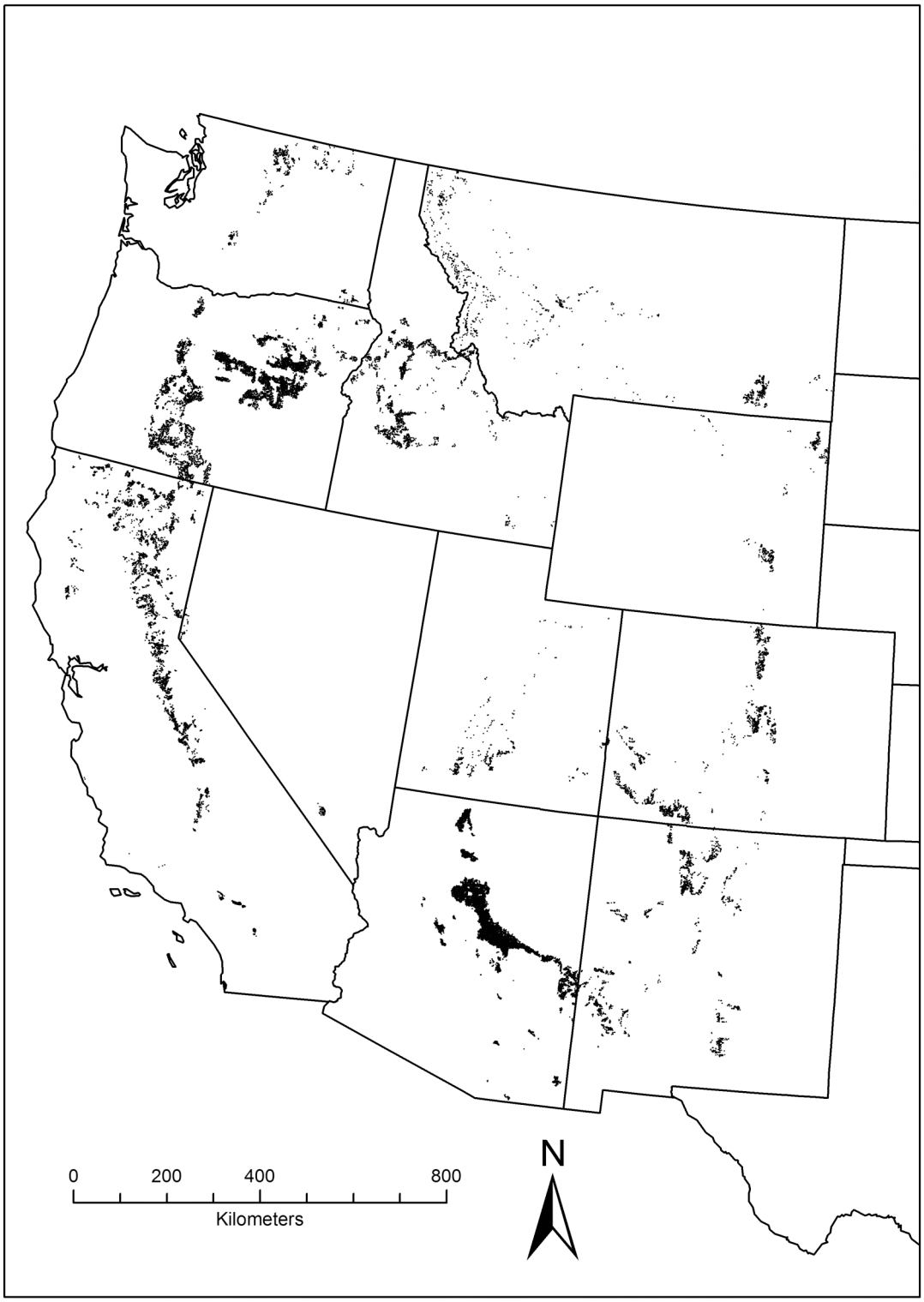


Fig. (1). Ponderosa pine forest fires (n = 40,389) in the western United States from 1980-2003. This is the dataset used in the regional analysis.

ment effectiveness. Treatments would have to be repeated for 180 to 340 years (9 to 17 times) before more than 50% of treated areas are expected to be affected by high-moderate severity fire. On average, these repeated treatments would affect watersheds and, potentially aquatic systems, depending on treatment practices, without providing reduction in fire severity on almost 50% of treated area.

An alternative method for estimating the risk of fire in the absence of fuel treatments is to use the fire rotation rather than mean annual probability of fire. The fire rotation indicates how long it takes, on average, for a particular area to burn one time and how often fire may return to a particular point in the landscape [23]. The fire rotation is calculated by:

$$B = 1/p \quad (3)$$

Table 1. Estimated *p* and *q* for Fires in Ponderosa Pine (PIPO) Forests. Data are Shown for Three Fire Severity Classes by USFS Region, and for All Forests on USFS Lands West-Wide

USFS Region	Any Severity		High-Moderate Severity		High Severity	
	p	q	p	q	p	q
1 N. Rockies	0.0070	0.1311	0.0036	0.0693	0.0020	0.0402
2 C&S Rockies	0.0059	0.1116	0.0041	0.0786	0.0014	0.0269
3 SW	0.0053	0.1008	0.0025	0.0487	0.0016	0.0307
4 Gt. Basin	0.0090	0.1654	0.0037	0.0715	0.0013	0.0257
5 Calif.	0.0046	0.0881	0.0031	0.0603	0.0017	0.0338
6 NW	0.0037	0.0715	0.0022	0.0421	0.0010	0.0198
West-wide: PIPO	0.0054	0.1026	0.0031	0.0602	0.0015	0.0295
West-wide: All types	0.0037	0.0715	0.0021	0.0416	0.0010	0.0203

where B is the fire rotation for fire of a specific severity and p is, again, the mean annual probability of fire of a specific severity.

Based on our analysis, the mean annual probability, p, of high-severity fire in ponderosa pine forests West-wide is 0.0015 (Table **1**), implying a fire rotation, B of about 667 years, varying from 500 to 1,000 years among individual regions. Based on the results in Table **1**, the fire rotation for high-moderate severity fire is about 323 years in ponderosa pine forests West-wide, varying from 244 to 454 years in individual regions, based on data in Table **1**. These results suggest that western ponderosa pine forests are not currently being rapidly burned by high or high-moderate severity fire, counter to other previous work [37].

Relaxing the Assumptions and Some Caveats

In some cases, the occurrence of fire of any severity may be of interest. Such cases include areas where fire of any severity might lead to high-severity fire. In ponderosa pine forests, the probability of fire of any severity encountering treatments within 20 years is approximately 7.15-16.5% across the six regions (Table **1**). Thus, if it is assumed that fuel treatments that encounter fire of any severity might be effective, the results indicate fuel treatments, on average, would not have the potential to reduce fire impacts on aquatic systems in 83.5-92.8% of the area treated. Based on Equation 1 and Table **1**, treatments would have be repeated every 20 years for 80-200 years, on average, before fire of any severity affects more than 50% of the treated areas in ponderosa forests in these USFS administrative regions.

However, the assumption that treatments that encounter low-severity fire convey benefits may not be warranted. Low-severity fires are commonly and easily extinguished under current management whether or not they encounter fuel treatments. Further, low-severity fire has minimal adverse impacts on watershed processes while conveying benefits, including maintenance of forest structure and fuel levels.

Our probabilistic approach does not explicitly address factors that can strongly influence fire area and severity, such as fuel conditions. Although spatially-explicit modeling of fire behavior can directly investigate the effects of such conditions, such models are unlikely to provide accurate estimates of the probability of occurrence of fire of a given severity because a host of other factors that influence fire area and severity cannot be deterministically predicted, including the frequency and location of ignitions and weather conditions during fire. Methods of assessing the risk of high-severity fire that are primarily based on fuel conditions have been shown to be an ineffective predictor of the actual severity at which fires burn [38]. In contrast, extensive recent data from numerous fires, as used in our analysis, does provide a robust estimate of the mean probability of the occurrence of fire of a given severity, because it integrates the many factors that influence fire occurrence and severity.

Our estimates likely represent the upper bound for fuel treatment effectiveness at the scale of analysis. In many cases, less than 4.16-7.86% of treated area is likely to experience high-moderate severity fire during the duration of treatment effectiveness, because q decreases with decreases in n, the duration of treatment effectiveness. This duration is often less than the 20 years assumed in our analysis. In the Sierra Nevada of California, fuels returned to pre-treatment levels within 11 years [39]. At the values of p in Table **1**, reducing n from 20 to 11 years (Eq. 1) reduces the probability that higher-severity fire affects treatments by ~45%.

Moreover, fuel levels rebound after treatment, eventually negating potential treatment effectiveness. If the reduction in effectiveness over time is such that mean effectiveness over the duration, n, is half the initial degree of effectiveness, the probability that fuel treatments reduce high-severity fire is approximately half the value of q for any value of p and n calculated using Equation 1.

Finally, available data indicate that fuel treatments do not always reduce fire severity when fire affects treated areas while fuels are reduced [4]. Our analysis does not address these effectiveness issues. For these combined reasons, Equation 1 likely estimates the upper bound of potential fuel treatment effectiveness in reducing fire impacts on aquatic systems.

Although our analysis focuses on higher-severity fire in bounding the effectiveness of fuel treatments and their net watershed effects, these fires do not have solely negative effects. Higher-severity fire benefits watersheds and aquatic

ecosystems in several ways, including providing a bonanza of recruitment of large wood and pulsed sediment supply that can rejuvenate aquatic habitats and increase their productivity [8, 14]. High severity fire is also a key process for the restoration of structural heterogeneity in forests, which is important for biodiversity [27, 40].

Our analysis intrinsically assumes some degree of climatic stationarity, which may not be warranted. Climatic variability influences the area annually burned in forests [25, 41]. However, the relatively recent fire data used in our regional analysis incorporates recent climatic fluctuation and possibly directional change, which would not be reflected in estimates based on natural fire return intervals. For instance, the data in our analysis of ponderosa pine forests come primarily from years in which annual fire area had increased due to climatic warming [25]. However, the analysis framework is flexible enough to accommodate projected values of the mean annual probability of fire, p, based on forecasts of climatic change or changes in fire management.

Current findings suggest treatment effects on fire severity are mostly confined to treated areas [3], but theory suggests a dense network of treatments might slow fire spread and reduce intensity, yielding a landscape-scale effect on fire severity [42]. However, empirical evidence of severity reduction was seen in the lee of only three of several dozen treatments in two Arizona wildfires [43]. Nonetheless, if dense treatment networks are shown to work in the future, our approach can aid in estimating their costs and benefits, because fire must still affect treated areas while fuels are reduced for networks to reduce fire severity.

CONCLUSIONS

Our analysis provides West-wide and regional first approximation of the likely upper bound of fuel treatment effectiveness. While valid at these two scales, they are not applicable to all smaller analysis areas, due to spatial variation in annual fire probability. However, the framework is flexible enough to allow more spatially explicit analyses of q where local estimates of n and p are available. The framework allows analysis of uncertainty, by using a range of plausible values for n and p. The analysis can also estimate the number of treatments to reach a specified q, abetting estimation of cumulative effects on ecosystems from repeated treatments.

Our approach also provides a method for quantitatively assessing the imminence of high-severity fire effects in the absence of fuel treatments and the degree of urgency of response. Based on available data, these are shown to be much lower than previously estimated in some work [37].

Our results and analyses can improve the assessment of risks to watersheds inherent in the treatment or non-treatment of forest fuels, because it accounts for the probability of fire and the transient nature of fuel treatments. For instance, previous work [22], evaluating treatment and non-treatment impacts, assessed the risks associated with fuel treatments based on the assumption that a single treatment significantly reduces fire risk on all treated areas, subsequently reducing consequent watershed impacts from fire. Other evaluations of these tradeoffs [21] compared the erosional effects of fuel treatments with high-severity fire under the explicit assumption that high-severity fire was inevitable without treatment and the implicit assumption that treatments always reduce or eliminate the potential for high-severity fire. Our analysis indicates that these assumptions are unwarranted and likely mischaracterize the outcomes and associated impacts of treatment options.

The approach can be extended to aid in assessing the risk to other ecosystem elements and processes that may be adversely affected by either fuel treatments or high-severity fire. For instance, non-native vegetation can be influenced by high fire severity [44] and some fuel treatments [10], especially if the treatments are repeated [9].

Even in ponderosa pine forests that burn relatively frequently, our regional analysis indicates that after 17 cycles of treatments, only slightly more than 50% of treated areas could potentially have fire severity reduced, on average. Our results indicate that high-severity fire is far from inevitable in areas left untreated and is, instead, expected to affect only a relatively small fraction of such areas at the broad scale of our analysis. Factoring in the probability of fire, using our framework, can significantly improve the assessments of the risks posed to aquatic systems by treating or not treating forest fuels. Where site-specific data on fire probabilities exist, the framework can be used to help locate treatments where they are most likely to encounter higher severity fire, increasing the likelihood of treatment benefits. In fact, our results indicate that such efforts are crucial.

There are several important factors that influence the aquatic tradeoffs among fuel treatments, fire, and aquatic systems that our framework does not address. Although the probability of outcomes is critical to assessing the expected value of options, the ecological costs of the outcomes of treatment *vs* non-treatment are also important in assessing the expected value of these options. With respect to the aquatic context, there is an ongoing need to fully evaluate tradeoffs such as the severity and persistence of the negative and positive impacts on watersheds and aquatic populations from fuel treatments and higher severity fire [8, 45]. An additional related issue is how effective treatments are when they encounter fire under a broad array of conditions affecting fire behavior [3]. While our analysis does not address these factors, it refines evaluation of net impacts of fuel treatment *vs* non-treatment by providing a framework for estimating the likelihood of fire occurrence in a given time frame.

At the scales of our analysis, results indicate that even if fuel treatments were very effective when encountering fire of any severity, treatments will rarely encounter fire, and thus are unlikely to substantially reduce effects of high-severity fire.

ACKNOWLEDGEMENTS

We thank Susan Goodman of the Bureau of Land Management for compiling and distributing the fire history database, Andrew Westerling for discussion of historical fire history records, the Pacific Rivers Council for funding aspects of the initial research on this topic, and three anonymous reviewers for their helpful comments on the manuscript.

REFERENCES

[1] U.S. Department of Agriculture. A collaborative approach for reducing wildland fire risks to communities and the environment: 10-year comprehensive strategy implementation plan [monograph on the internet]. Washington: U. S. Department of Agriculture; 2002 [cited 2006 Feb 11. Available from: http://fireplan.gov/.

[2] Pollet J, Omi PN. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. Inter J Wildl Fire 2002; 11: 1-10.

[3] Graham RT, McCaffrey S, Jain TB, Eds. Science basis for changing forest structure to modify wildfire behavior and severity RMRS-GTR-120. Fort Collins: USDA Forest Service Rocky Mountain Research Station; 2004.

[4] Schoennagel T, Veblen TT, Romme WH. The interaction of fire, fuels, and climate across Rocky Mountain forests. BioScience 2004; 54: 661-76.

[5] Raymond C, Peterson DL. How did prefire treatments affect the Biscuit fire? Fire Manage Today 2005; 65: 18-22.

[6] Kauffman JB. Death rides the forest: perceptions of fire, land use, and ecological restoration of western forests. Conserv Biol 2004; 18: 878-82.

[7] Agee JK, Skinner CN. Basic principles of forest fuel reduction treatments. Forest Ecol Manage 2005; 211: 83-96.

[8] Rieman B, Lee D, Burns D, *et al.* Status of native fishes in the western United States and issues for fire and fuels management. For Ecol Manage 2003; 178: 197-211.

[9] Dodson EK, Fiedler CE. Impacts of restoration treatments on alien plant invasion in *Pinus ponderosa* forests, Montana. J Applied Ecol 2006; 43: 887-97.

[10] Merriam, KE, Keeley JE, Beyers JL. The role of fuel breaks in the invasion of nonnative plants, US Geological Survey scientific investigations report 2006-5185. Reston: US Geol Survey; 2007.

[11] Gresswell RE. Fire and aquatic ecosystems in forested biomes of North America. Trans Amer Fish Soc 1999; 128: 193-221.

[12] Allen CD, Savage M, Falk DA, *et al.* Ecological restoration of southwestern ponderosa pine ecosystems: A broad perspective. Ecol Appl 2002; 12: 1418-33.

[13] Reid LM, Dunne T. Sediment production from forest road surfaces. Water Resour Res 1984; 20: 1753-61.

[14] Karr JR, Rhodes JJ, Minshall GW, *et al*. The effects of postfire salvage logging on aquatic ecosystems in the American West. BioScience 2004; 54: 1029-33.

[15] Megahan, WF, King JG, Seyedbagheri KA. Hydrologic and erosional responses of a granitic watershed to helicopter logging and broadcast burning. For Science 1995; 41:777-95.

[16] Kattlemann R. In: Sierra Nevada Ecosystem Project: Final report to Congress, vol. II, Assessments and scientific basis for management options. Davis: University of California Centers for Water Wildl Resour 1996; 855-920.

[17] Waters TF. Sediment in streams: sources, biological effects, and control. Bethesda: Amer Fish Soc; 1995

[18] Stephens SL, Ruth LW. Federal forest-fire policy in the United States. Ecol Appl 2005; 15: 532-42.

[19] Ziemer RR, Lewis J, Lisle TE, Rice RM. Long-term sedimentation effects of different patterns of timber harvesting. In: Proceedings of the symposium on sediment and stream water quality in a changing environment: Trends and explanation Inter Assoc Hydrol Sci Publ no. 203; 1991: Wallingford, UK: Inter Assoc Hydrol Sci; 1991; pp. 143-50.

[20] Benjamin JR, Cornell CA. Probability, statistics, and decision for civil engineers. 3rd ed. New York: McGraw-Hill; 1970.

[21] Elliot WJ, Miller IS. Estimating erosion impacts from implementing the National Fire Plan. In: Annual International Meeting Am Soc Agric Eng; 2002; Chicago, IL: Am Soc Agric Eng; 2002; meeting paper 025011.

[22] O'Laughlin J. Conceptual model for comparative ecological risk assessment of wildfire effects on fish, with and without hazardous fuel treatment. For Ecol Manage 2005; 211**:** 59-72.

[23] Baker WL, Ehle D. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. Can J For Res 2001; 31: 1205-26.

[24] Veblen TT. Key issues in fire regime research for fuels management and ecological restoration. In P. N. Omi, and L. A. Joyce, eds. Proceedings of conference on fire, fuel treatments, and ecological restoration RMRS-P-29; 2002: Fort Collins:USDA Forest Service Rocky Mountain Research Station; 2003; pp. 259-75.

[25] Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW. Warming and earlier spring increases western U.S. forest wildfire activity. Science 2006; 313:940-3.

[26] U.S. Department of Agriculture Office of Inspector General. Audit report: Implementation of the Healthy Forests Initiative USDA/OIG-A/08601-6-AT. Washington: USDA Office of Inspector General; 2006.

[27] Odion DC, Hanson CT. Fire severity in conifer forests of the Sierra Nevada, California. Ecosystems 2006; 9: 1177-89.

[28] National Interagency Fire Center [homepage on the Internet]. [Cited 2005 March 8] Available from: http://www.nifc.gov/fire_info/fires_acres.htm

[29] National Interagency Fire Center [homepage on the Internet]. [Cited 2007 October 13] Available from: http://www.nifc.gov/fire_info/fires_acres.htm

[30] Robichaud PR, Beyers JL, Neary DG. Evaluating the effectiveness of postfire rehabilitation treatments RMRS-GTR-63. Fort Collins: USDA Forest Service Rocky Mountain Research Station; 2000.

[31] U.S. Department of Interior Bureau of Land Management. 2003. [cited 2006 February 11] Fire History Database: Available from: ftp://ftp.blm.gov/pub/gis/wildfire/firehistory2003.

[32] U.S. Department of Agriculture Forest Service. NIFMID: National Interagency Fire Management Integrated Database—technical reference manual. Washington: USDA Forest Service, Fire and Aviation Management; 1993.

[33] U.S. Department of Interior Geological Survey. 2005. Gap analysis data warehouse: [cited 2006 Feb 11]. Available from: gapanalysis.nbii.gov/portal/server.pt

[34] U.S. Department of Agriculture, Forest Service. 2005. Geodata Clearinghouse: Available from: svinetfc4.fs.fed.us [cited 2006 February 11].

[35] Finney MA. The challenge of quantitative risk analysis for wildland fire. Forest Ecol Manage 2005; 211: 97-108.

[36] U.S. Department of Agriculture Forest Service. Sierra Nevada forest plan amendment final supplemental environmental impact statement. San Francisco: USDA Forest Service; 2004.

[37] Covington WW. Helping western forests heal: the prognosis is poor for US forest ecosystems. Nature 2000; 408: 135-6.

[38] Odion DC, Hanson CT. Fire severity in the Sierra Nevada Revisited: Conclusions robust to further analysis. Ecosystems *In Press*.

[39] van Wagtendonk JW, Sydoriak CA. Fuel accumulation rates after prescribed fires in Yosemite National Park. In: Proceedings of 9th conference on fire & forest meteorology; 1987: San Diego; Am Meteor Soc 1987; pp. 101-5.

[40] Noss, RF, Franklin JF, Baker WL, Schoennagel T, Moyle, PB. Managing fire-prone forests in the western United States. Front Ecol Environ 2006; 4: 481-7.

[41] Whitlock C, Shafer SL, Marlon J. The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. For Ecol Manage 2003; 178: 5-21.

[42] Finney MA. Design of regular landscape fuel treatment patterns for modifying fire growth and behavior. Forest Sci 2001; 47: 219-28.

[43] Finney MA, McHugh CW, Grenfell IC. Stand- and landscape-level effects of prescribed burning on two Arizona wildfires. Can J For Res 2005; 35: 1714-22.

[44] Keeley JE, Lubin D, Fotheringham CJ. Fire and grazing impacts on plant diversity and alien plant invasion in the southern Sierra Nevada. Ecol Appl 2003; 13: 1355-74.

[45] Rhodes JJ, Odion DC. Evaluation of the efficacy of forest manipulations still needed. BioScience 2004; 54: 980.

Received: October 28, 2007 Revised: January 16, 2008 Accepted: January 21, 2008

CHAPTER SIX

Stream Temperature and Aquatic Habitat: Fisheries and Forestry Interactions

ROBERT L. BESCHTA, ROBERT E. BILBY, GEORGE W. BROWN, L. BLAIR HOLTBY, and TERRY D. HOFSTRA

ABSTRACT The temperature of water entering a forest stream system typically resembles that of the watershed's subsoil environment. As this water continues to flow down the stream system, seasonal and diurnal water temperatures are strongly influenced by solar radiation. Pronounced differences in stream temperature patterns are evident for streams draining watersheds throughout the Pacific Northwest. Seasonal and diurnal patterns of stream temperature influence a wide range of responses by instream biota. Furthermore, logging activities can initiate pronounced temperature changes by the removal of forest vegetation along channels. Buffer strips of forest vegetation are an effective means of minimizing stream temperature impacts associated with logging. Although direct mortality of fish is probably not a major concern throughout the Pacific Northwest when stream temperatures are altered by management activities, temperature changes can influence rates of egg development, rearing success, species competition, and other factors.

The temperature of water in forest streams is an important factor regulating aquatic life. But until the 1960s, the impact of harvesting on the temperature of forest streams was seldom considered or reported in the literature. Whereas fisheries studies focused on the toxicological effects of high temperature in the laboratory, most watershed studies were concerned with changes in runoff and sediment.

The situation changed dramatically in the early 1960s, especially in the Pacific Northwest. Scientists observed changes in the migration of anadromous fish in the Columbia River because of increases in temperature below dams and the outfall of the Hanford thermonuclear reactor. Conversely, the beneficial impact of dams in reducing water temperature became an issue on the Rogue River in Oregon. Research on the energy balance of large rivers began to provide information about how their temperature was affected by the macro- and microclimatic factors, storage and release from reservoirs, and localized heat inputs.

The Alsea Watershed Study in western Oregon, which began in 1958, was the first detailed study of effects of timber harvesting on the temperature of small, forest streams. Temperature changes were

monitored before and after harvesting, and research on energy balance components provided a basis for understanding why temperature changes occurred. In the late 1960s, high postlogging stream temperatures were a central issue in a harvesting-fisheries controversy over the North Umpqua River in Oregon. This controversy, along with others, was part of a developing environmental awareness and involvement by the public, administrators, and legislators. These concerns also led to major changes in national policy for the USDI Bureau of Land Management and USDA Forest Service and were instrumental in the development of forest practices acts, on a state-by-state basis, for the Pacific Northwest in the early 1970s. These forest practices acts identify management activities intended to prevent significant temperature changes in fish-bearing streams.

The objectives of this paper are to characterize stream temperature regimes in forested ecosystems, to indicate the underlying physical mechanisms of temperature change resulting from the removal of forest canopies over streams, and to identify the various processes by which temperature changes following logging can affect aquatic communities and the production of fish.

STREAM TEMPERATURES AND FORESTED ECOSYSTEMS

The temperature of moisture arriving at a channel is dependent on many factors. In high mountain catchments of the Pacific Northwest, much of the annual precipitation occurs as snowfall, which accumulates on a watershed until sufficient energy is available for snowmelt. Most snowmelt typically occurs during the spring months. However, at lower elevations snowfall accumulations may be relatively transient, and rapid snowmelt can occur during rain-on-snow events. Typically, meltwater (at 0°C) and rainfall (at > 0°C) infiltrate forest soils and then move laterally through relatively porous soils and subsoils toward topographic depressions and stream channels. The pathways by which subsurface flow reaches a channel are highly variable, but when such water eventually enters a defined channel and becomes streamflow, its temperature generally reflects that of the watershed's subsoil environment.

As water flows downstream, its temperature will continue to change as a result of several factors that make up the heat balance of water. The net rate of gain or loss by a stream as it moves through a forest is the algebraic sum of net radiation, evaporation, convection, conduction, and advection (Brown 1983). Net radiation is generally dominated by the amount of direct-beam solar radiation that reaches a stream's surface. Heat gain or loss from evaporation and convection depends on the vapor pressure and temperature gradients, respectively, between the water surface and the air immediately above the surface. Wind speed at the air-water interface is also an important controlling variable. Conduction of heat between the water in the stream and the streambed depends on the type of material that makes up the bed. Bedrock channels are more efficient than gravel-bed channels at conducting heat. Advection is the result of heat exchange as tributaries or groundwater of different temperature mixes with the main streamflow, and can either increase or decrease stream temperature.

Channel characteristics and morphology also influence the amount of heat gain or loss of a stream. The surface area over which energy transfers take place is important: wide streams receive more energy than narrow ones. Discharge is another significant variable: for the same surface area and energy input, the temperature change expected of a high-discharge stream will be less than that of a low-discharge stream. In other words, for a given rate of net input, the change in temperature of a stream is directly proportional to surface area and inversely proportional to discharge.

How do these factors combine to produce temperature patterns for coastal streams in the Pacific Northwest? In winter, solar radiation levels at the stream surface are typically low, regardless of canopy cover. This is the result of a combination of factors affecting the availability of direct-beam solar radiation: short days, low sun angles (this maximizes reflection at the water surface and the shading effects of streamside vegetation and topography), and cloudy weather. During the summer months, when solar radiation levels are greatly increased (higher sun angles, longer days, and clear skies) and stream discharge is low, shading effects of the forest canopy become significant. The seasonal progression of potential direct solar radiation (for clear weather conditions) is shown in Figure 1. Although some losses occur as solar energy is routed through the atmosphere, much of the incoming solar radiation is intercepted by the canopy of streamside vegetation. Net radiation underneath a continuous canopy may be only 15% or less than that of an unshaded stream (Brown 1983) during daytime conditions. Throughout the year, evaoporative and convective transfers of energy are typically low for forested streams, because vapor pressure and temperature gradients close to the water surface are small and wind speeds are usually low. Likewise, conductive heat transfers are usually insignificant (Brown 1969). Because water has a relatively high specific heat, seasonal and daily temperature changes of forested streams are relatively small and gradual.

Seasonal temperature patterns for three small forested streams in the Pacific Northwest are shown in Figure 2. As expected, the watersheds show maximum temperatures occurring in summer and minimums in winter. However, the exact timing and magnitude of seasonal extremes vary. Porcupine Creek, the farthest north of the three, has the greatest range in monthly stream temperatures (nearly 13°C). The timing of summer maximum temperature for these streams follows, by one to two months, the timing of maximum solar radiation (Figure 1). An exception to the cyclical pattern of seasonal temperatures, shown in Figure 2, occurs in streams fed by large springs or groundwater sources. These systems often display a nearly uniform temperature year round, being cooler than other streams in summer and warmer in winter (Minkley 1963).

Characterizing the extent of natural or climatic variability in stream temperatures is an important preliminary step in attempting to document the effects that temperature changes related to logging may have on aquatic communities. If, after logging, stream temperatures lie within the bounds of natural variability, then any effects related to temperature change might be difficult to detect. Furthermore, even if

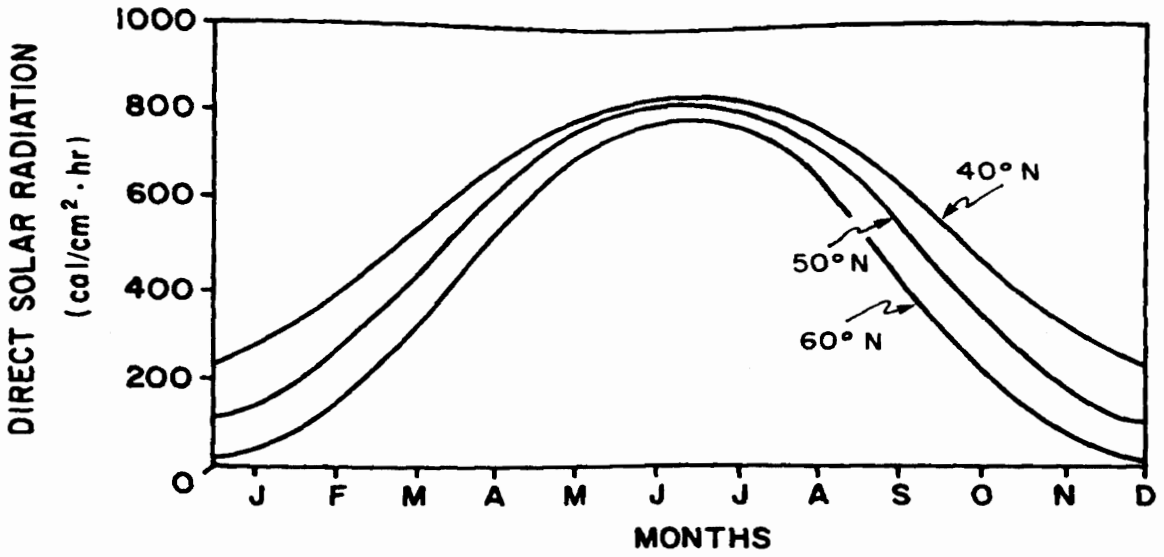


Figure 1. Seasonal pattern of potential direct-beam solar radiation at a stream surface during clear weather (assumed atmospheric transmission coefficient = 0.9) for selected latitudes (Buffo et al. 1972).

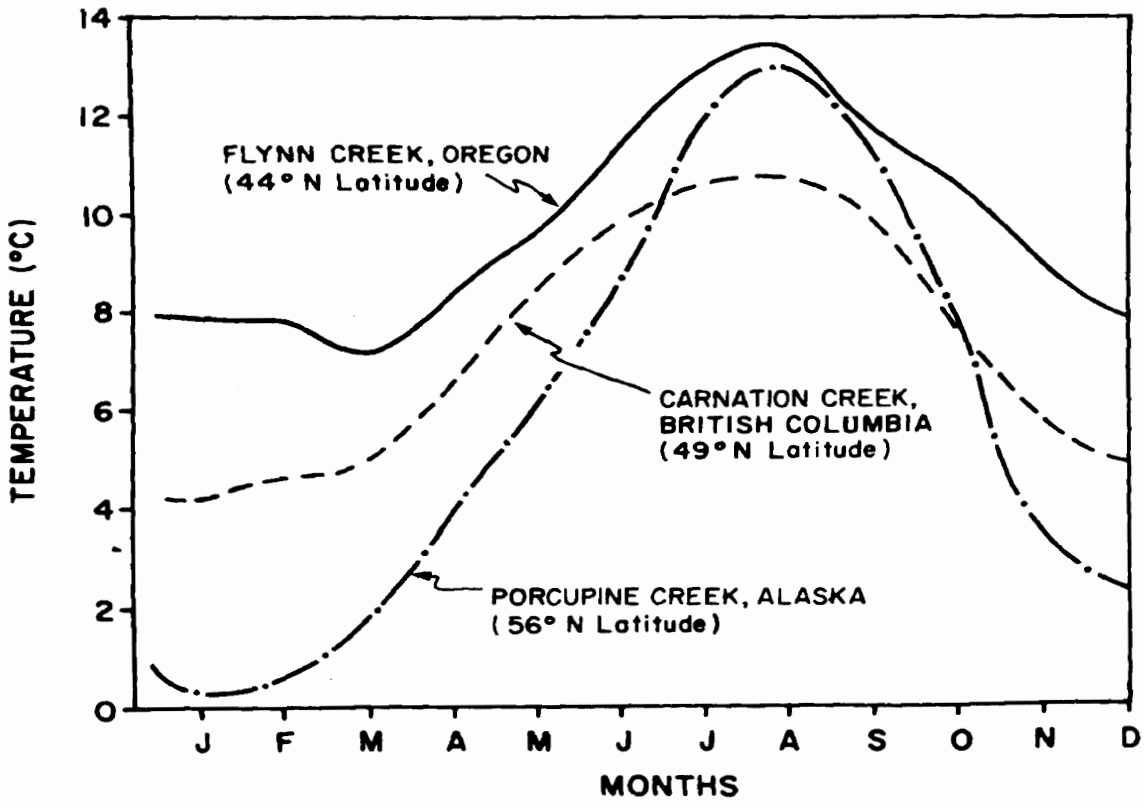


Figure 2. Seasonal temperature patterns for three coastal streams in the Pacific Northwest.

measurable, such effects might be relatively unimportant if they would be expected to result from climatic variability anyway.

The variation in monthly temperature between years can be as much as 4°C during the winter months (December-March) for Porcupine Creek in southeastern Alaska, but year-to-year variations in monthly temperature are generally less than 2°C for other times of the year (Koski 1984). Monthly temperature fluctuations between years generally remain lower than 2°C, regardless of season, at Flynn Creek in the Oregon Coast Range.

Superimposed on the seasonal progression of stream temperatures is a diurnal pattern. Generally, changes in water temperature over the course of a day tend to be greatest during summer, in part because of the relatively low volumes of water flowing in streams at that time of year. Peak daily temperatures are usually achieved during the late afternoon, and minimums just before dawn. Even in midsummer, when large diurnal changes in direct solar radiation occur above the forest canopy, the shading effects of the forest vegetation greatly moderate and reduce the energy exchanges at the stream surface. For example, diurnal temperature variations near the mouth of Carnation Creek (Vancouver Island, British Columbia) average approximately 1.3°C for the months of June, July, and August; maximum diurnal variations for these same months are less than 2.4°C (Holtby and Newcombe 1982). Diurnal variations for a well-shaded coastal Oregon stream were less than 1°C, even during the day of the annual maximum (Brown and Krygier 1970). Streams bordered with relatively low densities of forest vegetation or which have a significant number of natural openings along the channel would be expected to have higher diurnal variations.

A time series of monthly average water temperatures extending from 1923 to 1975 has been reconstructed for Carnation Creek, B.C., using fifty-two years of air temperature records from a nearby permanent weather station (Estevan Point, B.C.) and a regression of air and stream temperatures for the period 1971 to 1984. A temperature record of this duration provides an estimate of the extent to which climatic variability has influenced undisturbed stream temperatures in that region. Historical variability in Carnation Creek stream temperatures has been relatively small. For all months of the year, the average monthly temperature lies within 1°C of the long-term monthly median at least 50% of the time.

Forest streams change temperature in space as well as time, again in response to energy transfers. As stream order increases, so usually does stream width, stream discharge, and the number of tributaries. As width increases, surface area exposed to solar radiation usually increases, because riparian vegetation may shade less and less of the stream surface. On the other hand, discharge also increases in a downstream direction. The balance between these factors ultimately determines the rate of temperature change downstream, especially in summer. For instance, in the tributaries of Carnation Creek, B.C., diurnal ranges during the summer increase in proportion to drainage area and stream width (both correlates of stream surface area), indicating the overriding importance of direct solar radiation during

periods of low discharge indicating the temperature regimes of small streams. During the winter there is no relation between stream surface area and diurnal range; and other factors, principally discharge and elevation, become important determinants of diurnal variation. In large rivers, diurnal temperature fluctuations are generally dampened because of the relatively large volumes of water contained by these systems (Hynes 1970).

Where tributaries join, or enter a main stream, the mixed temperature is the simple resultant of their individual temperatures, weighted by their respective discharges (Brown 1983). Thus a small tributary will produce little change in the temperature of a larger stream unless the small stream's temperature is greatly different. Hence, as stream order increases, the impact on temperature of tributaries entering the main channel generally decreases.

Because much of their flow is derived from forested headwater catchments, rivers in the Pacific Northwest exhibit seasonal temperature patterns similar to those of small forest streams. In Figure 3, average monthly temperatures are illustrated for three rivers across Oregon. Winter temperatures for the Nestucca River in the Oregon Coast Range are similar to those for the smaller Flynn Creek watershed shown in Figure 2. This similarity is primarily a consequence of the combined low net radiation inputs and high streamflows common at that time of year. In summer, monthly temperatures for the Nestucca River average approximately 18°C, or nearly 5 to 6°C warmer than those for the smaller Flynn Creek watershed. These downstream increases in monthly water temperatures during the summer occur primarily from net radiation inputs to the water as it flows through increasingly wider reaches of the stream system. In addition, flows are low at this time of year and serve to magnify the effects of energy inputs.

Winter temperatures for the Nestucca River in the Oregon Coast Range tend to be higher than for Fall Creek and the Umatilla River, located farther east (Figure 3). Fall Creek drains a portion of the western Cascades; the Umatilla River has its headwaters in the Wallowa Mountains of eastern Oregon.

The range of temperatures experienced in coastal streams is relatively low because of the maritime influence of the Pacific Ocean on the coastal climate. Lower winter temperatures occur for rivers draining the Cascades and mountain ranges farther east, where cold water temperatures associated with rainfall or snowmelt and cold nighttime air temperatures (which promote radiational cooling of stream water) are conducive to lower stream temperatures. Monthly temperatures in January for the Umatilla River in eastern Oregon average more than 3°C lower than those of the Nestucca River in the Oregon Coast Range. Downstream changes in water temperature, as water moves from headwater channels toward the mouth of a river system, are also described by Theurer et al. (1985).

Even though general temperature patterns are evident in forest streams, local anomalies may occur. Thermal stratification, while common in lakes, is generally precluded in streams, because of constant

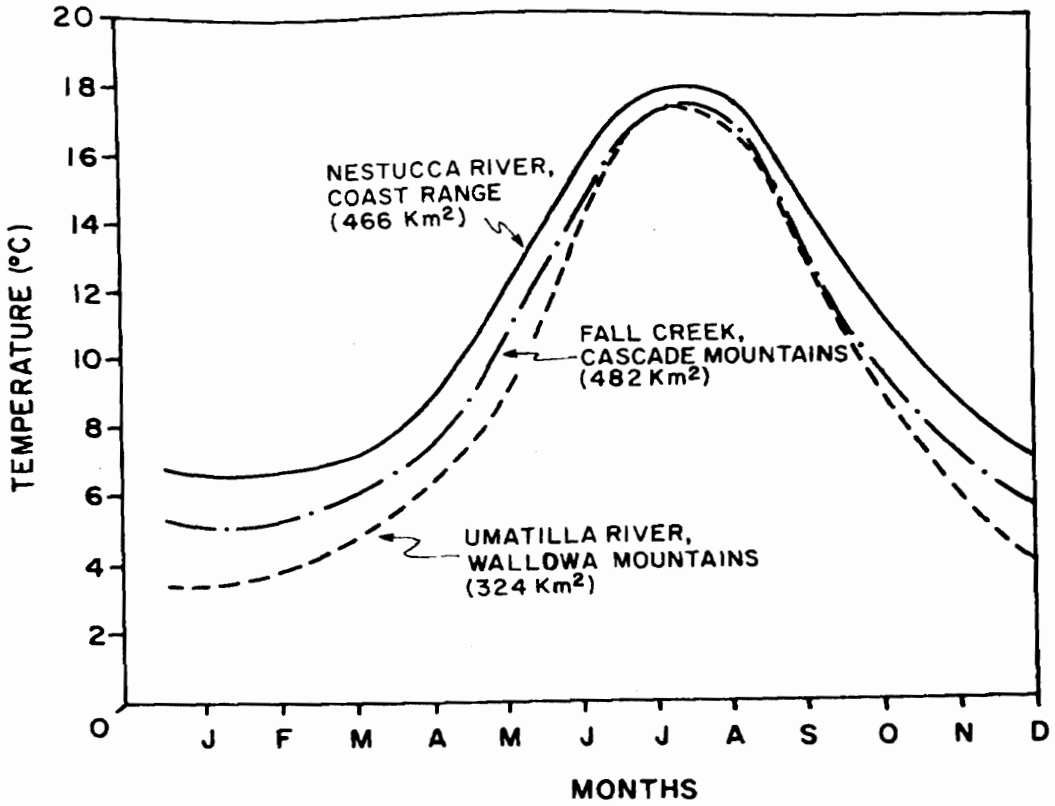


Figure 3. Seasonal temperature patterns for three rivers in Oregon (1965-71).

turbulence of flowing water. However, several studies have shown that water near the bottom of pools is sometimes 5 to 10°C cooler than water near the surface (Keller and Hofstra 1982, Bilby 1984, Keller et al., in press). Cool-water sources usually result from a tributary stream, groundwater, or an upwelling of stream water that has been cooled by flowing through the streambed (Figure 4). The occurrence of these sources seems to be rare, accounting for only 1.6% of the stream surface area of a western Washington stream (Bilby 1984). Where relatively cool water enters a channel, fish and other organisms may find local thermal environments more favorable than surface water temperatures would indicate (Gibson 1966, Keller and Hofstra 1982); however, reduced dissolved oxygen levels associated with cool-water sources may limit their immediate usefulness to instream biota (Figure 5). The occurrence of such phenomena serves as a reminder that generalizations about the thermal environments of forest streams may be misleading.

In summary, the seasonal cycles in the temperatures of streams draining forested watersheds in the Pacific Northwest can be defined on temporal and spatial scales. There are clear seasonal patterns, with low levels of between-year variability. Diurnal variations also follow a predictable pattern and are generally very small. Spatially, there are regular, predictable effects of such variables as latitude, proximity to the ocean, and stream order. Particularly during summer months, however, there appears to be a significant amount of fine-scale heterogeneity

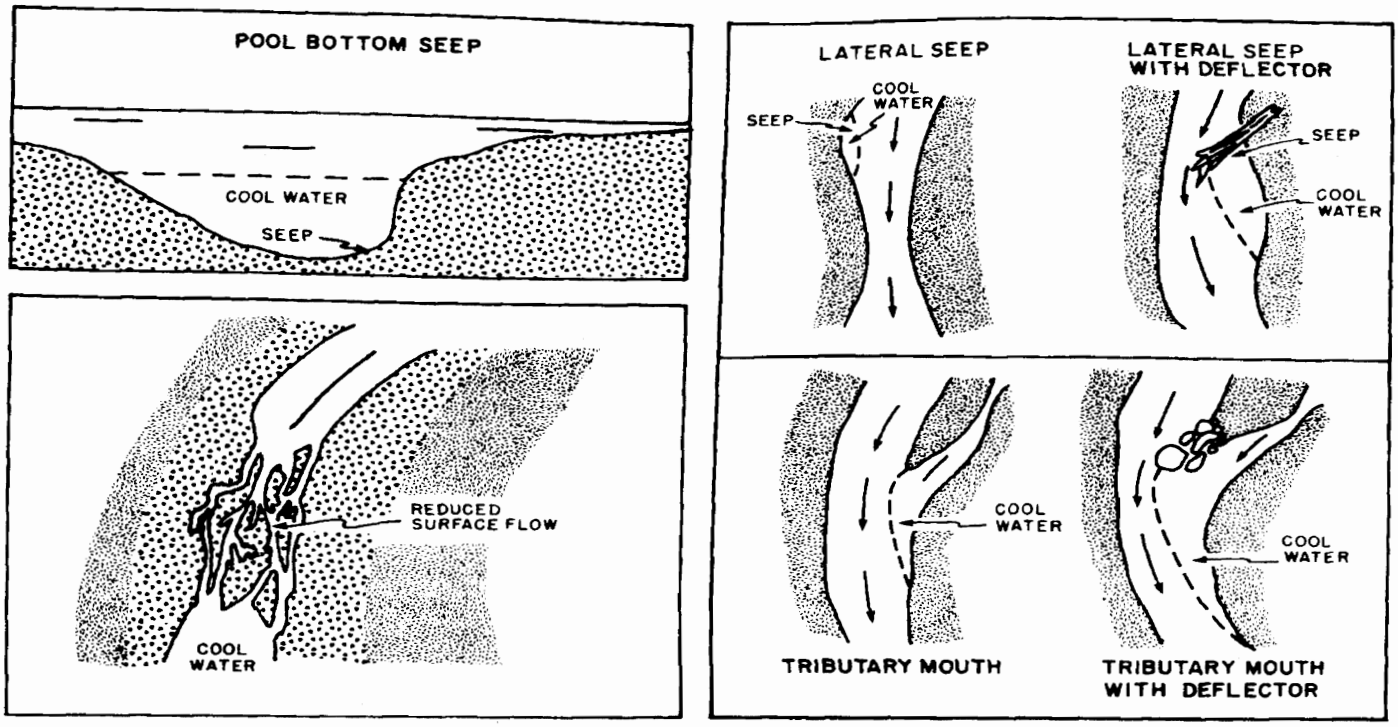


Figure 4. Examples of cool-water sources in mountain streams (from Bilby 1984).

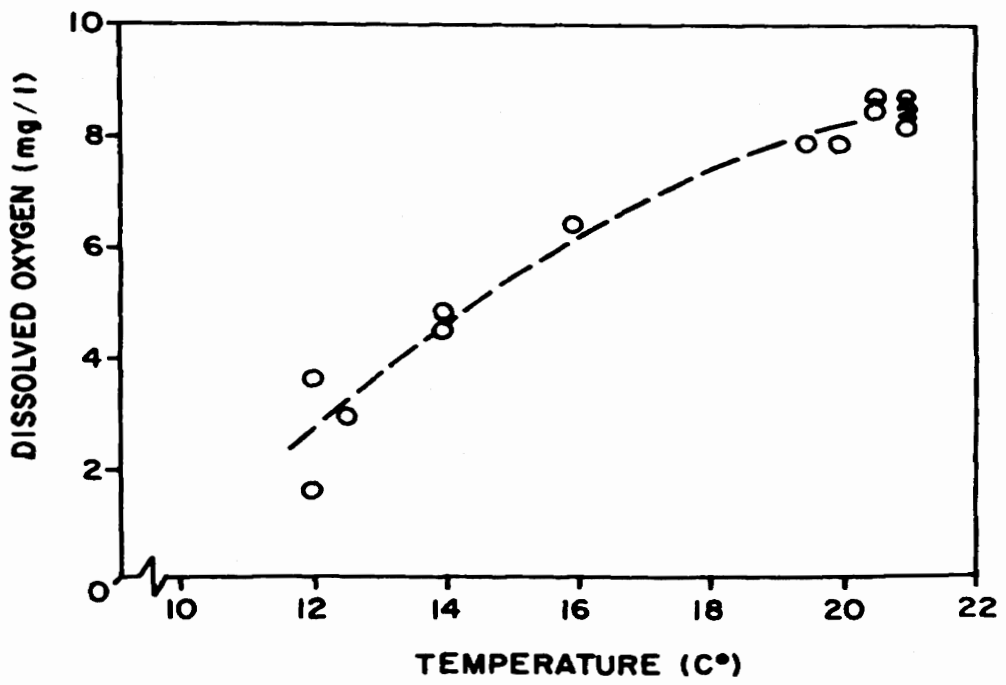


Figure 5. Relation between stream temperature and dissolved oxygen associated with a cool-water source in Redwood Creek, California (from Keller and Hofstra 1982).

in the thermal environment of streams brought about by variations in exposure to solar radiation, flow, channel widths, and the occurrence of cool-water upwelling. Nevertheless, the general temperature patterns represent a characteristic of the aquatic habitat that fish and other organisms must withstand and, perhaps more important, to which they have adapted their life strategies.

EFFECTS OF CANOPY COVER ON STREAM TEMPERATURES

Most stream temperature concerns in forest ecosystems have focused on summertime increases associated with forest harvesting. The energy balance components described earlier also operate for streams from which the canopy is removed. Again, the principal source of energy for heating small streams during summer conditions is incoming solar energy striking the water surface. The more canopy removed, the greater is the exposure of the stream to this heat source. Most of this incoming energy is stored in the stream, and its temperature rises accordingly.

Compared with solar radiation inputs, energy transfers involving convection or evaporation are of much less importance to the thermal regime of exposed mountain streams. Both require wind movement at the stream surface to be effective, in addition to temperature and vapor pressure gradients. Because of normally low wind velocities immediately above the water surface, neither process plays a significant role in controlling the temperature of an exposed stream (Brown 1983). Furthermore, these two processes tend to counterbalance each other. For example, if relatively warm air is present over a stream surface, the heat gain to the stream by convection will tend to be offset by heat loss through evaporation. This is important for several reasons. First, high air temperatures do not cause stream temperature to increase following canopy removal even though daily maximum air temperatures are usually at their highest during clear sunny weather, just as temperatures of streams are. However, the two variables are often highly correlated. Second, once a stream's temperature is increased, the heat is not readily dissipated to the atmosphere as it flows through a shaded reach. Hence, additional energy inputs to small streams can have an additive effect on downstream temperatures.

The net rate of heat exchange (N_h) per unit area of stream surface is shown in the following equation:

$$N_h = N_r + E + H + C \qquad (1)$$

where N_r = net radiation
E = evaporation
H = convection
C = conduction

Although the net radiation term comprises both short- and long-wave components, the shortwave or incoming solar radiation portion is by far the most important factor that changes as a result of canopy reductions, particularly during the summer.

Seasonal and diurnal temperature patterns of exposed streams differ markedly from those of shaded, forest streams. For a channel with a forest canopy shading the water surface, the individual terms on the right-hand side of equation (1) remain relatively small over a 24-hour period, even in midsummer. Hence diurnal temperature fluctuations are also small. However, should the canopy be removed through harvesting activities or natural causes, the net heat gain or loss may be significantly altered.

During winter months, exposed streams may experience lower temperatures when there is no canopy to inhibit energy losses by evaporation, convection, or long-wave radiation from the stream. Long-wave losses are greatest when clear skies prevail, particularly at night. While this phenomenon is not important in coastal streams of Oregon and Washington, where nighttime cloud cover and relatively warm air temperatures are common, it may be important for streams at high elevations in the Cascades and streams farther east, or at northerly latitudes where snow accumulations are insufficient to cover and insulate the channel from energy losses. Because most research studies in the Pacific Northwest have concentrated on evaluating changes in summer stream temperatures, less is known about winter temperature changes, if any, as a result of reductions in canopy cover.

Studies in deciduous forest types of the eastern United States have found relatively small changes in winter stream temperatures due to forest harvesting. In Pennsylvania, changes in winter maximum temperatures ranged from -0.7 to +0.9°C; changes in winter minimums ranged from -1.4 to +1.0°C (Table 1). In West Virginia, complete removal of riparian trees lowered winter stream temperature minimums approximately 2°C (Lee and Samuel 1976). In New Jersey, dormant season stream temperatures remained unchanged following herbicide application to riparian forest vegetation. Results from studies of coastal streams in the Pacific Northwest (Brown and Krygier 1970, Holtby and Newcombe 1982) show little change in winter temperatures following canopy reductions from logging.

During the summer, the amount of direct solar radiation available to a stream whose canopy has been removed is substantial (Figure 6), hence exposed streams may experience large diurnal fluctuations. The extent to which the incoming solar energy increases the temperature of an exposed stream further depends on the surface area of the exposed reach and the stream discharge. Streams with small discharges and large exposed areas inevitably experience the greatest temperature increases (Sheridan and Bloom 1975).

Research associated with a variety of forest types and geographic locations has identified the magnitude of temperature increases to be expected from canopy removal. For summertime conditions in the eastern United States, increases in average maximum temperatures following reductions or removal of forest canopy have generally ranged from 3 to 10°C (Table 1). Minimum temperatures in summer either remained unchanged or were generally limited to increases of less than 1°C.

Table 1. Summary of temperature changes associated with forest management activities and experimental treatments on forest watersheds, eastern United States.

Location	Treatment	Stream Temperature Variables	Temperature Change (°C)	Reference
Georgia	Clearcut with partial buffer strip	Average June-July maximum	+6.7	Hewlett and Fortson (1982)
Maryland	Riparian harvest up to 40 m from channels	Average summer maximum Average summer minimum	+4.4 to 7.6 +0.6 to 1.1	Corbett and Spencer (1975)
New Jersey	Riparian herbicide application	Average summer maximum Average summer minimum Dormant season	+3.3 Unchanged Unchanged	Corbett and Heilman (1975)
North Carolina	Deadened cove vegetation	Average summer maximum	+2.2 to 2.8	Swift and Messer (1971)
	Complete clearcut	Average summer maximum	+2.8 to 3.3	Swift and Messer (1971)
	Understory cut	Average summer maximum	0 to 0.3	
Pennsylvania	Riparian harvest (lower third of slope)	Average summer maximum Average summer minimum	+3.9 Unchanged	Lynch et al. (1975)
	Clearcut with herbicide treatment	Average June-July maximum Average June-July minimum	+10 to 10.5 +1.7 to 1.8	Rishel et al. (1982)
		Average Dec.-Feb. maximum Average Dec.-Feb. minimum	-0.5 to +0.9 -1.4 to +0.2	Rishel et al. (1982)
	Commercial clearcut with buffer strip	Average June-July maximum Average June-July minimum	+0.6 to 1.6 0 to 0.6	Rishel et al. (1982)
		Average Dec.-Feb. maximum Average Dec.-Feb. minimum	-0.7 to +0.9 -0.5 to +1.0	Rishel et al. (1982)
West Virginia	Clearcut	Average summer maximum	+4.4	Kochenderfer and Aubertin (1975)

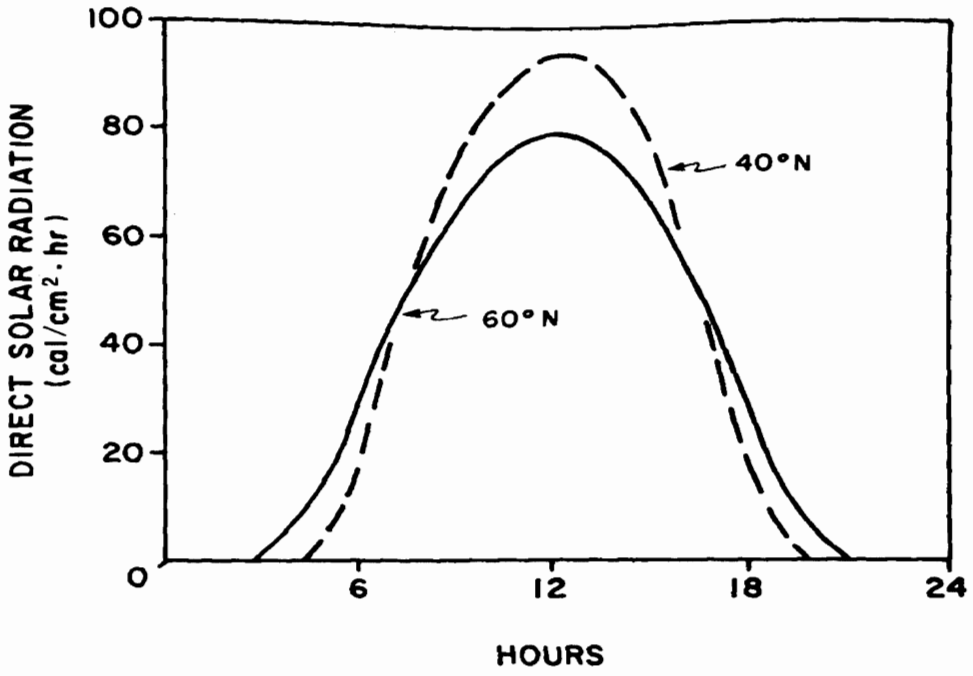


Figure 6. Daily pattern of potential direct-beam solar radiation at a stream surface during clear weather (assumed atmospheric transmission coefficient = 0.9) on June 22, for selected latitudes (Buffo et al. 1972).

For the Pacific Northwest, watershed studies in the Coast Range and the Cascade Mountains of Oregon have shown increases in mean monthly maximum temperatures of about 3 to 8°C (Table 2) following clearcut harvesting. Burning may add another 1°C increase. At Carnation Creek on Vancouver Island, British Columbia, Holtby and Newcombe (1982) found that summer temperature increases due to logging were proportional to the basin area logged. They predicted a 7°C increase in mean summertime water temperature if the entire watershed was clearcut. Studies in the Pacific Northwest also show that the minimum temperatures in summer are much less altered by canopy removal and are generally limited to increases of less than 1 or 2°C.

Concern over altered temperatures after logging streamside vegetation usually focuses on the inevitable increases in maximum temperatures observed during the summer. This focus is very much a result of the toxicological perspective on temperature changes that is prevalent in fisheries research. However, in the majority of cases in the Pacific Northwest, stream temperatures in deforested watersheds, while invariably warmer than they were in the forested state, do not approach the tolerance limits of the resident fish species.

Holtby (1986) compared temperature changes over three biologically interesting periods at Carnation Creek: (1) the winter (October through February), (2) the spring (April and May), and (3) the summer (May through September). Logging-related increases in temperature (as indexed by thermal summations), from 1977 to 1984, averaged 15% (range

Table 2. Summary of summer temperature changes associated with forest management activities on forest watersheds, Pacific Northwest.

Location	Treatment	Stream Temperature Variables	Temperature Change (°C)	Reference
Alaska (Southeast)	Clearcut and natural openings	Δ Temperature per 100 m of channel	0.1 to 1.1°C/100 m Average = 0.7°C/100 m	Meehan (1970)
British Columbia (Vancouver Island)	Logged (Tributary H)	Average June-August diurnal temperature range	0.5° to 1.8°C increase over pre-treatment levels	Holtby and Newcombe (1982)
	Logged and burned (Tributary J)	Average June-August diurnal temperature range	0.7° to 3.2°C increase over pre-treatment levels	Holtby and Newcombe (1982)
Oregon (Cascades)	Clearcut	Average June-August maximum	4.4 to 6.7°C	Levno and Rothacher (1967)
	Clearcut and burning	Average June-August maximum	6.7 to 7.8°C	Levno and Rothacher (1969)
Oregon (Coast Range)	Clearcut	Average July-Sept. maximum	2.8 to 7.8°C	Brown and Krygier (1967)
	Clearcut and burning	Average July-August maximum	9 to 10°C	Brown and Krygier (1970)
Oregon (Cascades)	Mixed clearcut and forested reaches	Δ Temperature per 100 m of channel	0 to 0.7°C/100 m	Brown et al. (1971)
	Tractor striped area	Δ Temperature per 100 m of channel	15.8°C/100 m	Brown et al. (1971)

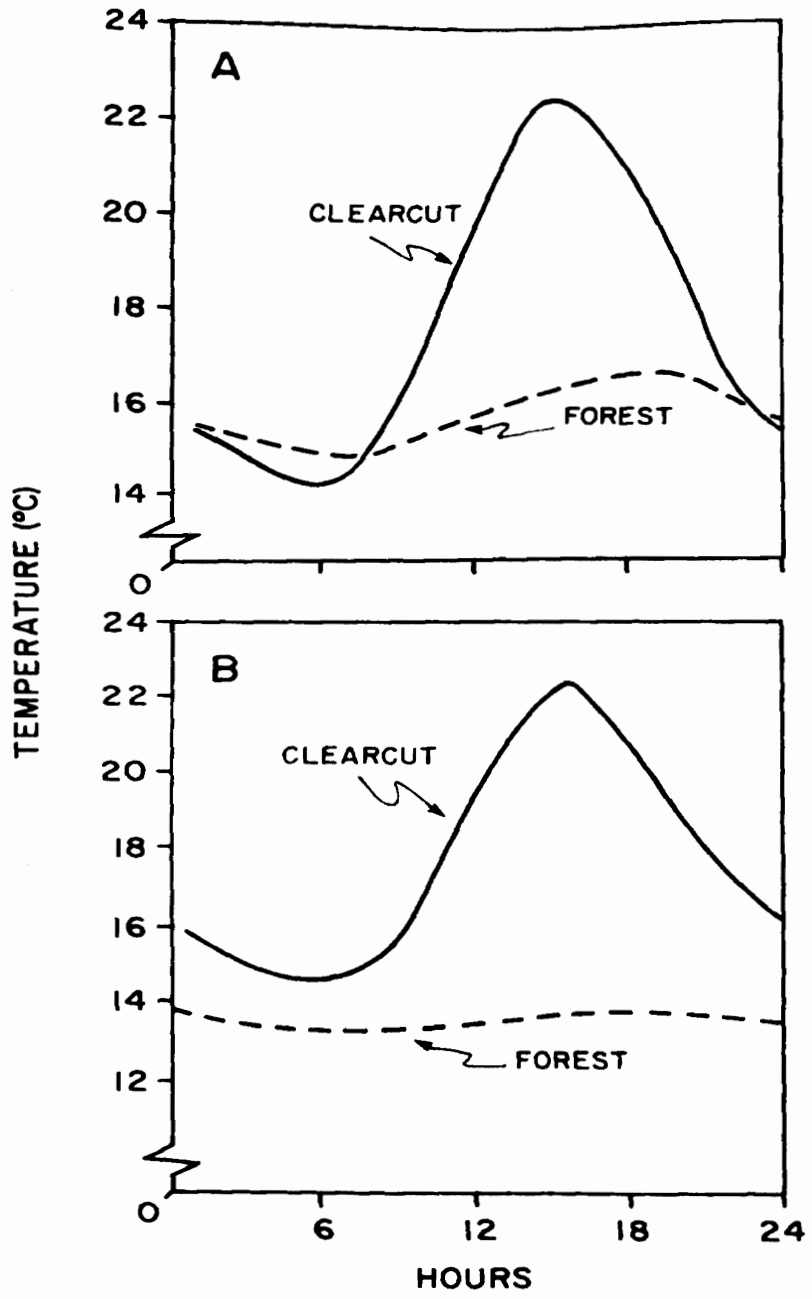


Figure 7. Summertime stream temperatures during clear weather in (A) West Virginia (from Lee 1980), and (B) Coast Range of Oregon (from Brown and Krygier 1967).

of 2 to 32%) during the winter, 27% (range of 18 to 36%) during the spring, and 37% (range of 16 to 56%) during the summer.

The increased exposure of small headwater streams draining clearcuts to incoming solar radiation leads to substantial increases in diurnal fluctuations (Figure 7). In some situations, the diurnal range in midsummer can increase by more than 15°C if the overstory shade is

completely removed (Brown and Krygier 1970, Moring 1975a). In other situations, increases in diurnal ranges have been considerably less. Increases in average diurnal ranges during summer after complete clearcutting along tributaries to Carnation Creek were less than 3°C (Holtby 1986). In the main creek, average diurnal range increased approximately 1°C during the summer. Increased diurnal ranges during most of the winter months were detectable but nevertheless were considerably smaller.

Because direct-beam solar radiation is the primary factor influencing temperature change in summer, the effect of partial canopy removal is directly proportional to the reduction in canopy providing shade to the stream. What this signifies is that leaving buffer strips represents an effective means of preventing temperature change for many mountain streams.

The importance of a buffer strip for preventing increases in stream temperature can be determined by measuring its angular canopy density (ACD). Whereas canopy density is usually expressed as a vertical projection of the canopy onto a horizontal surface, ACD is a projection of the canopy measured at the angle above the horizon at which direct-beam solar radiation passes through the canopy. This angle is determined by the position of the sun above the horizon during that portion of the day (usually between 10 a.m. and 2 p.m. in mid to late summer) during which solar heating of a stream is most significant. Thus ACD can provide a direct estimate of the shading effects of streamside vegetation. Although it is possible for natural forest vegetation to have ACDs of 100%, indicating complete shading from incoming solar radiation, the ACD of old-growth stands in western Oregon generally falls between 80 and 90% (Brazier and Brown 1973, Steinblums et al. 1984). In northern California, Erman et al. (1977) found ACDs to average 75% along undisturbed streams.

The relative degree of shading provided by a buffer strip depends on a range of factors (e.g., species composition, age of stand, density of vegetation). Although buffer-strip width is also important, by itself it is not generally a good predictor of shade protection. Figure 8 illustrates the variability of ACD associated with buffer-strip width for forest stands in the Coast Range and Cascade Mountains of Oregon. Buffer strips with widths of 30 m or more generally provide the same level of shading as that of an old-growth stand.

How can we predict the effect of complete removal of riparian vegetation, partial removal, or a buffer strip on the daily temperature pattern of a stream? The answer is relatively simple: by determining the change in energy available to the stream surface. In summer this means determining how much additional surface will be exposed to direct sunlight during clear weather. This task is comparatively easy when attempting to predict the effect of completely exposing a stream reach that was fully shaded. It is more difficult to predict the change in exposed surface area that will occur following partial removal of the canopy.

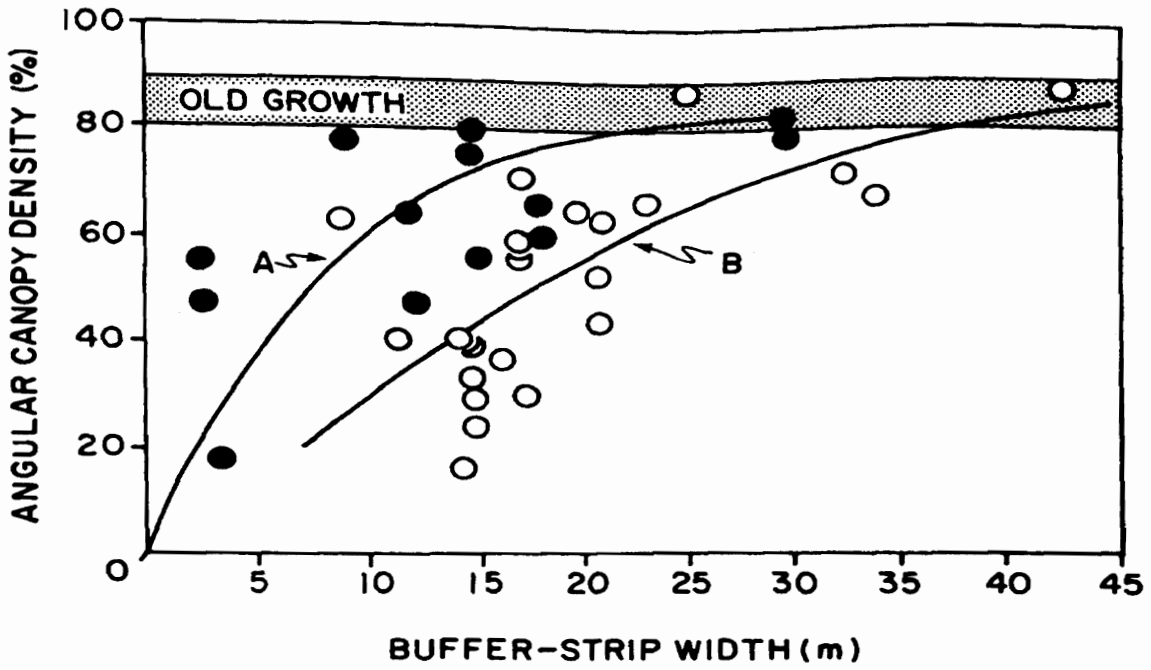


Figure 8. Relation between angular canopy density (ACD) and bufferstrip width in western Oregon. Data for (A) from Brazier and Brown (1973); data for (B) from Steinblums et al. (1984).

Once the surface area A exposed to direct-beam radiation is estimated, the increase in net energy N_h (mostly shortwave solar radiation) can be readily determined from tables and combined with an estimate of stream discharge Q to predict the temperature increase ΔT produced by harvesting:

$$\Delta T = \frac{N_h \times A}{Q} \times 0.000167 \qquad (2)$$

where N_h = net rate of heat added to the stream ($cal/cm^2 \cdot min$)

A = surface area of stream exposed to incoming solar radiation (m^2)

Q = streamflow (m^3/sec)

A detailed description of this predictive technique and the methods for laying out buffer strips to ensure temperature control are given by Currier and Hughes (1980) and Brown (1983).

Equation (2) works well for predicting temperature increases from harvest along short reaches of stream where incident solar radiation is the major contributor to the energy balance. On reaches greater than 1,000 meters, evaporative and conductive energy transfers begin to become significant dissipators of energy and must be accounted for in the prediction. Similarly, the temperature and inflow rate of groundwater must be quantified. These variables add a great deal of

complexity to the prediction (Beschta 1984), making it no longer a simple, easy-to-apply technique. From a practical standpoint, this situation also means that streams exposed over long reaches will not continue heating indefinitely (e.g., Theurer et al. 1985). They will eventually reach an equilibrium temperature as evaporation, convection, conduction, and groundwater inflow balance the incoming radiation load.

What happens to temperature when streams flow from a fully exposed reach into a shaded reach? Will they cool down just as they warmed in the sun? Probably not unless cooler water from a tributary or from subsurface seepage enters the channel. Even though the direct solar radiation may be greatly reduced in the shady reach, it is still greater than long-wave radiation losses from the warm water and is likely to be greater than energy losses from evaporation, convection, or conduction. Thus the water temperature will remain relatively unchanged in the shaded reach unless it mixes with other cooler water within the reach. Management strategies to prevent excessive temperature increases by alternating shaded with unshaded reaches will be effective only if cooler inflows occur within the shaded reaches. Where cooler inflows do not occur, temperature increases from each exposed reach will not decrease appreciably through the shaded reaches, and the result is a "stair-step" temperature increase in the downstream direction (Brown et al. 1971).

Because heat added to a stream is not readily dissipated, temperature increases in small headwater streams can increase the temperature regimes of downstream reaches. The magnitude of downstream effect depends on the relative increase in temperature and amount of streamflow from the exposed tributaries. The mixing of any heated water, from exposed headwater streams, with cooler subsurface seepage or at tributary junctions will moderate the pronounced diurnal temperature increases experienced in an exposed headwater stream. Nevertheless, where extensive reaches of channel have become exposed either as a result of clearcut logging without buffer strips or from sluiced channels due to mass soil failures and debris torrents, a cumulative effect on the downstream thermal regime should be expected. Unpublished data (Beschta and Taylor 1986) for Salmon Creek, a 325 square kilometer drainage in the Oregon Cascades, shows such a cumulative effect. A thirty-year trend of increasing summer stream temperatures has been measured during a period of extensive logging and roading throughout the basin. During the summer, maximum stream temperatures at the mouth of this drainage have increased from 16°C in the mid-1950s to 22°C in the late 1970s; minimum temperatures in summer increased approximately 2°C (from 12 to 14°C) during this same period.

Increased temperatures have also been observed in the Middle Santiam River of the Oregon Cascades as the basin was logged. Logging activities in this basin have been largely limited to areas along the lower 11 km of the river, with areas farther upstream essentially undisturbed. Thus temperature changes downstream of the logged area can be referenced against temperatures of the undisturbed section. Average daily maximum temperatures for the period May to October increased approximately 1°C from 1972 to 1982, apparently as a result

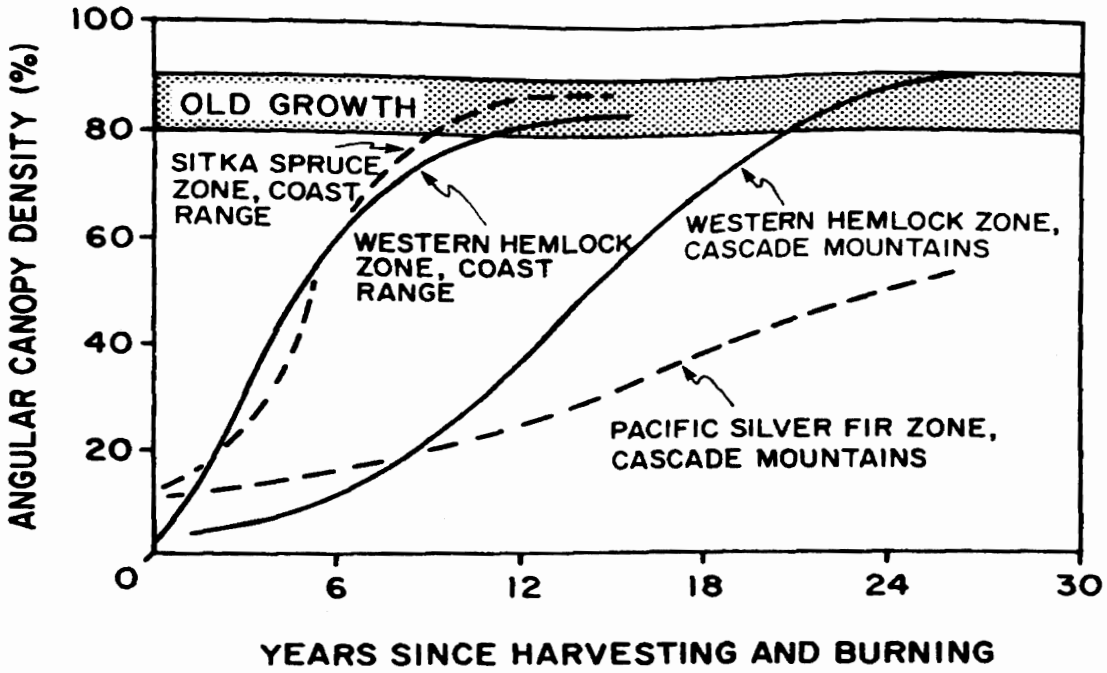


Figure 9. Relation between angular canopy density (ACD) and stand age for vegetation zones in western Oregon (Summers 1983).

of harvest (K. Sullivan, Weyerhaeuser Company, Tacoma, pers. comm.).

When temperature increases are produced by complete or partial exposure of a stream, they will subsequently decline as riparian vegetation returns. The rate of shade recovery depends on streamside conditions and vegetation. Sites in moist coastal ecosystems of the Pacific Northwest recover more rapidly than those in more arid ecosystems; sites at lower elevations more rapidly than those at higher elevations. In western Oregon, Summers (1983) examined sites with small streams that had been clearcut and burned at various times in the past to evaluate the recovery of shade (Figure 9). On the average, 50% of a stream was shaded within about five years of harvesting and burning in the Coast Range, within fifteen years from lower elevations of the Cascades (Western Hemlock Zone), and within twenty-five years for the higher elevations of the Cascades (Pacific Silver Fir Zone). Whereas small streams may be quickly overtopped by brush and effectively shaded from direct-beam solar radiation, larger streams, which require the canopies of tall conifers for shade protection, require longer periods.

Several alternatives are generally available to forest managers to prevent excessive temperature changes in order to avoid potential conflicts with fisheries interests, water quality changes, or other concerns. Where no change in temperature is permitted, a buffer strip is the obvious solution. But where some change in temperature is acceptable following logging, small clearcuts along streams, partial cuts or partial cuts within buffer strips (leaving only that vegetation that

provides shade during a critical time of the year), scheduling of cutting activity over time in a drainage, or some combination of these methods can provide a desired level of temperature protection.

THERMAL EFFECTS ON THE STREAM ECOSYSTEM

Research on the effects of thermal alterations on fish communities falls into three general areas that serve as foci for our discussion: (1) trophic effects (effects of thermal alteration on other components of the community that affect fish), (2) thermal tolerances and preferences of fishes, and (3) fish metabolism, development, and activity.

Trophic Effects

Water temperature changes in mountain streams may not only influence fish populations and productivity but also that of the microbial community, algae, and invertebrates. These latter biotic components form the energy base for fish communities, and changes in these compoents can potentially be translated into impacts on fish through a change in available food. The energy base for stream biota comes primarily from two sources: algal production and terrestrial sources of organic matter (needles, leaves, twigs, etc.) (Fisher and Likens 1973). In most forest streams, the largest proportion of available energy is from terrestrial organic inputs. The nutritional value of this organic matter to animals that ingest it is due largely to an encrusting layer of microorganisms that develops after entry into the stream (Kaushik and Hynes 1971). With increased temperatures, these microflora develop more rapidly and utilize available organic matter at a higher rate (Suberkropp et al. 1975). Rapid decomposition of organic material may promote increased invertebrate production more quickly than in cooler streams, thus leading to additional fish food at an earlier time. However, the organic matter would thus be consumed over a shorter period, so this effect may be transitory.

Where streamside vegetation has been removed, light availability and stream temperatures typically increase. Although Murphy et al. (1981) demonstrated increased stream primary production mainly from increased light availability after canopy removal, it is difficult to separate the influence of light and temperature. Light limitation of aquatic plant production has been demonstrated in several Pacific Northwest streams (Stockner and Shortreed 1978, Rounick and Gregory 1981, Walter 1984). Both increased light and temperature generally cause higher production of stream algae and, in many cases, a change in species composition. Phinney and McIntire (1965) examined the influence of both light and temperature on production of a natural assemblage of periphyton in an artificial stream channel. They found that algae production was higher at 18°C than it was at 8-10°C for all tested light levels. However, the influence of increased light on algae growth in the two channels differed. At 18°C, algal production increased with light intensity up to an intermediate level and decreased at higher illumination. In the cooler channel, algal productivity increased up to the highest light level tested. Kevern and Ball (1965) and Bisson and Davis (1976) also noted a marked increase in periphyton

production in heated stream channels compared with channels exposed to similar light regimes at lower temperatures. In contrast, Stockner and Shortreed (1978) conclude that nutrients and light are important regulators of algal growth in Carnation Creek, B.C., but that temperature does not have an important regulatory effect.

Changes in the taxonomic composition of the algal community in a stream following exposure to direct sunlight have been noted in several studies. In a spring-fed stream where temperature was constant (7°C), but light was experimentally varied through shade manipulation, Busch (1978) found that increased light both altered the species of algae present and caused an increase in algal biomass and invertebrate production. Warren et al. (1960) noted that in Oregon streams filamentous green algae dominated where at least 3% of full sunlight reached the substrate. In shaded stretches, diatoms predominated. Temperature also probably plays a role in this shift from a flora dominated by diatoms to one of green algae. Bisson and Davis (1976) noted a heavy growth of filamentous green algae in their heated channel. Their control channel had far less of this type of algae despite being exposed to similar light levels. The heavy growth of filamentous algae in the heated stream trapped considerable amounts of fine sediment, resulting in a shift in the invertebrate community to one dominated by oligochaete worms. These worms were rarely consumed by fish during this experiment. However, the general significance of such shifts in algal community composition on fish production in mountain streams is not well understood.

The influence of the changes in the energy base on higher tropic levels of the stream after canopy removal is difficult to interpret (Lee and Samuel 1976). Higher production levels of both microorganisms and algae suggest corresponding increases at higher levels of the food chain. However, the faster processing rate of organic matter by microbes coupled with a decrease in the input of leaves, needles, and other organic materials after clearcutting may lead to a scarcity of this material at certain times of the year. For example, Fisher and Likens (1973) found that under natural forested conditions, organic matter of leaf and twig size persisted in a small New England stream for about a year. With the more rapid processing at higher temperature, the residence time of this material in the stream should decrease. Since most terrestrial organic matter enters the stream as a pulse in autumn, an increased rate of processing could reduce summer stocks of this material, hence lowering food supplies for invertebrates dependent on this material. Thus when streams become exposed following removal of riparian vegetation, a short-term increase (from logging slash) followed by a longer term decrease in the availability of terrestrial organic matter may occur. The effect on the invertebrate populations and the extent to which it is offset by greater algal productivity are not known.

Nevertheless, despite the potential for deleterious effects, invertebrate standing crops in headwater streams that drain clearcuts are generally greater than those either in old-growth forests or in second-growth deciduous forests (Hughs 1966, Newbold et al. 1980, Smith 1980, Murphy and Hall 1981, Murphy et al. 1981). It would

appear that the possible deleterious effects of removing riparian vegetation are outweighed by the increased primary production resulting from increased temperatures, light levels, and nutrients.

Invertebrates may be directly influenced by temperature increases, apart from the influence of their food supply. At higher temperatures, invertebrates feed more actively and, as a result, exhibit elevated growth rates (Cummins et al. 1973).

Temperature increases have at times been related to noticeable decreases in invertebrate production. Minshall (1968), studying a spring-fed brook in Kentucky, found a large decrease in both species diversity and numbers of individuals when stream temperature was elevated in a clearcut. However, spring-fed streams, in general, tend to have a constant, cold temperature year round and hence a fauna specialized for these unusual circumstances. This type of system may be especially sensitive to elevated temperatures.

Higher stream temperatures can also cause accelerated development of aquatic insect larvae, leading to early adult emergence (Nebeker 1971a, 1971b, Moore 1980). Salmonid fishes prey heavily on emerging adults, and accelerated insect development may benefit fish by making more food available earlier in the year. However, for most trouts (Salmo spp.) the emergence of fry from spawning gravel and the onset of active feeding coincides with spring and early summer hatches of aquatic insects.

Bisson and Davis (1976), working with two experimental stream channels, one heated about 4°C over the other, reported a reduction in the number of taxa in the heated channel. They also reported that nearly all the species represented in the channels produced higher biomasses in the control stream. There were exceptions to this rule, however, the most notable being a species of oligochaete worm and a snail, both of which exhibited increased production in the channel. Neither species was eaten by the juvenile chinook salmon in the channels, and as a result the increased production was of no benefit to the fish.

Sherberger et al. (1977) indicate that a temperature of at least 28°C was needed to influence mortality in Isonychia, a mayfly, while Hydropsyche, a caddisfly, withstood brief exposures up to temperatures of 26.5°C. Temperatures below the lethal limit did not have an effect on survival. At least in the case of these two invertebrates, lethal levels are above that needed to severely affect salmonids. Thus increased temperatures would probably eliminate the fish before their food resource was affected.

Some invertebrates are able to avoid high summer temperatures, such as those created by canopy removal, by adjusting their life cycle to spend the stressful period in a resistant, resting stage. Macan (1961) demonstrated that the mayfly, Rithrogena semicolorata, emerged earlier in the year in a warm stream than normally seen in cooler waters. The eggs deposited by the adults in spring in the warmed stream remained dormant for a longer period than those in cooler streams,

hatching only when water temperatures decreased in autumn. Many invertebrates, however, such as those that spend one or more years in a larval form, would not generally be able to avoid temperature extremes by using this tactic.

Increased temperatures have been implicated in several studies as leading to increased entry of invertebrates into the drift (Pearson and Franklin 1968, Waters 1968, Bisson and Davis 1976). However, other investigators have not found this phenomenon (Bishop and Hynes 1969, Wojtalik and Waters 1970, Reisen and Prins 1972). The drift reaction of various invertebrates is probably species specific, which would account for the discrepancies noted in these studies. Increased drift rate would make more food available for fish, since drift forms the major food source for salmonids.

The influence of elevated temperatures on salmonid production of natural systems is difficult to delineate because of the variety of other factors concurrently affected. However, more abundant invertebrates have been observed in streams draining clearcuts (e.g., Murphy et al. 1981). Increased algal productivity leading to higher invertebrate production, and consequently to elevated food availability for fish, has been hypothesized as a cause of the frequent observation of increased salmonid production in streams exposed to sunlight (Murphy and Hall 1981, Weber 1981, Hawkins et al. 1983, Bisson and Sedell 1984). The consistency of these observations has led to general acceptance of the hypothesis that salmonid abundance is greater in streams draining clearcuts because there is more available food. Consequently, it is also generally accepted that an understanding of the effects of logging on the entire stream ecosystem is essential if we are to make progress in understanding the narrower problem of logging impacts on fish production.

Thermal Tolerances and Preferences of Fishes

The systematic study of the thermal tolerances and preferences of fishes began in the last century (see Brett 1970). Our understanding has slowly broadened from the concept of a single end point (e.g., a single upper lethal temperature) to a two or three factor concept (the zone of thermal tolerance of Fry 1964, where lethal temperatures are modified by acclimation temperature and exposure) and finally to a multifactorial concept where a multidimensional zone of thermal tolerance is defined by many interacting environmental factors (Brett 1970). Such studies are of necessity conducted under the tightly controlled conditions of the laboratory. The relevant objective of this work is to define for a particular species the boundaries of the thermal habitat. It may then be inferred that any land use activity that drives temperatures outside these boundaries will have deleterious and possibly lethal consequences.

Have any generalities relevant to our general topic emerged from this work? Apparently salmonids are tolerant of the extremes in temperature they are likely to encounter over their life spans and geographic ranges. In particular, the life stages of salmonid species that rear in freshwater seem especially tolerant of extreme high

temperatures (extreme in the sense that most species can tolerate temperatures that are many degrees higher than any they are likely to encounter).

Because fish are cold-blooded, or poikilothermic, the temperature of their external environment dictates their internal temperature, which in turn regulates metabolic rate. Thus changes in water temperature directly influence the physiology and activity of fish. Furthermore, the relative sensitivity of fish to temperature changes depends, to a great extent, on their stage of development.

Early studies evaluated the effects of elevated temperatures on the survival of salmon eggs. For example, Combs and Burrows (1957) examined the influence of various temperatures on the survival of chinook salmon eggs. They found the upper lethal limit to be between 14 and 15.5°C. Similarly, Seymour (1959) reported that chinook eggs would not survive to the stage of vertebral development at temperatures in excess of 16.5°C. Sockeye salmon eggs appear to be even more susceptible to elevated temperatures, as Combs (1965) set the lethal level for development of this species at 13.5°C. Even in cases where temperature elevation is not sufficient to cause direct egg mortality, morphological characteristics of the fish can be altered as a result of high temperature during embryonic development (Orska 1963). Although laboratory studies provide an upper bound on temperature tolerance of eggs and embryos exposed to constant temperatures, the temperature environment in redds may be quite different.

Spawning and egg development in salmonids occurs during the autumn, winter, and spring. In coastal Oregon, Ringler and Hall (1975) found intragravel water temperatures during the time of coho salmon egg incubation in a stream draining a clearcut watershed to be well below those reported to cause developmental abnormalities. In the case of some races of spring-spawning salmonids, egg development may continue into late spring when the possibility of coincident low stream flow and sunny days could produce water temperatures detrimental to the development of the eggs. The extent to which this occurs is unknown. In addition to the influence elevated temperatures may have on egg development, depressed temperatures have been seen to lengthen incubation periods or increase freezing mortalities (Alderdice and Velsen 1978, Reiser and Wesche 1979, Reiser and White 1981). However, the effect removal of streamside vegetation has on minimum stream and intergravel temperatures in winter has generally received little attention (Needham and Jones 1959, Sheridan 1961).

Lethal threshold temperatures for Pacific salmon and steelhead trout have been identified for laboratory conditions (Figure 10), where the fish are held at a given temperature for long periods of time. This situation does not exist under natural conditions (even where temperatures have been elevated because of the removal of streamside vegetation), hence the direct application of laboratory temperature limits to field conditions is tenuous. Streams flowing through clearcut areas may display sizable fluctuations of water temperature over the period of a day, and maximum temperatures may exceed the reported lethal threshold temperatures for a brief time. However, these streams may

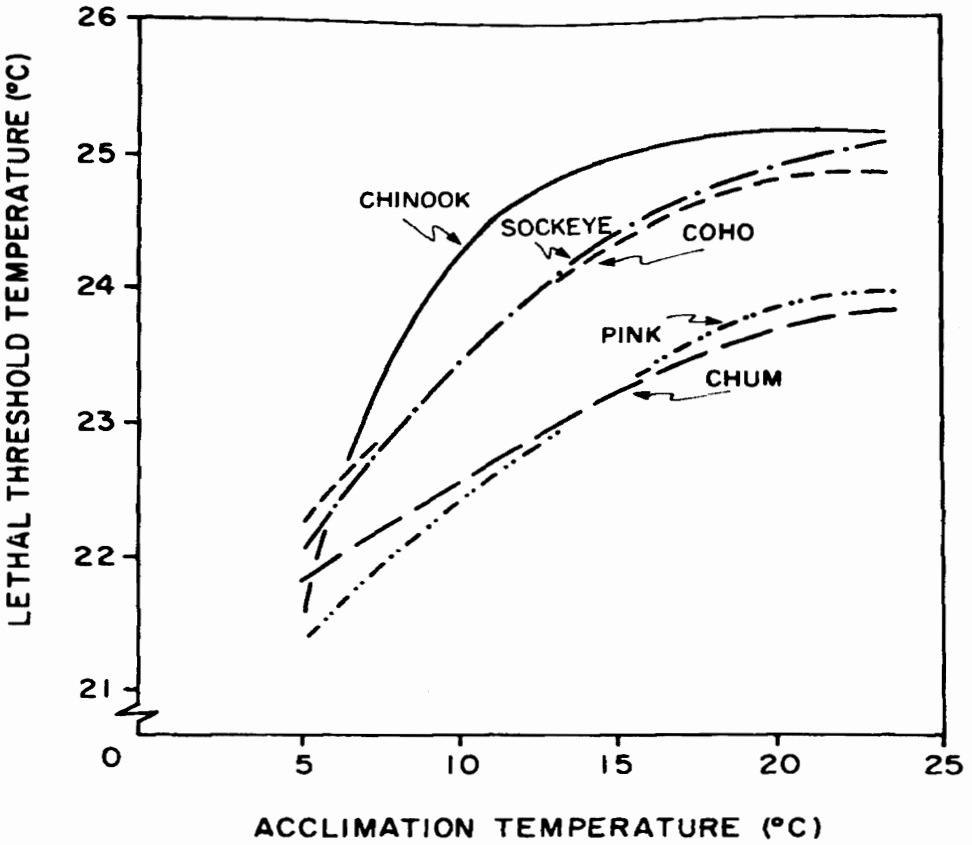


Figure 10. Lethal threshold temperatures for juvenile salmonids (from EPA 1973): chum salmon (Oncorhynchus keta), pink salmon (O. gorbuscha), coho salmon (O. kisutch), sockeye salmon (O. nerka), and chinook salmon (O. tshawytscha).

contain sizable populations of salmonids (Bisson et al. 1985). Apparently fish are able to withstand periodic, short-term exposures to fairly high temperatures with minimal detrimental impact.

The temperature levels preferred by rearing juvenile salmonids have also been evaluated in a number of laboratory studies. Brett (1952) found that the range of greatest preference by all species of Pacific salmon was from 12 to 14°C for acclimation temperatures ranging from 5 to 24°C. Brett (1952) also noted a definite avoidance of water over 15°C. Mantelman (1960) observed that juvenile rainbow trout were most commonly found in water ranging from 13 to 19°C and actively avoid water in excess of 22°C. These preferred temperatures may be exceeded in streams draining clearcut watersheds (Brown and Krygier 1970, Sheridan and Bloom 1975).

Elevated temperatures can also influence salmonid behavior. Upstream movement of adult sockeye salmon and steelhead trout was curtailed in the Columbia River when water temperatures reached 21°C (Lantz 1971). At these times the migrating fish congregated in the mouths of cooler tributaries until water temperatures decreased. Keenleyside and Hoar (1954) reported that both chum and coho salmon

fry exhibited progressively increased rates of downstream migration as water temperature increased. Temperature preferences of fish have been the target of many studies; these have been summarized by Coutant (1977) and Jobling (1981).

For the coho salmon of Carnation Creek there is no evidence that increased summer temperatures (several degrees outside of their probable historical limits) and increased diurnal fluctuations affected fish distributions, at least on a macroscale. The availability of small-scale cover ("fine logging debris") was the important factor in determining the abundance of fry in stream sections whose banks had been completely clearcut, not the increases in stream temperatures in those sections (Scrivener and Andersen 1984).

Larkin (1956) noted that, as a rule, freshwater fish are adaptable to a wide range of environmental conditions and that the outcome of competitive interactions may vary depending on these conditions. A species that is dominant under one set of conditions may not necessarily prevail when conditions differ. Two recent studies have examined the influence of water temperature on interspecific interactions between fish. Reeves (1985) showed that the outcome of interactions between juvenile steelhead trout (age 1+) and the redside shiner (Richardsonius balteatus) was mediated by water temperatures. Water temperatures and the presence of the other species influenced production and activity in laboratory streams and distribution in the field and laboratory. Trout dominated in cool water (12 to 15°C) and shiners in warm water (19 to 22°). Baltz et al. (1982) found that competition between two species of nongame fish was affected by water temperature: one species dominated in cool water and the other in warm. Alteration of the temperature regime may influence not only growth and survival of a given species but also the structure of the fish community.

The development of thermal tolerance criteria in laboratory studies seems to have been markedly unsuccessful in helping understand the effects of logging on fish communities in the Pacific Northwest. To our knowledge, there are no records of elevated temperatures following shade removal that have led to extensive fish kills. An exception is the fish kill observed following a hot slash fire in Needle Branch, Oregon, during the Alsea Watershed Study (J. D. Hall, Oregon State University, Corvallis, pers. comm.). In fact, there is a general tendency for salmonid biomass to be higher in streams draining clearcuts (Burns 1972, Smith 1980, Martin et al. 1981, Murphy and Hall 1981, Holtby and Hartman 1982, Hawkins et al. 1983, Bisson and Sedell 1984, Scrivener and Andersen 1984). While such increases may have been due to many factors, the generality of the observation suggests that temperature increases resulting from clearcut logging do not, by themselves, have significant deleterious effects on salmonid abundance. One reason is that stream temperatures throughout the region seldom exceed, for extended periods, the tolerance limits of the resident salmonid species. The fish themselves also appear to be behaviorally "plastic" and can act to reduce either or both the temperatures they are exposed to and the duration of the exposure. For instance, salmonids appear to seek out cool water regions in streams where temperatures approach and exceed tolerance limits (Gibson 1966, Kaya et al. 1977). Even in studies where

elevated summer temperatures, resulting from streamside disturbance, appear to have precluded salmonids, strong arguments can be made that the temperature effects were indirect. For example, Barton et al. (1985) concluded that the suitability of streams in southern Ontario for trout was characterized by maximum summer temperatures. While the effects of temperatures could have been direct, the authors suggest that elevated temperatures over several decades allowed the successful invasion of warm water competitors of the salmonids, possibly resulting in their competitive exclusion.

Although salmonid populations may respond favorably to opening of the riparian canopy, increased water temperatures, or both, resulting from management activities in these streams, the cumulative effect of these changes on other areas of the watershed has received little or no consideration in the Pacific Northwest. Water temperature in mid-order streams lower in a watershed depends largely on the temperature of water entering from upstream. Mid-order streams are important rearing areas for juvenile anadromous salmonids, especially chinook salmon and >1+ steelhead trout. They also have a more diverse fish community than lower order streams do (Vannote et al. 1980). Changes in environmental conditions may result in a decrease in available habitat for salmonids and alter the outcome of interactions between salmonids and potential competitors. Environmental changes less favorable to salmonids, such as increased water temperature in higher order streams, could offset any increase in abundance or production of anadromous salmonids that might occur from opening the canopy along lower order streams, or could even result in an overall decrease in population.

Temperature Effects on Fish Metabolism, Development, and Activity

The second general approach that has been used to study the effects of thermal change of stream fishes considers the effects of temperatures on metabolism, development, and activity. Within the bounds of thermal tolerance for any species, temperature is an important modifier of metabolism which then acts through numerous pathways to affect development, growth, activity, and reproduction or, more generally, survival and success (Brett 1958, Brett 1970, Lantz 1971). This rather broad field has been reviewed extensively (e.g., Fry 1967, Warren and Davis 1967, Brett 1970).

Except when fish are starving, the response of growth and activity to increasing temperatures is enhancement up to some optimum temperature and them diminution as the optimum is exceeded. In general, the optimal temperatures for growth and activity are similar to those likely to be encountered at a particular stage of the fish. It is also generally the case that the optima are rather broad, especially for species and life stages where the temperatures encountered are wide ranging.

Laboratory studies with salmon and trout at constant temperature levels have generally shown decreased growth with higher temperatures when food was limiting. A fish will not grow until metabolic energy requirements are first met (Warren and Davis 1967), and the metabolic rate increases with temperature. Dwyer and Kramer (1975) examined the

metabolic rate of cutthroat trout at several temperatures. They measured the lowest metabolic rate at 5°C and the highest at 15°C with a decrease in rate at 20 to 24°C. Normally, metabolic rate would be expected to continue to increase as a function of temperature; however, in this experiment the trout held at 20 and 24°C fed very little, and it is likely that the decrease in metabolic rate was brought on by starvation. Wurtsbaugh and Davis (1977) found that maintenance food levels (the amount needed to maintain constant body weight) for rainbow trout were 2.7% of body weight per day at 6.9°C and 7.5% at 22.5°C. Averett (1968) found that juvenile coho salmon required twice the amount of food to grow at 17°C than at 5°C. In many salmonids, however, the dimunution in growth and swimming performance with increasing temperature occurs primarily at temperatures near the lethal thresholds (e.g., Brett 1967, Brett et al. 1969).

Wurtsbaugh and Davis (1977) indicated that if steelhead trout were fed limited amounts of food, growth decreased at higher temperatures. The difference in productivity lessened, however, if the ration was increased. Similarly, the production of coho salmon has been shown to decrease at higher temperatures under conditions of limited food (Iversen 1972). The decreased production in Iversen's (1972) study was attributed to both increased metabolic rate and a reduction in food availability due to a decrease in the invertebrate population in the artificial stream channel in which the experiment was conducted. Bisson and Davis (1976) also reported a decrease in fish production with increased temperature for juvenile chinook salmon. They subjected artificial stream channels to diurnal and annual temperature cycles with one of the channels heated and maintained at a temperature approximately 4°C higher than the control. Production in the cooler channel exceeded that in the heated channel by 100% the first year of the experiment and 30% by the second year. The decreased production in the heated channel was attributed to increased metabolic requirements and reduced food levels.

Fish productivity at elevated temperatures could probably be maintained, provided the food supply increased enough to compensate for increased metabolic requirements. In a study in which water temperature in artificial streams varied daily, production of juvenile steelhead trout (>1+) was two and one half times greater in cooler water (12 to 15°C) than in warmer (19 to 22°C) water (Reeves 1985). One reason for these differences was that fish in the cooler water were able to maintain territories in areas of higher food concentration, which were in areas of greater water turbulence.

Nearly all these studies on the influence of temperature on fish production were conducted in artificial streams. More recent studies of natural streams have not always corroborated the results from artificial channels. Martin et al. (1981) compared a population of cutthroat trout inhabiting a shaded section of stream with fish in a section of stream exposed to direct sunlight. They could find no difference in trout biomass or density between the two sections, although the exposed section had a daily maximum temperature that averaged 2°C higher than the shaded section. However, in a final analysis of the data set, Martin (1985) concluded that in the canopy area with no temperature change,

density increased. In the open area where temperature increased, growth increased but density did not. Some studies of salmonid populations in streams exposed to sunlight have reported increases in production. For example, Murphy and Hall (1981) reported higher salmonid biomass in streams exposed to sunlight than in streams flowing through old-growth forest in Oregon. The temperature increases in the exposed streams were slight, ranging from 0.1 to 1°C, thus the fish biomass increase is probably attributable to factors other than increased temperature. Bisson and Sedell (1984) also reported higher salmonid biomass in streams draining clearcut areas than in shaded systems in southwestern Washington, but these authors did not monitor stream temperatures.

While the growth efficiency of salmonids is theoretically highest at low temperatures, activity of fish in cold water is at a minimum and feeding rates are correspondingly depressed. Thus optimum growth usually occurs at some intermediate temperature where activity levels are high enough to ensure active feeding, and metabolic conversion efficiencies are also relatively high. "Optimum" stream temperatures for various stages of development and species of fish are shown in Table 3.

The relation between increases in diurnal variations and growth rate is unknown. For some species, increases in diurnal variation might be beneficial. Biette and Green (1980) have demonstrated for sockeye salmon that temperature fluctuations, resulting from diurnal migrations throughout the thermoclines of stratified lakes, are associated with growth increases at low, and therefore realistic, ration levels. In contrast, Edwards et al. (1979) have shown for brown trout that increases in diurnal temperature fluctuations with constant mean temperatures result in diminution in growth. As noted earlier, streams often contain pockets of water cooler than the ambient stream (Keller and Hofstra 1982, Bilby 1984). These areas have been seen to be used by salmonids during times of stressful temperatures (Gibson 1966, Kaya et al. 1977), and may in part be responsible for the presence of salmon and trout in streams that occasionally attain very high temperatures (Bisson et al. 1985). However, the potential for this mechanism to assist in reducing thermal impacts to fish may be limited by the relative scarcity and, potentially, low oxygen concentration of cool-water areas (Bilby 1984).

Temperature is known to affect other physiological processes. For instance, as temperatures increase, diseases often become more virulent. The higher susceptibility to disease is brought on by a combination of higher metabolic rates and elevated levels of physiological stress. Ordal and Pacha (1963) and Parker and Krenkel (1969) report that a large number of common diseases of salmonids, including kidney disease, furunculosis, vibrosis, and columnaris, become more virulent as temperature increases. Nakatani (1969) found that columnaris became well established in salmonids at temperatures of 17 to 18°C under crowded conditions. When temperatures reached 21°C, the disease killed most of the infected individuals. Chinook and coho salmon and steelhead trout, infected with furunculosis, a bacterial infection, were held at temperatures ranging from 3.9 to 20.5°C (Groberg et al. 1978). At temperatures below 10°C, mortality of the fish ranged from 2 to 26% of

Table 3. Water temperature criteria, in degrees Celsius, for fish in western North America.

Species	Upstream Migration	Spawning	Incubation	Juvenile Rearing		
				Preferred	Optimum	Upper Lethal
Chinook	---	5.6-13.9	5.0-14.4	7.3-14.6	12.2	25.2
Fall	10.6-19.4	---	---	---	---	---
Spring	3.3-13.3	---	---	---	---	---
Summer	13.9-20.0	---	---	---	---	---
Chum	8.3-15.6	7.2-12.8	4.4-13.3	11.2-14.6	13.5	25.8
Coho	7.2-15.6	4.4- 9.4	4.4-13.3	11.8-14.6	---	25.8
Pink	7.2-15.6	7.2-12.8	4.4-13.3	5.6-14.6	10.1	25.8
Sockeye	7.2-15.6	10.6-12.2	4.4-13.3	11.2-14.6	15.0	24.6
Steelhead	---	3.9- 9.4	---	7.3-14.6	10.0	24.1
Kokanee	---	5.0-12.8	---	---	---	---
Rainbow	---	2.2-20.0	---	---	---	---
Cutthroat	---	6.1-17.2	---	9.5-12.9	---	23.0
Brown	---	7.2-12.8	---	3.9-21.3	---	24.1

Source: Adapted from Reiser and Bjornn 1979.

the infected fish. However, at 20.5°C, 93 to 100% of the infected fish died within two to three days. These investigations were conducted under conditions of constant temperature and high population densities. As with much of the temperature research, it is difficult to transfer work done in a controlled environment to a situation in the field. The virulence of various fish diseases under conditions of varying temperatures and relatively low population densities has seldom been examined.

An exception to the general rule of increased disease virulence with increased temperature was noted by Bisson and Davis (1976). They found a reduced infection rate of juvenile chinook salmon by the trematode parasite (Nanophyetus salmicola) for fish held in water 4°C warmer than a control. This seems to represent an instance where the infecting organism is less tolerant of temperature elevation than the host.

It is generally accepted that the temperature regime is one habitat component to which fish populations are locally adapted (Ricker 1972). For instance, Leggett and Carscadden (1978) demonstrated for the anadromous American shad (Alosa sapidissima) that the principal factor determining interpopulation differences in reproduction strategies was the variability in thermal regimes of the natal streams. Since developmental and metabolic rates in fish are highly dependent on temperature, variations in temperature lead to variation in the timing of such life history events as emergence and migrations. In lakes of the Fraser River drainage, interannual variations in sockeye salmon smolt sizes that are not accounted for by density appear determined by the length of the growing season, which, in turn, is determined by temperatures around the time of emergence (Goodlad et al. 1974).

Temperature variations around the time of smolt migration have been shown to be the principal source of interannual variability of Atlantic smolt migration timing in Norway (Jonsson and Ruud-Hansen 1985). Thedinga and Koski (1984) have shown, in their studies of the coho salmon of Porcupine Creek, Alaska, that variations in the timing of smolt outmigrations can have deleterious impacts on marine survival.

Since the timing of life history events is an adaptation to local conditions, it can be expected that changes in those environmental conditions, such as changes in temperature regimes caused by logging, may reduce the fitness of affected populations, with deleterious consequences to production (Leggett and Carscadden 1978). The possible effects of altering events such as fry emergence and smolt and adult migration have been mentioned in the context of logging effects (Narver 1972, Moring 1975b, Holtby and Newcombe 1982, Hartman et al. 1984), but with the exception of research at Carnation Creek, B.C., there has been little systematic study.

In a recently completed study, Holtby (1986) attempted to assess the effects of temperature on the timing of life history events of a population of coho salmon in a small coastal stream (Carnation Creek). Temperature-related impacts on this fish population were seen to bring about a series of changes: (1) logging-related (58%) and climate-related (42%) increases in late winter temperatures accelerated fry emergence (Holtby and Newcombe 1982, Tschaplinski and Hartman 1983); (2) increased length of growing season, resulting from earlier emergence, led to increased fry size entering their first winter (Hartman et al. 1984); (3) increased fry size led to higher overwinter survival (Holtby and Hartman 1982); (4) higher overwinter survival and size led to increased numbers and sizes of 1+ smolts; and (5) seaward migration of the smolts in spring was accelerated by seven to ten days.

The impacts of temperature increase on the freshwater phases of the coho population generally suggest increased production of smolts. However, earlier release to the sea of hatchery-stock coho smolts has been linked to decreased marine survival (Bilton et al. 1982). Therefore, the benefits that resulted from changes in smolt size and numbers following logging (Figure 11) may be substantially or wholly offset by increased saltwater mortality attributable to earlier migration.

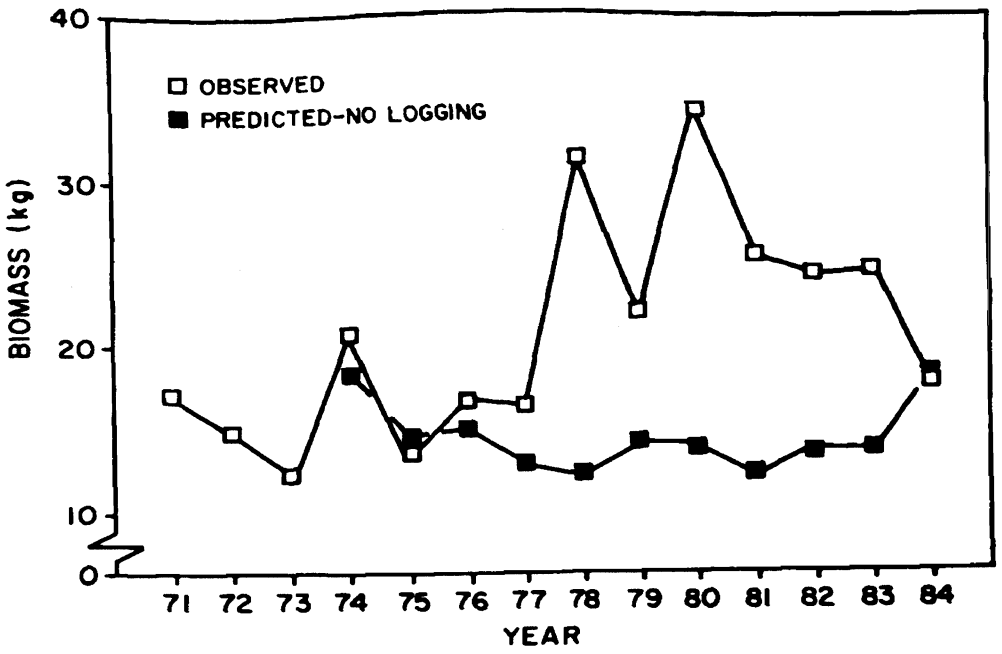


Figure 11. The combined weight of coho salmon smolts produced by Carnation Creek, B.C. Logging began in the winter of 1975-76 and was largely complete in those areas of the watershed immediately surrounding anadromous salmon habitat by the summer of 1979. The line of predicted smolt output assumes that temperature changes associated with logging did not occur (Holtby 1986).

Several important points emerge from the studies at Carnation Creek, B.C. First, the alteration in the timing of life history events due to temperature changes may significantly affect fish production. Second, temperature effects are not necessarily confined to the stream, but ultimately may affect returns of adults to the stream. Third, the temperature changes that resulted in effects on fish production were relatively small and clearly not life threatening changes that occurred in the winter and spring. The much larger thermal effects of logging that were observed during the summer had no detectable effects on coho smolt production.

SUMMARY AND CONCLUSIONS

Stream temperatures in forested watersheds in the Pacific Northwest can be characterized as (1) predictable along such various spatial scales as latitude, elevation, and stream order, (2) predictable on temporal scales such as season and day, and (3) of low variability both between years and within days. It has been repeatedly demonstrated that removal of riparian vegetation alters stream temperature regimes. In coastal streams, where prolonged periods of below zero temperatures are rare, removal of riparian vegetation invariably results in increased mean and maximum stream temperatures and increased diurnal ranges. Over a sufficiently long period, effects of streamside

logging on thermal regimes can be detected throughout the year, and not just in the summer as is the general perception. In regions where winter temperatures are below freezing, the removal of riparian vegetation may result in the depression of stream temperatures and greater periods of freeze-up, but such situations have been little studied.

For a given stream, the magnitude of the temperature increase after streamside logging is proportional to the increase in exposure of the stream to incoming solar radiation, or, conversely, to the amount of shade reduction. Thus buffer strips (composed of vegetation not susceptible to blow down) are an effective means of providing shade and preventing temperature changes. The exact configuration and width of such buffer strips can be highly variable and site specific. In western Oregon, it appears that buffer strips 30 m or more in width along small streams provide approximately the same level of shading as an old-growth forest. More important, an understanding of the energy transfer influencing stream temperature permits the dimensions of streamside logging to be controlled to produce the desired effects on stream temperatures, ranging upward from no effects at all.

There are many reasons why the observed logging-related temperature increases have not had significant deleterious effects on resident salmonids. Among these are (1) the wide thermal tolerances of the freshwater forms of most of the resident salmonid species, (2) the natural diurnal cycling of stream temperatures, which limits exposure to maximum temperatures, (3) the occurrence of localized cool-water sources, which fish seem readily able to locate and utilize, (4) the inability to extrapolate tolerance limits determined under homogeneous laboratory conditions to the spatially and temporally complex thermal environments of streams, and (5) the ability of fish to migrate to other locations or to curtail activities temporarily when temperatures become stressful. Although increased summer temperatures remain a concern to fisheries managers, it appears that fish are generally able to tolerate such increases without major adverse impacts on growth or mortality.

Because of the extensive geographical range of salmonids, the effects of temperature on these fish should be viewed in a regional context. In at least some regions of the Pacific Northwest, concern over the lethal effects of elevated summer temperatures in small streams draining deforested watersheds is unwarranted. This is certainly the case in the low elevation, coastal streams of British Columbia and Washington. However, in other regions of the Pacific Northwest, increased temperatures from logging may remain a significant concern. For example, in southern areas (southern Oregon and northern California) and areas east of the Cascade Mountains, increased temperatures due to logging may have a greater impact on fish populations than in areas of cooler climate, because of ambient water temperatures. Unfortunately, for most of these areas little information is available that might demonstrate the influences increased water temperatures have on fish populations.

Temperature is clearly an important component of the habitat of many stream organisms, including the fish, and most organisms respond

to the changes in stream temperatures caused by streamside logging. But because temperature is only one of several closely interconnected physical factors that are affected simultaneously by streamside logging, it is questionable whether our understanding of the impacts of logging on fish production can be increased by trying to study the effects of temperature in isolation.

Increased temperatures following logging, together with increased light levels and increased nutrient concentrations, often lead to general increases in productivity in the trophic levels that form the basis of fish production. Increased temperatures, light, and nutrients all play a role. Temperature directly affects development rates of fish; in some systems, the temperature increases lead to earlier emergence, longer growing seasons, and increased survivals at critical times in the life histories of fish. Increased temperatures also directly affect metabolism and activity levels of fish.

The apparent generality of enhanced fish production after streamside logging could be an artifact of geographically limited data or a "coastal rain-forest" perspective. For instance, there is relatively little known about the effects of logging on stream temperatures and fish production in areas where streams freeze in the winter. In such regions, production "bottlenecks" might occur during the winter period of low flows and freezing temperatures. Slight changes in stream exposure might cause decreased stream temperatures, and, coupled with other physical effects of logging such as channelization and decreased pool depths, could conceivably decrease winter habitat for fish and decrease production (Bustard 1985). Under such circumstances, enhanced summer production would be essentially nullified by worsened winter conditions.

The same streamside activities that lead to changes in temperature and light levels precipitate other changes in the stream (Bisson et al., Everest et al., Swanson et al., and Sullivan et al., in this volume). Streamside logging has often been associated with changes in sedimentation, bank stability, channel morphology, large woody debris, and other factors that ultimately alter the productive capacity of a stream for fish. Where sources of large organic debris have been removed, the effects of streamside logging on the physical configuration of the stream can extend for decades.

There are many promising areas for research on the impacts of streamside management on fisheries. There is a great need to develop empirical predictors of the productivity gains to be had from controlled streamside disturbance (In what situations should the streamside be left unaltered? If there are productivity gains to be had, how can streamsides be managed to maximize those benefits?). A great deal has yet to be learned about the processes governing the productivity of salmonids in the diverse stream types and climatic zones in the region. This knowledge is essential if the riparian zone is to be successfully managed. A technological challenge lies in the development of techniques that maximize the beneficial effects while minimizing or mitigating deleterious impacts.

Considering the productivity gains that may be had by judicious streamside treatments, it seems to us an overly conservative view to eliminate all forest management activity in the riparian zone. However, much remains to be discovered before managers can abandon their cautious stance on streamside logging. Therein lie the challenges for joint fisheries-forestry research.

ACKNOWLEDGMENTS

Review comments by G. H. Reeves, P. A. Bisson, and J. D. Hall, while the manuscript was at various stages of development, are greatly appreciated.

LITERATURE CITED

Alderdice, D. F., and F. P. J. Velsen. 1978. Relation between temperature and incubation time for eggs of chinook salmon (Oncorhynchus tshawytscha). J. Fish. Res. Board Can. 35:69-75.

Averett, R. C. 1968. Influence of temperature on energy and material utilization by juvenile coho salmon. Ph.D. thesis, Oregon State University, Corvallis.74 p.

Baltz, D. M., P. B. Moyle, and N. J. Knight. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, Cottus gulosus, and speckled dace Rhinichthys osculus. Can. J. Fish. Aquat. Sci. 39:1502-1511.

Barton, D. R., W. D. Taylor, and R. M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. North Am. J. Fish. Manage. 5:364-378.

Beschta, R. L. 1984. TEMP-84: A computer model for predicting stream temperatures from the management of streamside vegetation. USDA For. Serv. WSDG Rep. 9. Watershed Systems Development Group, Fort Collins, Colorado. 76 p.

Beschta, R. L., and R. Lynn Taylor. 1986. Increased stream temperatures of Salmon Creek, Oregon: An example of cumulative effects? Unpublished report. Department of Forest Engineering, Oregon State University, Corvallis. 20 p.

Biette, R. M., and G. H. Green. 1980. Growth of underyearling sockeye salmon (Oncorhynchus nerka) under constant and cyclic temperatures in relation to live zooplankton ration size. Can. J. Fish. Aquat. Sci. 37:203-210.

Bilby, R. E. 1984. Characteristics and frequency of cool-water areas in a western Washington stream. J. Freshw. Ecol. 2:593-602.

Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (Oncorhynchus kisutch) on returns at maturity. Can. J. Fish. Aquat. Sci. 39:426-447.

Bishop, J. E., and H. B. N. Hynes. 1969. Downstream drift of the invertebrate fauna in a stream ecosystem. Arch. Hydrobiol. 66:56-90.

Bisson, P. A., and G. E. Davis. 1976. Production of juvenile chinook salmon, Oncorhynchus tshawytscha, in a heated stream. NOAA Fishery Bull. 74:763-774.

Bisson, P. A., J. L. Nielsen, and J. W. Ward. 1985. Experimental release of coho salmon (Oncorhynchus kisutch) into a stream impacted by Mount St. Helens volcano. In Proceedings, Western Association of Fish and Wildlife Agencies, p. 422-435. Victoria, B.C.

Bisson, P. A., and J. R. Sedell. 1984. Salmonid populations in streams in clearcut vs. old-growth forests of western Washington. In W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley (eds.) Fish and wildlife relationships in old-growth forests: Proceedings of a symposium, p. 121-129. American Institute of Fishery Research Biologists.

Brazier, J. R., and G. W. Brown. 1973. Buffer strips for stream temperature control. Res. Pap. 15. Forest Research Laboratory, Oregon State University.9 p.

Brett, J. R. 1952. Temperature tolerances in young Pacific salmon, Oncorhynchus. J. Fish. Res. Board Can. 9:268-323.

_____. 1958. Implications and assessments of environmental stress. In P. A. Larkin (ed.) The Investigation of Fish-Power Problems Proceedings, p. 69-83. H. R. MacMillan Lectures in Fisheries. University of British Columbia, Vancouver.

_____. 1967. Swimming performance of sockeye salmon (Oncorhynchus nerka) in

relation to fatigue, time and temperature. J. Fish. Res. Board Can. 24:1731-1741.

_____. 1970. Temperature: Fishes. In O. Kinne (ed.) Marine Ecology, 1:513-560. Environmental factors, Part 1. Wiley-Interscience, London.

Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, Oncorhynchus nerka, in relation to temperature and ration size. J. Fish. Res. Board Can. 26:2363-2394.

Brown, G. W. 1969. Predicting temperatures of small streams. Water Resour. Res. 5(1):68-75.

_____. 1983. Forestry and water quality. Oregon State University Bookstore, Inc., Corvallis. 142 p.

Brown, G. W., and J. T. Krygier. 1967. Changing water temperatures in small mountain streams. J. Soil Water Conserv. 22(6):242-244.

_____. 1970. Effects of clearcutting on stream temperature. Water Resour. Res. 6(4):1133-1139.

Brown, G. W., G. W. Swank, and J. Rothacher. 1971. Water temperature in the Steamboat drainage. USDA For. Serv. Res. Pap. PNW-119. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon. 17 p.

Buffo, J., L. J. Fritschen, and J. L. Murphy. 1972. Direct solar radiation on various slopes from 0 to 60 degrees north latitude. USDA For. Serv. Res. Pap. PNW-142. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon. 74 p.

Burns, J. W. 1972. Some effects of logging and associated road construction on northern California streams. Trans. Am. Fish. Soc. 101:1-17.

Busch, D. E. 1978. Successional changes associated with benthic assemblages in experimental streams. Ph.D. thesis, Oregon State University, Corvallis.91 p.

Bustard, D. R. 1985. Some differences between coastal and interior streams and the implications to juvenile fish production. In J. Paterson (ed.) Habitat Improvement Workshop, Whistler, B.C. Can. Tech. Rep. Fish. Aquat. Sci. In press.

Combs, B. D. 1965. Effects of temperature on the development of salmon eggs. Prog. Fish-Cult. 27:134-137.

Combs, B. D., and R. E. Burrows. 1957. Threshold temperatures for the normal development of chinook salmon eggs. Prog. Fish-Cult. 19:3-6.

Corbett, E. S., and J. M. Heilman. 1975. Effects of management practices on water quality and quantity: The Newark, New Jersey, Municipal Watersheds. In Proceedings of a Symposium on Municipal Watershed Management, p. 47-57. USDA For. Serv. Gen. Tech. Rep. NE-13. Northeastern For. Exp. Stn., Broomall, Pennsylvania.

Corbett, E. S., and W. Spencer. 1975. Effects of management practices on water quality and quantity: Baltimore, Maryland, Municipal Watersheds. In Proceedings of Symposium on Municipal Watershed Management, p. 25-31. USDA For. Serv. Gen. Tech. Rep. NE-13. Northeastern For. Exp. Stn., Broomall, Pennsylvania.

Coutant, C. C. 1977. Compilation of temperature preference data. J. Fish. Res. Board Can. 34:739-745.

Cummins, K. W., R. C. Petersen, F. O. Howard, J. C. Wuycheck, and V. I. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54:336-345.

Currier, J. B., and D. Hughes. 1980. Temperature. In An approach to water resources evaluation on nonpoint silvicultural sources. EPA-600/8-80-12. U.S. Environmental Protection Agency, Environmental Research Laboratory, Athens, Georgia.

Dwyer, W. P., and R. H. Kramer. 1975. The influence of temperature on scope for activity in cutthroat trout, Salmo clarki. Trans. Am. Fish. Soc. 104:552-554.

Edwards, R. W., J. W. Densen, and P. A. Russell. 1979. An assessment of the importance of temperature as a factor controlling the growth rate of brown trout in streams. J. Anim. Ecol. 48:501-507.

Erman, D. C., J. D. Newbold, and K. B. Roby. 1977. Evaluation of streamside bufferstrips for protecting aquatic organisms. Contribution 165. California Water Resources Center, University of California, Davis. 48 p.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to ecosystem metabolism. Ecol. Monogr. 43:421-439.

Fry, F. E. J. 1964. Animals in aquatic environments: Fishes. In D. B. Dill, E. F. Adolph, and C. G. Wilber (eds.) Handbook of physiology. Sec. 4: Adaptation to the environment, p. 715-728. American Physiological Society, Washington, D.C.

_____. 1967. Responses of vertebrate poikilotherms to temperature. In A. H. Rose (ed.) Thermobiology, p. 375-409. Academic Press, London.

Gibson, R. J. 1966. Some factors influencing the distribution of brook trout and young Atlantic salmon. J. Fish. Res. Board Can. 23:1977-1980.

Goodlad, J. C., T. W. Gjernes, and E. L. Brannon. 1974. Factors affecting sockeye salmon (Oncorhynchus nerka) growth in four lakes of the Fraser River System. J. Fish. Res. Board Can. 31:871-892.

Groberg, W. J., Jr., R. H. McCoy, K. S. Pilcher, and J. L. Fryer. 1978. Relation of water temperature to infections of coho salmon (Oncorhynchus kisutch), chinook salmon (O. tshawytsch) and steelhead trout (Salmo gairdneri) with Aernomora salmonicida and A. hydrophila. J. Fish. Res. Board Can. 35:1-7.

Hartman, G. F., L. B. Holtby, and J. C. Scrivener. 1984. Some effects of natural and logging-related winter stream temperature changes on the early life history of coho salmon (Oncorhynchus kisutch) in Carnation Creek, British Columbia. In W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley (eds.) Fish and wildlife relationships in old-growth forests: Proceedings of a symposium, p. 141-149. American Institute of Fishery Research Biologists.

Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Can. J. Fish. Aquat. Sci. 40:1173-1185.

Hewlett, J. D., and J. C. Fortson. 1982. Stream temperature under an inadequate buffer strip in the southeast Piedmont. Water Resour. Bull. 18(6):983-988.

Holtby, L. B. 1986. Some effects of logging related stream temperature changes on the population dynamics of coho salmon (Oncorhynchus kisutch) of Carnation Creek, British Columbia. Unpublished manuscript.

Holtby, L. B., and G. F. Hartman. 1982. The population dynamics of coho salmon (Oncorhynchus kisutch) in a west coast rain forest stream subjected to logging. In G. F. Hartman (ed.) Proceedings of the Carnation Creek Workshop: A ten-year review, p. 308-347. Pacific Biological Station, Nanaimo, B.C.

Holtby, L. B., and C. P. Newcombe. 1982. A preliminary analysis of logging related temperature changes in Carnation

Creek, British Columbia. In G. F. Hartman (ed.) Proceedings of the Carnation Creek Workshop: A ten-year review, p. 81-99. Pacific Biological Station, Nanaimo, B.C.

Hughs, D. A. 1966. Mountain streams of the Barberton area, eastern Transvaal. Part 2: The effect of vegetational shading and direct illumination on the distribution of stream fauna. Hydrobiologia 27:439-459.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto. 555 p.

Iverson, R. A. 1972. Effects of elevated temperatures on juvenile coho salmon and benthic invertebrates in model stream communities. Ph.D. thesis, Oregon State University, Corvallis. 98 p.

Jobling, M. 1981. Temperature tolerance and the final preferendum: Rapid methods for the assessment of optimum growth temperatures. J. Fish. Biol. 19:439-455.

Jonsson, B., and J. Rudd-Hansen. 1985. Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (Salmo salar) smolts. Can. J. Fish. Aquat. Sci. 42:593-595.

Kaushik, N. K., and H. B. N. Hynes. 1971. The fate of the dead leaves that fall into streams. Arch. Hydrobiol. 68:465-515.

Kaya, C. M., L. R. Kaeding, and D. E. Burkhalter. 1977. Use of a coldwater refuge by rainbow and brown trout in a geothermally heated stream. Prog. Fish-Cult. 39:37-39.

Keenleyside, M. H. A., and W. S. Hoar. 1954. Effects of temperature on the response of young salmon to water currents. Behavior 7:77-87.

Keller, E. A., and T. Hofstra. 1982. Summer "cold pools" in Redwood Creek near Orick, California. In C. Van Riper III, L. D. Whittig, and M. L. Murphy (eds.) Proceedings of the First Biennial Conference of Scientific Research in California's National Parks, University of California, Davis.

Keller, E. A., T. D. Hofstra, and C. Moses. In press. Summer "cold pools" in Redwood Creek near Orick, California. In K. M. Nolan, H. Kelsey, and D. C. Marron (eds.) Geomorphic processes and aquatic habitat in the Redwood Creek basin, northwestern California. U.S. Geological Survey Prof. Pap.

Kevern, N. R., and R. C. Ball. 1965. Primary productivity and energy relationships in artificial streams. Limnol. Oceanogr. 10:74-87.

Kochenderfer, J. N., and G. M. Aubertin. 1975. Effects of management practices on water quality and quantity: Fernow Experimental Forest, West Virginia. In Proceedings of Symposium on Municipal Watershed Management, p. 14-24. USDA For. Serv. Gen. Tech. Rep. NE-13. Northeastern For. Exp. Stn., Broomall, Pennsylvania.

Koski, K V. 1984. A stream ecosystem in an old-growth forest in southeast Alaska. Part 1: Description and characteristics of Porcupine Creek, Etolin Island. In W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley (eds.) Fish and wildlife relationships in old-growth forests: Proceedings of a symposium, p. 47-55. American Institute of Fishery Research Biologists.

Lantz, R. L. 1971. Influence of water temperature on fish survival, growth, and behavior. In J. T. Krygier and J. D. Hall (eds.) Forest land uses and stream environment: Proceedings of a symposium, p. 182-193. Oregon State University, Corvallis.

Larkin, P. A. 1956. Interspecific competition and population control in freshwater fish. J. Fish. Res. Board Can. 13:327-342.

Lee, R. 1980. Forest hydrology. Columbia University Press, New York. 349 p.

Lee, R., and D. E. Samuel. 1976. Some thermal and biological effects of forest cutting in West Virginia. J. Environ. Qual. 5(4):362-366.

Leggett, W. C., and J. E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American shad (Alosa sapidissima): Evidence of population specific life history strategies in fish. J. Fish. Res. Board Can. 35:1469-1478.

Levno, A., and J. Rothacher. 1967. Increases in maximum stream temperatures after logging old growth Douglas-fir watersheds. USDA For. Serv. Res. Note PNW-65. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon. 12 p.

_____. 1969. Increases in maximum stream temperatures after slash burning in a small experimental watershed. USDA For. Serv. Res. Note PNW-110. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon. 7 p.

Lynch, J. A., W. E. Sopper, E. S. Corbett, and D. W. Aurand. 1975. Effects of management practices on water quality and quantity: The Penn State Experimental Watersheds. In Proceedings of Symposium on Municipal Watershed Management, p. 32-46. USDA For. Serv. Gen. Tech. Rep. NE-13. Northeastern For. Exp. Stn., Broomall, Pennsylvania.

Macan, T. T. 1961. Factors that limit the range of fresh water animals. Bio. Rev. 36:151-198.

Mantelman, I. I. 1960. Distribution of the young of certain species of fish in temperature gradients. Transl. Ser. 257. J. Fish. Res. Board Can. 67 p.

Martin, D. J. 1985. Production of cutthroat trout Salmo clarki in relation to riparian vegetation in Bear Creek, Washington. Ph.D. thesis, University of Washington, Seattle.

Martin, D. J., E. O. Salo, S. T. White, J. A. June, W. J. Foris, and G. L. Lucchetti. 1981. The impact of managed streamside timber removal on cutthroat trout and the stream ecosystem. Part 1: Summary. FRI-UW-8107. Fisheries Research Institute, University of Washington, Seattle.

Meehan, W. R. 1970. Some effects of shade cover on stream temperature in southeast Alaska. USDA For. Serv. Res. Note PNW-113. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon. 9 p.

Minkley, W. L. 1963. The ecology of spring streams, Doe Run, Meade County, Kentucky. Wild. Monogr. 2. 124 p.

Minshall, G. W. 1968. Community dynamics of the benthic fauna in a woodland springbrook. Hydrobiologia 32:305-337.

Moore, J. W. 1980. Factors influencing the composition, structure and density of a population of benthic invertebrates. Arch. Hydrobiol. 88:202-218.

Moring, J. R. 1975a. The Alsea Watershed Study: Effects of logging on the aquatic resources of three headwater streams of the Alsea River, Oregon. Part 2: Changes in environmental conditions. Fish. Res. Rep. 9. Oregon Department of Fish and Wildlife, Corvallis. 39 p.

_____. 1975b. The Alsea Watershed Study: Effects of three headwater streams of the Alsea River, Oregon. Part 3: Discussion and recommendations. Fish. Res. Rep. 9. Oregon Department of Fish and Wildlife, Corvallis. 24 p.

Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Can. J. Fish. Aquat. Sci. 38:137-145.

Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. Trans. Am. Fish. Soc. 110:469-478.

Nakatani, R. E. 1969. Effects of heated discharge on anadromous fish. In P. A. Krenkel and F. L. Parker (eds.) Biological aspects on thermal pollution, Vanderbilt University Press, Nashville, Tennessee.

Narver, D. W. 1972. A survey of some possible effects of logging on two eastern Vancouver Island streams. Fish. Res. Board Can. Tech. Rep. 323. 55 p.

Nebeker, A. V. 1971a. Effect of water temperatures on nymphal feeding rate, emergence and adult longevity of the stonefly, Pteronarcyla dorsata. J. Kansas Entomol. Soc. 44:21-26.

_____. 1971b. Effect of temperature at different altitudes on the emergence of aquatic insects from a single stream. J. Kansas Entomol. Soc. 44:26-35.

Needham, P. R., and A. C. Jones. 1959. Flow, temperature, solar radiation, and ice in relation to activities of fishes in Sagehen Creek, California. Ecology 40(3):465-474.

Newbold, J. D., D. C. Erman, and K. B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Can. J. Fish. Aquat. Sci. 37:1076-1085.

Ordal, E., and R. E. Pacha. 1963. The effects of temperatures on disease in fish. In Water temperature: Influences, effects and control. Proceedings, Twelfth Pacific Northwest Symposium on Water Pollution Research. U.S. Public Health Service, Pacific Northwest Water Laboratory, Corvallis, Oregon.

Orska, J. 1963. The influence of temperature on the development of meristic characters of the skeleton in salmonidae. Part 2: Variations in dorsal and anal fin ray counts correlated with temperature during development of Salmo irideus. Transl., Bio. Abstr. 47(6): Abstr. 28237. 1966.

Parker, F. L., and P. A. Krenkel. 1969. Thermal pollution: Status of the art. Rep. 3. Department of Environmental and Water Resources Engineering. Vanderbilt University Press, Nashville, Tennessee.

Pearson, W. D., and D. R. Franklin. 1968. Some factors affecting drift rates of Baetis and Simuliidae in a large river. Ecology 49:75-81.

Phinney, H. K., and C. D. McIntire. 1965. Effect of temperature on metabolism of periphyton communities developed in laboratory streams. Limnol. Oceanogr. 10:341-344.

Reeves, G. H. 1985. Interaction and behavior of the redside shiner (Richardsonius balteatus) and the steelhead trout (Salmo gairdneri) in western Oregon: The influence of water temperature. Ph.D. thesis, Oregon State University, Corvallis. 101 p.

Reisen, W. K., and R. Prins. 1972. Some ecological relationships of the invertebrate drift in Praters Creek, Pitkene County, South Carolina. Ecology 53:876-884.

Reiser, D. W., and T. C. Bjornn. 1979. Influence of forest and rangeland management on anadromous fish habitat in western United States and Canada. Part 1: Habitat requirements of anadromous salmonids. USDA For. Serv. Gen. Tech. Rep. PNW-96. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon. 54 p.

Reiser, D. W., and T. A. Wesche. 1979. In situ freezing as a cause of mortality in brown trout eggs. Prog. Fish-Cult. 41(2):58-60.

Reiser, D. W., and R. G. White. 1981. Incubation of steelhead trout and spring chinook salmon eggs in a moist environment. Prog. Fish-Cult. 43(3):131-134.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. In R. C. Simon and P. A. Larking (eds.) The stock

concept in Pacific salmon, p. 19-160. H. R. MacMillan Lectures in Fisheries. University of British Columbia, Vancouver.

Ringler, N. H., and J. D. Hall. 1975. Effects of logging on water temperature and dissolved oxygen in spawning beds. Trans. Am. Fish. Soc. 104:111-121.

Rishel, G. B., J. A. Lynch, and E. S. Corbett. 1982. Seasonal stream temperature changes following forest harvesting. J. Environ. Qual. 11(1):112-116.

Rounick, J. S., and S. V. Gregory. 1981. Temporal changes in periphyton standing crop during an unusually dry winter in streams of the western Cascades, Oregon. Hydrobiologia 83:197-205.

Scrivener, J. C., and B. C. Andersen. 1984. Logging impacts and some mechanisms that determine the size of spring and summer populations of coho salmon fry (Oncorhynchus kisutch) in Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. 41:1097-1105.

Seymour, A. H. 1959. Effects of temperature upon formation of vertebrae and fin rays in young chinook salmon. Trans. Am. Fish. Soc. 88:58-69.

Sherberger, F. F., E. F. Benfield, K. L. Dickson, and J. Cairns, Jr. 1977. Effects of thermal shocks on drifting aquatic insects: A laboratory simulation. J. Fish. Res. Board Can. 34:529-536.

Sheridan, W. L. 1961. Temperature relationships in pink salmon stream in Alaska. Ecology 42(1):91-98.

Sheridan, W. L., and A. M. Bloom. 1975. Effects of canopy removal on temperature of some small streams in southeast Alaska. USDA For. Serv. Alaska Region, Juneau. 19 p.

Smith, B. D. 1980. The effects of afforestation on the trout of a small stream in southern Scotland. Fish. Manage. 11:39-58.

Steinblums, I., H. A. Froehlich, and J. K. Lyons. 1984. Designing stable buffer strips for stream protection. J. For. 82(1):49-52.

Stockner, J. G., and K. R. S. Shortreed. 1978. Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. J. Fish. Res. Board Can. 35:28-34.

Suberkropp, K., M. J. Klug, and K. W. Cummins. 1975. Community processing of leaf litter in woodland streams. Verh. Int. Ver. Limnol. 19:1653-1658.

Summers, R. P. 1983. Trends in riparian vegetation regrowth following timber harvesting in western Oregon watersheds. M.S. thesis, Oregon State University, Corvallis. 151 p.

Swift, L. W., and J. B. Messer. 1971. Forest cuttings raise temperatures of small streams in the southern Appalachians. J. Soil Water Conserv. 26(3):111-116.

_____. 1973. Lower water temperatures within a streamside buffer strip. USDA For. Serv. Res. Note SE-193. Southeastern For. Exp. Stn., Asheville, North Carolina. 7 p.

Thedinga, J. F., and K V. Koski. 1984. A stream ecosystem in an old-growth forest in southeast Alaska. Part 6: The production of coho salmon, Oncorhynchus kisutch, smolts and adults from Porcupine Creek. In W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley (eds.) Fish and wildlife relationships in old-growth forests: Proceedings of a symposium, p. 99-108. American Institute of Fishery Research Biologists.

Theurer, F. D., I. Lines, and T. Nelson. 1985. Interaction between riparian vegetation, water temperature, and salmonid habitat in the Tucannon River. Water Resour. Bull. 21:53-64.

Tschaplinski, P. J., and G. F. Hartman. 1983. Winter distribution of juvenile coho salmon (Oncorhynchus kisutch) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Can. J. Fish. Aquat. Sci. 40:452-461.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Walter, R. A. 1984. A stream ecosystem in an old-growth forest in southeast Alaska. Part 2: Structure and dynamics of the periphyton community. In W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley (eds.) Fish and wildlife relationships in old-growth forests: Proceedings of a symposium, p. 57-69. American Institute of Fishery Research Biologists.

Warren, C. E., and G. E. Davis. 1967. Laboratory studies on the feeding, bioenergetics, and growth of fish. In S. D. Gerking (ed.) The biological basis of freshwater fish production. Blackwell Science Publ., Oxford, England.

Warren, C. E., J. H. Wales, G. E. Davis, and P. Doudoroff. 1960. Progress report: Ecological studies of an experimental stream. Mimeographed report. Oregon State College, Corvallis.

Waters, T. F. 1968. Diurnal periodicity in the drift of a day-active stream invertebrate. Ecology 49:152-153.

Weber, P. K. 1981. Comparisons of the lower trophic levels of small stream communities in forest and clearcut sites, southeast Alaska. Ph.D. thesis, University of Washington, Seattle.

Wojtalik, T. A., and T. F. Waters. 1970. Some effects of heated water on the drift of two species of stream invertebrate. Trans. Am. Fish. Soc. 99:782-788.

Wurtsbaugh, W. A., and G. E. Davis. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of Salmo gairdneri Richardson. J. Fish. Biol. 11:87-98.

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by University of British Columbia on 01/24/13
For personal use only.

Characteristics and Function of Large Woody Debris in Streams Draining Old-Growth, Clear-Cut, and Second-Growth Forests in Southwestern Washington

Robert E. Bilby and James W. Ward

Weyerhaeuser Co., Technology Center 2H4, Tacoma, WA 98477, USA
and
Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA 98531, USA

Bilby, R. E., and J. W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Can. J. Fish. Aquat. Sci. 48: 2499–2508.

Amount of large woody debris (LWD) surveyed in 70 stream reaches flowing through old-growth, clear-cut, and second-growth forests decreased with increasing stream size for all stand types but was greatest at old-growth sites. Average piece volume was larger at old-growth sites than at other stand types in streams >10 m wide, but no differences were seen in smaller streams. Scour pools accounted for 90% of the wood-associated pools at second-growth and clear-cut sites but only 50% at old-growth sites, which contained more pools than other stand types, particularly for larger streams. Pool size was similar for all stand types in smaller streams, but averaged 10 m^2 in streams >10 m wide at old-growth sites and 4 m^2 for other stand types. Pool size was similar for all stand types in smaller streams. Sediment and fine organic matter retained by woody debris decreased with increasing stream size for all stand types, but old-growth sites contained greater amounts of both materials than other stand types. The frequency of pool formation, the type of pool formed, and sediment accumulation were influenced by the amount of fine debris associated with LWD. Changes in LWD amount, characteristics, and function occurred very rapidly following removal of streamside vegetation.

Les quantités de gros débris ligneux (GDL), étudiées dans 70 tronçons de cours d'eau s'écoulant dans de vieilles forêts, des forêts coupées à blanc et des forêts de seconde venue, ont diminué en fonction de l'augmentation de la taille des cours d'eau dans tous les types de peuplements, mais ce sont les vieilles forêts qui ont donné lieu aux quantités de GDL les plus importantes. Le volume moyen des débris présents dans les cours d'eau d'une largeur supérieure à 10 m a également été plus grand dans les vieilles forêts que dans les autres sites, mais dans le cas des cours d'eau plus étroits, on n'a pas observé de différence entre les trois types de peuplements. Les zones calmes d'affouillement représentaient plus de 90 % des zones calmes formées par les débris de bois dans les forêts de deuxième venue et les forêts coupées à blanc, mais seulement 50 % dans les vieilles forêts, qui comptent un plus grand nombre de zones calmes que les autres types de peuplements, surtout en ce qui a trait aux cours d'eau plus larges. La taille des zones calmes dans les petits cours d'eau était semblable dans tous les types de peuplements, alors que dans les cours d'eau de plus de 10 m de largeur, elle était en moyenne de 10 m^2 dans les vieilles forêts et de 4 m^2 dans les autres peuplements. Les sédiments et les matières organiques fines retenus par les débris ligneux ont diminué en fonction de l'augmentation de la largeur du cours d'eau dans tous les sites; toutefois, les vieilles forêts contenaient de plus grandes quantités de ces deux matériaux que les autres sites. La quantité de débris accompagnant les GDL a influé sur la fréquence de formation des zones calmes, le type de zones calmes et l'accumulation de sédiments. Des modifications de la quantité de GDL ainsi que de leurs caractéristiques et de leur rôle sont apparues très rapidement après l'élimination de la végétation riparienne.

Received November 27, 1990
Accepted June 12, 1991
(JA823)

Reçu le 27 novembre 1990
Accepté le 12 juin 1991

Large woody debris (LWD) controls many of the structural and functional properties of smaller streams in forested areas (Bilby and Likens 1980; Harmon et al. 1986; Bisson et al. 1987; Bilby and Ward 1989). Wood affects channel form through the formation and stabilization of pools, waterfalls, and gravel bars (Heede 1972; Bilby 1981; Lisle and Kelsey 1982; Lisle 1986). LWD influences sediment routing through the formation of depositional sites and the creation of waterfalls, which reduce the efficiency of downstream transport of particulate materials (Heede 1972; Swanson and Lienkaemper 1978; Beschta 1979; Bilby 1981; Megahan 1982). A large proportion of the standing stock of particulate organic matter in streams is often associated with LWD (Naiman and Sedell 1979; Bilby and Likens 1980). Wood also provides habitat for some invertebrates (Benke et al. 1984) and fishes (Bustard and Narver 1975; Bisson et al. 1982; Tschaplinski and Hartman 1983; Dolloff 1986; Elliott 1986; McMahon and Hartman 1989).

Features of the stream channel and the bordering riparian vegetation influence the amount and function of LWD. Channel size affects both wood amount and the relative influence of LWD on channel features (Swanson et al. 1976; Bilby 1979; Long 1987; Bilby and Ward 1989). Density of streamside trees is positively correlated with LWD amounts in some systems (Long 1987; Bilby and Wasserman 1989). Morphology of the bed may also influence LWD amount (Bilby and Wasserman 1989). Susceptibility of riparian trees to windthrow can play

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by University of British Columbia on 01/24/13
For personal use only.

a major role in determining quantities of LWD in streams (Lienkaemper and Swanson 1987; Robison and Beschta 1990).

Various management activities in and adjacent to the channel have also influenced LWD amounts and characteristics in Pacific Northwest streams. Removal of wood from rivers for navigation or to provide upstream access for anadromous fishes has greatly reduced LWD amounts in some systems (Sedell and Luchessa 1982; Bilby 1984). Use of splash dams for log transport, a practice which was used widely in the Pacific Northwest until the 1950s, also reduced wood amounts in many streams (Wendler and Deschamps 1955). Removal of streamside timber during logging occurred until the early 1980s in the Pacific Northwest. While this practice no longer occurs, there are many streams where amount of LWD and the composition and structure of the riparian vegetation were influenced as a result of this activity.

Several conceptual models of the influence of streamside timber removal on amount of LWD have been developed (Swanson and Lienkaemper 1978; Likens and Bilby 1982; Grette 1985; Murphy and Koski 1989). In general, these models predict a decrease in LWD over time as a result of decay of wood present in the channel prior to disturbance coupled with decreased input from the riparian area.

Relatively few data have been collected to validate these models. Comparisons of the amount of LWD in streams flowing through old-growth and previously logged forests in several areas in the Pacific Northwest have verified the decrease in wood after removal of the streamside vegetation (Grette 1985; Long 1987). Some information is also available on the influence of stream size and channel characteristics on the rate of change in LWD amount after removal of streamside vegetation (Long 1987; Murphy and Koski 1989). However, little is known about the changes in the characteristics of pieces of LWD or their function over time after removal of streamside vegetation or the rate at which these changes occur. The purpose of this study was to compare LWD abundance, characteristics, and function in streams bordered by forests of differing ages: old-growth forest, recently clear-cut areas, and 40- to 60-yr-old second-growth forest. Comparison of the three stand age-classes provides an indication of the rate at which changes in LWD occur following timber removal from the riparian area.

Description of Study Sites

Measurements of LWD abundance, characteristics, and associated channel features were made on 70 stream reaches in southwestern Washington. All sites were located in the foothills of the Cascade Range or the Willapa Hills. Streams ranged from second order to fifth order with drainage areas from 0.4 to 137 km^2. Bankfull channel widths ranged from 3.1 to 23.5 m. All stream reaches surveyed drained watersheds underlain with volcanic bedrock (Huntting et al. 1961).

One of the most important factors in selection of the sites was the condition of the vegetation adjacent to the surveyed reach. Three stand-age classes were examined: (1) undisturbed, old-growth forest, (2) clear-cut to the channel's edge within 5 yr of the survey, and (3) second-growth forest which had been clear-cut to the edge of the channel 40–60 yr prior to our survey. The clear-cut and second-growth classes had been logged only once.

Sites where factors other than stream size and vegetative characteristics of the riparian zone were likely to have influenced LWD were not surveyed. Stream reaches which had been splash dammed at some time in the past were excluded (Wendler and Deschamps 1955). In addition, streams flowing through clear-cut areas which exhibited evidence of post-harvest channel cleaning were avoided, although selective removal of merchantable wood from the stream during or after logging could not be detected. We also avoided reaches which showed evidence of being influenced by landslides or debris torrents during the recent past.

Mean annual precipitation at the sites varied from 180 to 280 cm, primarily as a result of changes in elevation (Sternes 1969). However, all sites were located within 100 km of one another and thus were likely exposed to a relatively similar history of high discharge events, which play a major role in determining LWD distribution (Bilby 1984; Lienkaemper and Swanson 1987).

Methods

Aerial photographs were utilized to identify streams bordered by appropriate forest conditions. These sites were then examined on the ground to determine if they met the criteria outlined above. Once sites were located, watershed area above the surveyed reach was determined from U.S. Geological Survey topographic maps (scale 1:62500). Additional detail on the techniques employed in this study may be found in Bilby and Ward (1989).

We defined LWD as any piece of wood larger than 10 cm in diameter and 2 m long. Organic material not qualifying as LWD by this definition was considered fine organic debris.

All pieces of LWD within the bankfull channel of the surveyed stream reaches were measured with the exception of those pieces which were either floating free in the channel or resting in an unstable position atop a LWD accumulation. These pieces were considered to have a minimal impact on the channel form or stream function and thus were omitted. However, these pieces were rare and nearly all pieces meeting our size criteria were included in the survey.

We attempted to measure at least 50 pieces of wood at each study site. However, LWD was rare at some of the sites and riparian stand conditions changed before 50 pieces were encountered. Due to our criterion of 50 pieces of LWD per site, the length of stream channel surveyed varied with changing LWD abundance, ranging from less than 100 m to nearly 1.5 km.

Characteristics of the LWD pieces which were measured included diameter, taken at the center of the piece, length in and out of the channel, and the species of tree that produced the piece. Advanced decay prevented identification of species for about 10% of the surveyed pieces. Channel characteristics associated with LWD which were measured included surface area of pools, surface area of sediment accumulations, height of waterfalls, and volume of fine organic debris (organic material less than 10 cm in diameter and 2 m in length, including twigs, leaves, needles, etc.).

Average size of LWD pieces was compared between sites with a debris volume index (Bilby and Ward 1989). This variable was calculated by determining the geometric mean diameter and geometric mean total length (both in and outside the channel) for debris pieces in each surveyed reach. Frequency distributions of LWD diameters and lengths were skewed heavily towards smaller size classes; thus, a geometric mean was used to calculate average values for these variables (Bilby and Ward 1989). The debris volume index is the volume of a cyl-

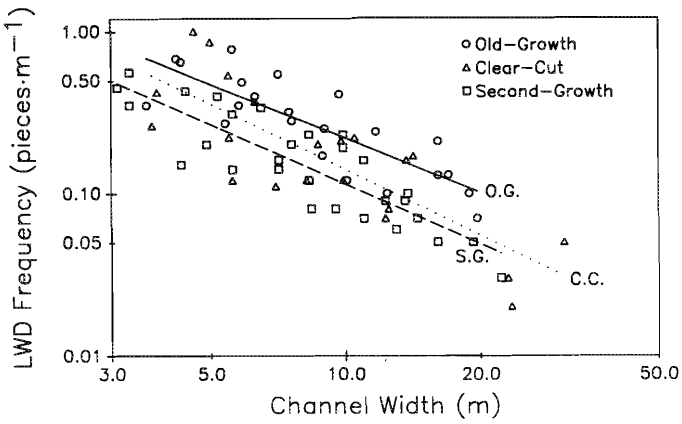


FIG. 1. Relationship between numbers of pieces of LWD per length of surveyed channel and channel width for the three stand-age classes (O.G. = old-growth, C.C. = clear-cut, S.G. = second-growth). There are significant differences among the slope values (ANOVA; $p < 0.05$). Equations for the regressions are as follows: old-growth, $\log_{10}$ LWD frequency $= -1.12 \log_{10}$ channel width $+ 0.46$ ($r^2 = 0.69$); clear-cut, $\log_{10}$ LWD frequency $= 1.35 \log_{10}$ channel width $+ 0.50$ ($r^2 = 0.66$); second-growth, $\log_{10}$ LWD frequency $= -1.23 \log_{10}$ channel width $+ 0.28$ ($r^2 = 0.75$).

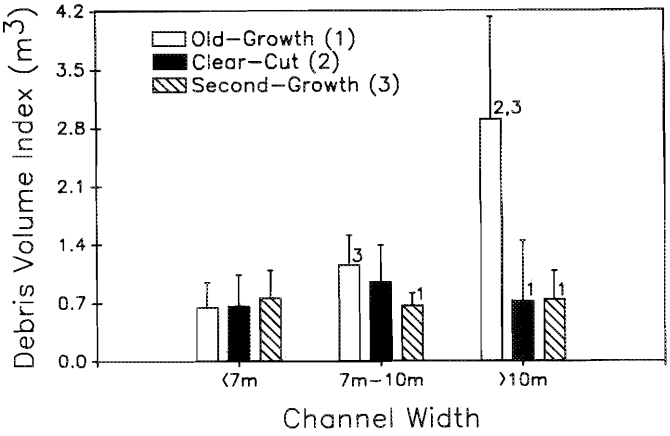


FIG. 2. Comparison of debris volume index (see text for definition) between stand-age classes for channels <7, 7–10, and >10 m wide. Numbers above the bars indicate significant differences from other stand-age classes (t-test; $p < 0.05$).

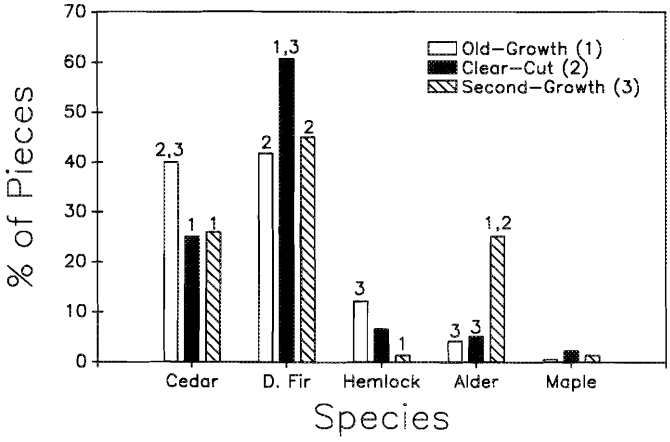


FIG. 3. Species distribution of pieces of LWD in the three stand-age classes. Values significantly different (t-test; $p < 0.05$) from corresponding values for different stand-age classes are denoted with a number above the bar. Cedar = western redcedar (*Thuja plicata*), D. Fir = Douglas fir (*Pseudotsuga menziesii*), Hemlock = western hemlock (*Tsuga heterophylla*), Alder = red alder (*Alnus rubra*), Maple = bigleaf maple (*Acer macrophyllum*).

inder with dimensions equal to the geometric mean diameter and length for each reach.

LWD-associated pools were assigned to one of four classes based on their morphology and method of formation (Bisson et al. 1982). The four classes we recognized were scour pools, plunge pools, backwater pools, and dammed pools.

The influence of fine organic debris on LWD function was examined by comparing the proportion of pieces of LWD retaining large amounts of fine debris (≥ 0.5 m^3) associated with pools, waterfalls, and sediment accumulations with the proportion of pieces of LWD retaining lesser amounts of fine debris associated with these channel features. The same comparison was made between the different pool types to determine if the presence of fine debris favored the formation of certain kinds of pools.

The amount, characteristics, and function of LWD change with changing stream size (Bilby and Ward 1989). Thus, stream size had to be considered in comparing LWD features and function between the three stand-age classes. Because of the variation in precipitation between the study sites, channel width, rather than watershed area, was used as an index of relative stream size.

Regression of LWD features or function against channel width was used for some of the analyses in this study. In cases where regression techniques were not used, streams were segregated into three channel-width classes: <7 m, 7–10 m, and >7 m. There were about an equal number of sites in each stream-size class for each stand-age class. Statistical comparisons of percentage values between stand-age classes and stream-size classes were made using a t-test for equality of two percentages (Sokal and Rohlf 1969).

Results

Abundance, Size, and Species

LWD abundance decreased with increasing stream size for all three stand-age classes (Fig. 1). However, old-growth sites had more wood than similarly sized streams at second-growth or clear-cut sites (t-test; $p < 0.05$). The frequency of LWD pieces in clear-cut and second-growth sites was 59 and 50%, respectively, of that measured in old-growth sites for streams at 15 m wide. In channels 5 m wide, LWD frequency in clear-cut and second-growth sites was 77 and 56%, respectively, of that seen at old-growth sites.

Debris volume index increased with increasing stream size at the old-growth sites (Fig. 2). However, no relationship between piece size and stream size was observed for clear-cut or second-growth sites. The debris volume index for old-growth sites was about four times greater than the other two stand-age classes for streams >10 m wide (ANOVA; $p < 0.05$). LWD piece size was also significantly greater at old-growth sites than at second-growth sites in channels 7–10 m wide. No statistical differences in piece size were observed between stand-age classes for streams <7 m wide.

There were significant differences between stand-age classes in the species distribution of the LWD (Fig. 3; t-test; $p < 0.05$).

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by University of British Columbia on 01/24/13
For personal use only.

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by University of British Columbia on 01/24/13
For personal use only.

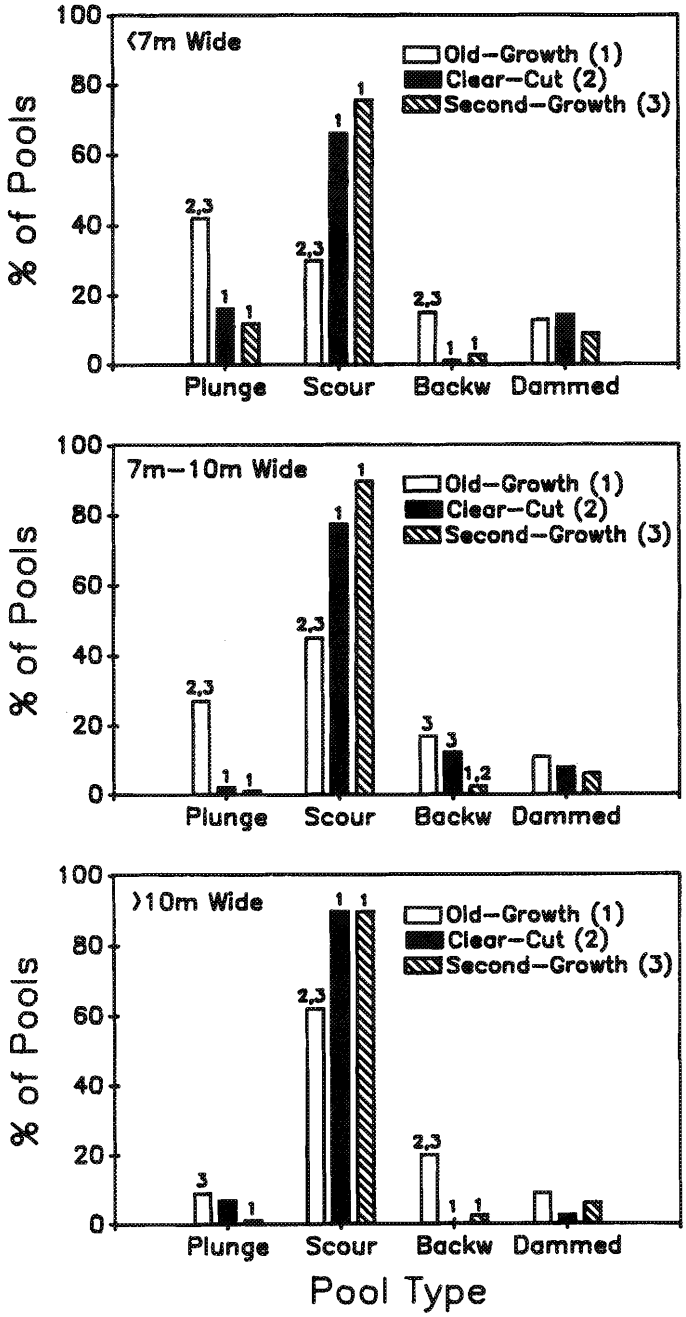


FIG. 4. Distribution of pool types for the three stand-age classes in each of the channel-width classes. Values significantly different (t-test; $p < 0.05$) from corresponding values for other stand-age classes are denoted with a number above the bar.

Western redcedar accounted for 40% of the debris pieces in the old-growth systems but contributed significantly lower proportions of LWD to clear-cut and second-growth sites. Douglas fir, the most commonly encountered species in all stand-age classes, contributed significantly more pieces of LWD in clear-cut systems than in the other two stand-age classes. The proportion of western hemlock was relatively low and progressively decreased from old-growth to clear-cut to second-growth sites. Red alder contributed significantly more pieces of LWD to second-growth sites than to old-growth or clear-cut sites. No differences were observed by stand-age class in the proportion of LWD contributed by bigleaf maple.

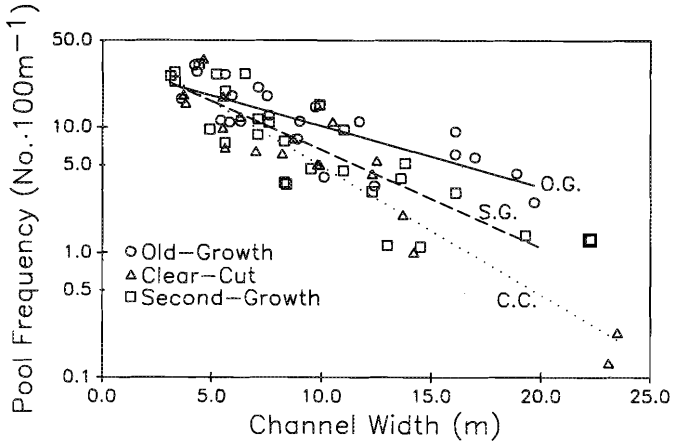


FIG. 5. Relationship between channel width and frequency of LWD-associated pools for the three stand-age classes (O.G. = old-growth, C.C. = clear-cut, S.G. = second-growth). There are significant differences among the slope values (ANOVA; $p < 0.05$). Regression equations are as follows: old-growth, $\log_{10}$ pool frequency $= -0.05$ channel width $+ 1.49$ ($r^2 = 0.64$); clear-cut, $\log_{10}$ pool frequency $= -0.10$ channel width $+ 1.71$ ($r^2 = 0.90$); second-growth, $\log_{10}$ pool frequency $= -0.08$ channel width $+ 1.59$ ($r^2 = 0.70$).

However, this species did not produce more than 5% of the wood in any of the stand-age classes.

Pools

The frequency of occurrence of different types of pools associated with LWD changed with stand-age class and stream size (Fig. 4). Pool types were the most diverse in streams bordered by old-growth forest. In these systems, scour pools increased and plunge pools decreased in abundance with increasing stream size (t-test; $p < 0.05$). Scour pools occurred significantly more frequently in clear-cut and second-growth systems than at old-growth sites for all three stream-size classes and were the predominant pool type in all stream-size classes at clear-cut and second-growth sites. Plunge pools formed by LWD were significantly more common at old-growth sites than at second-growth sites for all stream-size classes and at clear-cut sites in streams <7 m wide.

Backwater and dammed pools formed by LWD occurred less frequently than other pool types in all stand-age classes (Fig. 4). Backwater pools were more common at old-growth sites than at second-growth sites for all stream-size classes and at clear-cut sites for streams <7 m wide and >10 m wide (t-test; $p < 0.05$).

Frequency of LWD-associated pools decreased with increasing stream size for all three stand-age classes (Fig. 5) but was significantly greater at old-growth sites than at the other two stand-age classes (t-test; $p < 0.05$). Pool frequency was most similar among stand-age classes in smaller streams. Differences increased with increasing stream size, and frequency of pools associated with LWD in old-growth sites was more than twice that of second-growth sites and three times that of clear-cut sites for streams 15 m wide.

Surface area of debris-associated pools was not significantly different among the stand-age classes for streams <7 m wide or 7–10 m wide (Fig. 6). However, average pool surface area was significantly greater in streams >10 m wide at old-growth sites (t-test; $p < 0.05$), averaging more than twice the area of pools in clear-cut and second-growth systems.

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by University of British Columbia on 01/24/13
For personal use only.

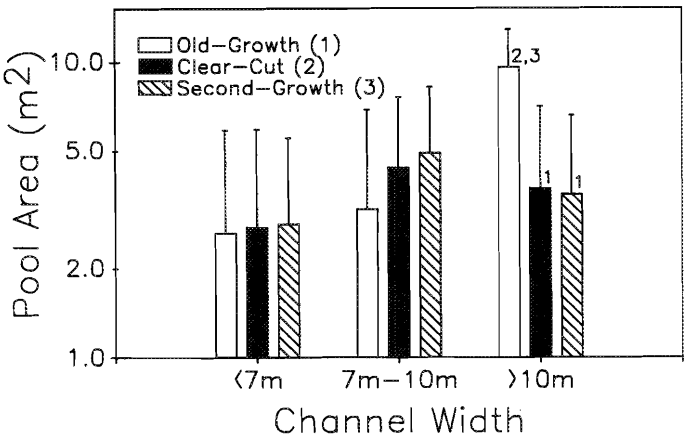


FIG. 6. Comparison of average surface area of scour pools between stand-age classes for different channel widths. Error bars indicate standard deviation. Values significantly different (t-test; $p < 0.05$) from corresponding values in other stand-age classes are denoted with a number above the bar.

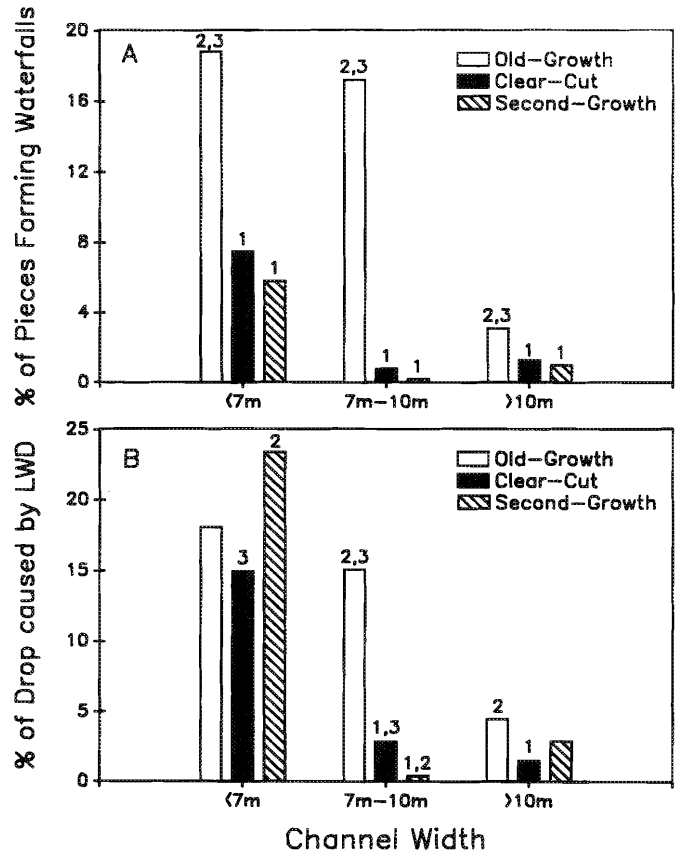


FIG. 7. (A) Proportion of pieces of LWD forming waterfalls and (B) proportion of the total drop in elevation of the surveyed stream sections accounted for by the summed height of LWD-formed waterfalls for the three age classes for each channel-width class. Values significantly different (t-test; $p < 0.05$) from corresponding values in other stand-age classes are denoted with a number above the bar.

Waterfalls

The proportion of pieces of LWD forming waterfalls was significantly greater at old-growth sites than at the other two stand-age classes for all stream-size classes (Fig. 7A; t-test; $p < 0.05$). The proportion of pieces forming waterfalls was greater in streams <7 m wide than in larger systems for all three stand-age classes (t-test; $p < 0.05$).

The proportion of the drop in elevation of a stream reach accounted for by summing the heights of waterfalls formed by LWD decreased with increasing stream size (Fig. 7B). Old-growth sites displayed a greater cumulative elevation drop caused by LWD than the other stand-age classes in streams 7–10 m wide and greater than the clear-cut sites in channels >10 m wide (t-test; $p < 0.05$).

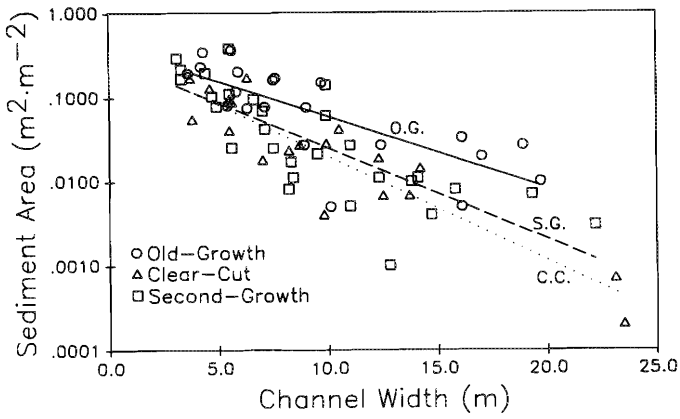


FIG. 8. Relationship between channel width and the surface area of the streambed occupied by LWD-associated sediment accumulations for the three stand-age classes (O.G. = old-growth, C.C. = clear-cut, S.G. = second-growth). There are significant differences among the intercept values (ANOVA; $p < 0.05$). Regression equations are as follows: old-growth, $\log_{10}$ sediment area = -0.08 channel width $- 0.38$ ($r^2 = 0.53$); clear-cut, $\log_{10}$ sediment area = -0.12 channel width $- 0.47$ ($r^2 = 0.84$); second-growth, $\log_{10}$ sediment area = -0.11 channel width $- 0.53$ ($r^2 = 0.62$).

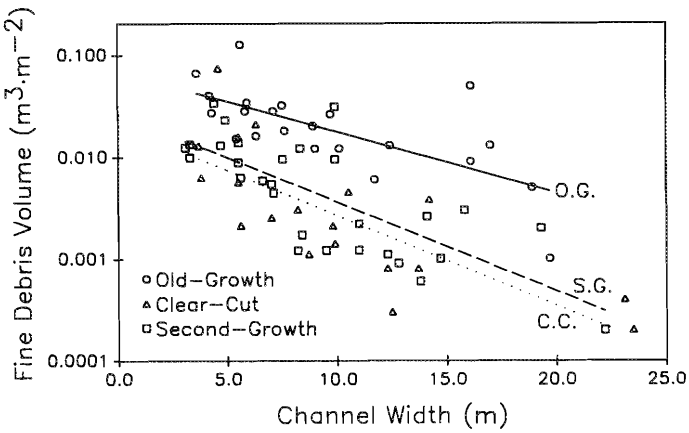


FIG. 9. Relationship between channel width and volume of fine debris associated with LWD for the three stand-age classes (O.G. = old-growth, C.C. = clear-cut, S.G. = second-growth). There are significant differences among the intercept values (ANOVA; $p < 0.05$). Regression equations are as follows: old-growth, $\log_{10}$ sediment volume = -0.06 channel width -1.16 ($r^2 = 0.48$); clear-cut, $\log_{10}$ volume = -0.09 channel width -1.70 ($r^2 = 0.59$); second-growth, $\log_{10}$ volume = -0.09 channel width -1.57 ($r^2 = 0.57$).

Sediment

Proportion of the streambed covered by sediment stored by LWD decreased with increasing stream size for all three stand-

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by University of British Columbia on 01/24/13
For personal use only.

TABLE 1. Proportion of pieces of LWD retaining <0.5 and ≥0.5 m^3 of fine debris associated with pools. Values are significantly different for all stand-age classes (*t*-test; $p < 0.05$).

	Pieces of LWD retaining <0.5 m^3		Pieces of LWD retaining ≥0.5 m^3	
	% forming pools	*N*	% forming pools	*N*
Old-growth	21	881	60	221
Clear-cut	28	858	82	51
Second-growth	39	1346	89	95

age classes (Fig. 8). Area of LWD-associated sediment was greater at old-growth sites than at the other two stand-age classes for all stream sizes (*t*-test; $p < 0.05$). Differences in this variable among the stand-age classes increased with stream size, with an estimated 16, 8, and 9% of the bed surface covered with LWD-associated sediment in channels 5 m wide at old-growth, clear-cut, and second-growth sites, respectively, compared with 2.5, 0.5, and 0.7% in channels 15 m wide.

Fine Organic Debris

The volume of fine organic debris per square metre of channel surface area decreased with increasing stream size for all stand-age classes (Fig. 9), but more fine debris was retained by LWD at old-growth sites than at the other two stand-age classes (*t*-test; $p < 0.05$). Volume of fine organic debris stored by LWD in channels 5 m wide was estimated at 0.035, 0.007, and 0.010 $m^3 \cdot m^{-2}$ at old-growth, clear-cut, and second-growth sites, respectively. The corresponding values for a 15-m-wide channels were 0.0087, 0.0010, and 0.0013 $m^2 \cdot m^{-3}$, respectively.

Fine Organic Debris and LWD Function

Differences between stand-age classes in the frequency of debris-associated pools (Fig. 5) were partly due to a greater amount of fine debris at old-growth sites, although the relative abundance of LWD also was an important factor. In all stand-age classes, pools were associated with pieces of LWD retaining ≥0.5 m^3 of fine debris significantly more frequently than with LWD retaining <0.5 m^3 of fine debris (Table 1; *t*-test; $p < 0.05$). About 20% of the pieces of LWD at the old-growth sites had fine debris accumulations ≥0.5 m^3 compared with 6% at clear-cut and 7% at second-growth sites.

The increased diversity of pool types observed at the old-growth sites may have been related to the large amount of fine organic debris at these sites (Table 2). Plunge and dammed pools were associated with accumulations of fine debris ≥0.5 m^3 significantly more frequently than scour pools in all three stand-age classes (*t*-test; $p < 0.05$). Both plunge pools and dammed pools tend to be formed by obstructions that completely span the channel (Bilby and Ward 1989). Fine debris fills in the gaps in the framework provided by the LWD, resulting in more efficient blockage of stream flow. Since larger fine debris accumulations were rare at clear-cut and second-growth sites (Table 1), it is not surprising that plunge pools were rare and scour pools comprise the vast majority of pools in these systems.

Amount of fine organic debris associated with LWD also may have influenced the formation of depositional sites. LWD with fine debris accumulations ≥0.5 m^3 retained sediment significantly more frequently than LWD pieces with less fine debris (Table 3; *t*-test; $p < 0.05$). Thus, accumulations of sediment associated with LWD were more frequent at old-growth sites due to both high levels of LWD and large amounts of fine debris.

TABLE 2. Proportion of the different pool types associated with fine debris accumulations ≥0.5 m^3. Significant differences between pool types within a stand-age class are indicated with a letter (*t*-test; $p < 0.05$; s = scour pools, p = plunge pools, b = backwater pools, d = dammed pools).

	Pool type			
	Scour	Plunge	Backwater	Dammed
Old-growth				
≥0.5 m^3 (%)	36	49	33	56
Sign. diff.	p, d	s, b	p, d	s, b
N	131	88	58	41
Clear-cut				
≥0.5 m^3 (%)	8	37	33	35
Sign. diff.	p, b, d	s	s	s
N	216	27	12	31
Second-growth				
≥0.5 m^3 (%)	12	26	13	41
Sign. diff.	p, d	s	d	s, b
N	510	31	15	51

Discussion

Effect of Riparian Timber Harvest on LWD

Reduction in LWD amount and piece size as a result of timber harvest has generally been assumed to occur gradually due to a decrease in LWD input coupled with decomposition of material in the channel. However, our data indicate that many changes in LWD abundance, characteristics, and function occur during or shortly after timber harvest. During the 5-yr period separating our old-growth and clear-cut sites, wood amount decreased, average piece size in channels >10 m wide decreased, and the species mix of the LWD changed. It is unlikely that these changes could be attributed solely to decomposition of residual LWD and reduced LWD input over this short time period. The decrease in abundance of large, redcedar logs between the old-growth and clear-cut sites suggests that selective removal of this material from the channel during or shortly after logging may have been a factor in the reduction in LWD. Salvage of redcedar after timber harvest is a common practice in the Pacific Northwest. Removal of LWD from streams also has been shown to destabilize wood remaining in the channel (Bilby 1984), thus promoting flushing of wood downstream and contributing to the decrease in LWD amount. Selective removal of larger logs from channels may also be partly responsible for the lack of relationship between stream size and debris volume index at clear-cut sites. However, since no records of wood salvage from stream channels are kept, the extent to which this practice occurred on our study sites cannot be determined.

Changes in LWD characteristics from the clear-cut to second-growth conditions likely reflect decomposition of residual wood in the channel coupled with reduced input and a change in the composition of the riparian vegetation. The progressive decrease in western hemlock abundance with time after harvest

TABLE 3. Proportion (%) of the pieces of LWD containing fine debris accumulations ≥0.5 and <0.5 m^3 associated with depositional sites. Pieces of wood with large fine debris accumulations are significantly more likely to be associated with areas of deposited sediment in all cases (*t*-test; $p < 0.05$).

	Channel width					
	<7 m		7–10 m		>10 m	
	≥0.5 m^3	<0.5 m^3	≥0.5 m^3	<0.5 m^3	≥0.5 m^3	<0.5 m^3
Old-growth	69.0	30.1	63.8	20.1	36.9	11.9
Clear-cut	60.0	19.7	66.7	16.5	46.2	17.2
Second-growth	64.7	36.9	57.5	20.9	58.1	18.3

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by University of British Columbia on 01/24/13
For personal use only.

indicates elimination of this species from the system without replacement. Since hemlock is less decay resistant than many other conifer species, reduction in its abundance should occur relatively rapidly. The increase in red alder debris in streams in second-growth sites is due to the abundance of this species at the second-growth sites.

There were very large differences between stand-age classes in the amount of fine debris stored by LWD, with old-growth sites containing more fine debris than the other two stand-age classes. Three factors contributed to the large amount of LWD-associated fine debris at the old-growth sites: abundant LWD to retain fine organic matter, a high rate of input from the terrestrial system (Gregory et al. 1987), and high proportions of debris from decay-resistant coniferous trees (Harmon et al. 1986). In contrast, the clear-cut sites have less LWD, very low contributions of organic matter from the terrestrial system, and a high proportion of material from deciduous trees or herbaceous vegetation, which decomposes rapidly. The second-growth sites have conditions intermediate to the two other stand-age classes, with little LWD and inputs of relatively easily decayed terrestrial debris (primarily red alder litter).

Differences between the three stand-age classes in certain characteristics and functions of LWD are accentuated in larger streams. Average piece size, pool frequency, and average pool area exhibit less difference in smaller streams than in larger systems. Differences by stand-age class in the amount of sediment accumulated by LWD or amount of fine organic matter associated with wood are less affected by stream size. In general, however, changes in LWD features and function after timber harvest of streamside vegetation tend to be most pronounced in larger streams.

Changes in LWD over Time

Models of changes in LWD abundance following removal of riparian trees have assumed a relatively slow decline caused by decomposition of residual in-channel wood. Swanson and Lienkaemper (1978) hypothesized that relatively little change in pre-harvest levels of LWD in Pacific Northwest streams would occur for 50 yr due to slow decomposition of pre-harvest LWD. A model by Grette (1985) proposed a linear decline in LWD amount with time, at a rate of slightly less than $1\% \cdot yr^{-1}$. Input of LWD from the deciduous riparian vegetation resumes approximately 40 yr after harvest, but is insufficient to offset decomposition, leading to LWD amounts 50 yr after harvest of approximately 75% of the old-growth level. Murphy and Koski (1989) suggested a faster rate of decline for southeastern Alaska streams, with larger pieces of LWD being eliminated at the rate of $1–3\% \cdot yr^{-1}$, depending on characteristics of the channel.

None of these models, however, accurately predicted the patterns of change in LWD abundance reported here. Using the regressions developed from our data for LWD frequency (Fig. 1) and average debris volume index (Fig. 2), we estimated wood volume in streams 5, 10, and 15 m wide for each stand-age class (Fig. 10A). The regressions in Fig. 5, 8, and 9 were used to calculate pool frequency, area of sediment accumulations, and volume of fine organic material (Fig. 10B, 10C, 10D). Three channel widths were examined, since mean LWD piece size is influenced by stream size (Bilby and Ward 1989) and, as a result, has an influence on input and elimination rate (Likens and Bilby 1982; Murphy and Koski 1989). We have assumed that our clear-cut sites were all 5 yr post-harvest and the second-growth sites were all 50 yr post-harvest.

Total volume of LWD per 100 m of channel decreased 22% from old-growth levels 5 yr after harvest and 35% after 50 yr in streams 5 m wide (Fig. 10A). The magnitude of decrease became progressively greater with increasing channel width, with a depression in LWD volume of 47 and 86% in channels 10 and 15 m wide, respectively, 5 yr after harvest. The very large drop in volume in the larger streams is an indication of the decrease in both piece frequency and piece size. LWD volume decreased 71 and 94% from old-growth levels in channels 10 and 15 m wide, respectively, 50 yr after logging. The rate of decrease in LWD abundance between our old-growth and second-growth sites is comparable with that reported in other studies (Grette 1985; Murphy and Koski 1989). However, our data showed that the majority of this decrease occurred within the first 5 yr after harvest.

Pool frequency in channels 5 m wide is only slightly greater at old-growth sites than at clear-cut and second-growth sites (Fig. 10B). However, in 10- and 15-m-wide streams, pool frequency decreased by more than 50% in the 5 yr after harvest and then changed relatively little over the next 45 yr. Estimated decreases in sediment stored by LWD over time were greater than 50% for all three sized streams, with nearly all the change occurring shortly after timber harvest (Fig. 10C).

Fine debris volume decreases at a much greater relative rate than LWD following removal of the streamside vegetation (Fig. 10D). Fine debris was reduced by about 90% within 5 yr of harvest, regardless of stream size. Little change in the amount of stored fine debris occurred between 5 and 50 yr post-harvest.

Management of Riparian Areas

Pacific Northwest states and provinces have recently instituted regulations or guidelines requiring retention of standing trees along stream channels during timber harvest to provide a source of future LWD. In Washington, from 50 to 200 trees

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by University of British Columbia on 01/24/13
For personal use only.

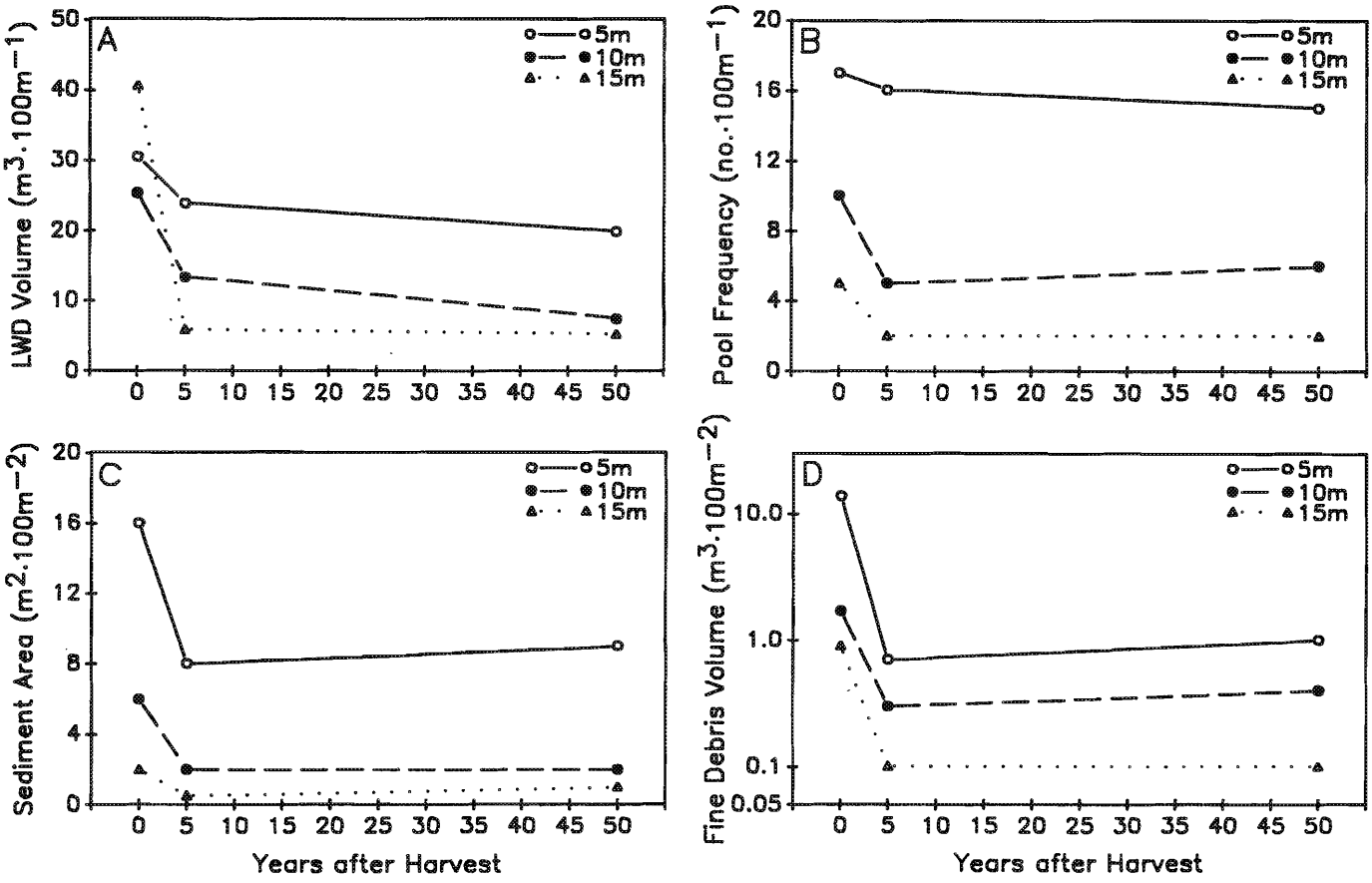


FIG. 10. Changes in LWD abundance and function with time after timber harvest for streams of three different widths. (A) Volume of LWD per length of channel; (B) pool frequency; (C) area of sediment accumulated by LWD; (D) volume of fine organic matter.

per 300 m of stream length must be retained after timber harvest, varying as a function of channel width (Bilby and Wasserman 1989). The width of the protected area also varies with stream size, ranging from 8 to 30 m on either side of the channel. Thus, the patterns of change in LWD abundance and function seen in this study resulted from timber harvest practices that are no longer in use. However, until the early 1980s, the trees along many streams were removed during timber harvest. The effect of this practice was the creation of riparian stands composed largely of red alder. Our data indicate that riparian zones with this type of vegetative composition (our second-growth sites) may not supply sufficient LWD, especially to larger streams. Also, the rapidly decomposing fine organic matter produced by deciduous vegetation is less effective at influencing channel structure than that from coniferous trees. Encouragement of conifer growth in riparian zones dominated by red alder may help alleviate some of these problems.

The vegetative and structural diversity of alder-dominated riparian stands may be increased by active management. Planting of conifer seedlings in riparian areas might be successful if the proper conditions for survival and growth can be created (Emmingham et al. 1989). Clearing small areas of riparian vegetation would be necessary in most cases to provide the conditions required by shade-intolerant conifer species, such as Douglas fir. Control of understory vegetation for several years could also be necessary. Release of suppressed conifers already present in the riparian area by removing the overstory is another possible option (Ferguson and Adams 1980).

The influence of fine organic debris on LWD function also suggests that vegetative characteristics of the riparian zone should be considered when selecting locations for stream habitat enhancement projects that include placement of wood. Our study indicates that LWD placement in streams would achieve improved results if conducted on a site receiving large inputs of fine coniferous debris.

Acknowledgments

We thank J. Heffner and W. Stonecypher for assistance with the field surveys. Helpful comments on the manuscript were provided by P. Bisson, J. Rochelle, K. Sullivan, D. Mumper, D. Wilbur, and two anonymous reviewers.

References

BENKE, A. C., T. C. VAN ARSDALL, D. M. GILLESPIE, AND F. K. PARRISH. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecol. Monogr. 54: 25–63.

BESCHTA, R. L. 1979. Debris removal and its effects on sedimentation in an Oregon Coast Range stream. Northwest Sci. 53: 71–77.

BILBY, R. E. 1979. The function and distribution of organic debris dams in forest stream ecosystems. Ph.D. thesis, Cornell University, Ithaca, NY. 143 p.

1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. Ecology 62: 1234–1243.

1984. Post-logging removal of woody debris affects stream channel stability. J. For. 82: 609–613.

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by University of British Columbia on 01/24/13
For personal use only.

BILBY, R. E., AND G. E. LIKENS. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61: 1107–1113.

BILBY, R. E., AND J. W. WARD. 1989. Changes in the characteristics and function of woody debris with increasing size of streams in western Washington. Trans. Am. Fish. Soc. 118: 368–378.

BILBY, R. E., AND L. J. WASSERMAN. 1989. Forest practices and riparian management in Washington state: data based regulation development, p. 87–94. *In* R. E. Gresswell, B. A. Barton, and J. L. Kershner [ed.] Practical approaches to riparian resource management. U.S. Department of the Interior, Bureau of Land Management, Billings, MT.

BISSON, P. A., J. L. NIELSEN, R. A., PALMASSON, AND L. E. GROVE. 1982. A system of naming habitat types in small streams with examples of habitat utilization by salmonids during low streamflow, p. 62–73. *In* N. B. Armantrout [ed.] Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Bethesda, MD.

BISSON, P. A., ET AL. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present and future, p. 143–190. *In* E. O. Salo and T. Cundy [ed.] Proceedings of an interdisciplinary symposium on streamside management: forestry and fisheries interactions. University of Washington Press, Seattle, WA.

BUSTARD, D. R., AND D. W. NARVER. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 667–680.

DOLLOFF, C. A. 1986. Effects of stream cleaning on juvenile coho salmon and Dolly Varden in southeast Alaska. Trans. Am. Fish. Soc. 115: 743–755.

ELLIOTT, S. T. 1986. Reduction of a Dolly Varden population and macrobenthos after removal of logging debris. Trans. Am. Fish. Soc. 115: 392–400.

EMMINGHAM, W. H., M. BONDI, AND D. E. HIBBS. 1989. Underplanting western hemlock in an alder thinning: early survival, growth, and damage. New For. 3: 31–43.

FERGUSON, D. E., AND D. L. ADAMS. 1980. Response of advanced grand fir regeneration to overstory removal in northern Idaho. For. Sci. 26: 537–545.

GREGORY, S. V., ET AL. 1987. Influence of forest practices on aquatic production, p. 233–255. *In* E. O. Salo and T. Cundy [ed.] Proceedings of an interdisciplinary symposium on streamside management: forestry and fisheries interactions. University of Washington Press, Seattle, WA.

GRETTE, G. B. 1985. The role of large organic debris in juvenile salmonid rearing habitat in small streams. Master's thesis, University of Washington, Seattle, WA. 105 p.

HARMON, M. E., ET AL. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133–302.

HEEDE, B. H. 1972. Influences of a forest on the hydraulic geometry of two mountain streams. Water Resour. Bull. 8: 523–530.

HUNTTING, M. T., W. A. BENNETT, V. A. LIVINGSTON, AND W. S. MOEN. 1961. Geologic map of Washington. Washington Department of Mines and Geology, Olympia, WA.

LIENKAEMPER, G. W., AND F. J. SWANSON. 1987. Dynamics of large woody debris in streams in old-growth Douglas-fir forests. Can. J. For. Res. 17: 150–156.

LIKENS, G. E., AND R. E. BILBY. 1982. Development, maintenance, and role of organic debris dams in New England streams, p. 122–128. *In* F. J. Swanson, R. J. Janda, T. Dunne, and D. N. Swanston [ed.] Sediment budgets and routing in forested drainage basins. U.S. For. Serv. Res. Pap. PNW-141.

LISLE, T. E. 1986. Stabilization of a gravel channel by large streamside obstructions and bedrock bends, Jacoby Creek, northwestern California. Geol. Soc. Am. Bull. 8: 999–1011.

LISLE, T. E., AND H. M. KELSEY. 1982. Effects of large roughness elements on the thalweg course and pool spacing, p. 134–135. *In* L. B. Leopold [ed.] American geomorphological field group field trip guidebook, 1982 conference, Pinedale, Wyoming. American Geophysical Union, Berkeley, CA.

LONG, B. A. 1987. Recruitment and abundance of large woody debris in an Oregon coastal stream. Master's thesis, Oregon State University, Corvallis, OR. 65 p.

MCMAHON, T. E., AND G. F. HARTMAN. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 46: 1551–1557.

MEGAHAN, W. F. 1982. Channel sediment storage behind obstructions in forested drainage basins draining the granitic bedrock of the Idaho Batholith, p. 114–121. *In* F. J. Swanson, R. J. Janda, T. Dunne, and D. N. Swanston [ed.] Sediment budgets and routing in forested drainage basins. U.S. For. Serv. Res. Pap. PNW-141.

MURPHY, M. L., AND K. V. KOSKI. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. N. Am. J. Fish. Manage. 9: 427–436.

NAIMAN, R. J., AND J. R. SEDELL. 1979. Relationships between metabolic parameters and stream order in Oregon. Can. J. Fish. Aquat. Sci. 37: 834–847.

ROBISON, E. G., AND R. L. BESCHTA. 1990. Characteristics of coarse woody debris for several coastal streams of southeast Alaska, USA. Can. J. Fish. Aquat. Sci. 47: 1684–1693.

SEDELL, J. R., AND K. J. LUCHESSA. 1982. Using the historical record as an aid to salmonid habitat enhancement, p. 210–223. *In* N. B. Armantrout [ed.] Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Bethesda, MD.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, CA. 776 p.

STERNES, G. L. 1969. Climatological handbook: Columbia basin states precipitation. Vol. 2. Pacific Northwest River Basins Commission, Meteorology Committee, Vancouver, WA.

SWANSON, F. J., AND G. W. LIENKAEMPER. 1978. Physical consequences of large organic debris in Pacific Northwest Streams. U.S. For. Serv. Gen. Tech. Rep. PNW-69.

SWANSON, F. J., G. W. LIENKAEMPER, AND J. R. SEDELL. 1976. History, physical effects, and management implications of large organic debris in western Oregon streams. U.S. For. Serv. Gen. Tech. Rep. PNW-56.

TSCHAPLINSKI, P. J., AND G. F. HARTMAN. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Can. J. Fish. Aquat. Sci. 40: 452–461.

WENDLER, H. O., AND G. DESCHAMPS. 1955. Logging dams on coastal Washington streams. Wash. Dep. Fish. Fish. Res. Pap. 1: 1–12.

Appendix

TABLE A.1. Characteristics of the surveyed stream sections and the number of pieces of LWD measured at each site (o.g. = old-growth, c.c. = clear-cut, s.g. = second-growth).

Stream	Stand condition	Channel width (m)	Basin area (km^2)	Pieces measured (*N*)
Deschutes River Basin				
Hard Cr.	o.g.	5.6	1.7	60
Unnamed stream	o.g.	5.8	1.0	50
Mine Cr.	o.g.	7.5	2.7	50
Thorn Cr.	o.g.	7.6	3.6	52
West Fork Cr.	o.g.	9.0	8.7	51
Lewis Cr.	c.c.	3.8	3.0	50
Hard Cr.	c.c.	5.5	2.2	50
Upper Deschutes R.	c.c.	5.5	2.6	50
Little Deschutes R.	c.c.	5.6	3.9	50
Deschutes R.	c.c.	8.7	12.7	50
Thurston Cr.	s.g.	4.9	9.6	50
Mitchell Cr.	s.g.	8.3	21.9	50
North River Basin				
Fall R.	o.g.	12.4	30.4	50
Fall R.	c.c.	8.2	24.2	51
Unnamed stream	o.g.	3.6	2.1	50
Skookumchuck River Basin				
Unnamed stream	o.g.	4.2	0.8	50
Unnamed stream	o.g.	4.3	0.4	53
Unnamed stream	o.g.	5.4	2.3	50
Deer Cr.	o.g.	6.3	2.9	51
U. Skookumchuck R.	o.g.	7.1	1.7	50
L. Skookumchuck R.	o.g.	17.0	26.6	50
Unnamed stream	c.c.	4.6	1.3	50
Big Water Cr.	c.c.	6.3	5.2	60
Skookumchuck R.	c.c.	10.5	15.9	50
Upper Hanaford Cr.	s.g.	3.3	3.5	50
Laramie Cr.	s.g.	4.3	7.8	50
Three Deer Cr.	s.g.	4.4	4.5	51
Lower Hanaford cr.	s.g.	9.9	33.8	51
U. Skookumchuck R.	s.g.	11.0	60.6	50
L. Skookumchuck R.	s.g.	13.0	72.1	50

TABLE A.1. (*Continued*)

Stream	Stand condition	Channel width (m)	Basin area (km^2)	Pieces measured (*N*)
Abernathy Creek Basin				
Abernathy Cr.	s.g.	11.0	31.2	50
Newaukum River Basin				
Newaukum R.	o.g.	8.9	18.1	53
N.F. Newaukum R.	c.c.	7.0	19.0	50
Hemlock Hole Cr.	s.g.	5.6	9.1	50
N.F. Newaukum R.	s.g.	13.6	18.9	50
S.F. Newaukum R.	s.g.	13.8	60.6	50
Kalama River Basin				
Arnold Cr.	c.c.	3.7	2.6	50
Gobar Cr.	c.c.	12.3	54.3	48
Nisqually River Basin				
Hiawatha Cr.	c.c.	9.8	12.3	50
Little Nisqually R.	c.c.	13.7	21.9	50
Beaver Cr.	s.g.	7.6	29.0	50
Busy Wild Cr.	s.g.	12.3	41.9	50
Upper Mashel R.	s.g.	14.5	48.7	50
Middle Mashel R.	s.g.	19.3	96.3	47
Lower Mashel R.	s.g.	22.3	136.8	36
Coweeman River Basin				
Baird Cr.	s.g.	8.3	19.9	50
Lewis River Basin				
Upper Canyon Cr.	o.g.	10.1	12.7	50
Middle Canyon Cr.	o.g.	16.1	33.0	50
Fly Cr.	o.g.	18.9	50.3	46
Lower Canyon Cr.	o.g.	19.7	68.0	50
Canyon Cr.	c.c.	23.5	74.6	19

TABLE A.1. (*Concluded*)

Stream	Stand condition	Channel width (m)	Basin area (km^2)	Pieces measured (*N*)
Upper Chehalis River Basin				
Salmon Cr.	c.c.	9.9	55.4	50
Upper Chehalis R.	c.c.	12.5	29.6	51
Unnamed stream	s.g.	3.1	2.0	50
Capps Cr.	s.g.	3.3	2.6	50
Big Cr.	s.g.	5.6	9.3	50
S.F. Stillman Cr.	s.g.	9.5	23.1	50
S.F. Chehalis R.	s.g.	16.1	43.7	50
Willapa River Basin				
Trap Cr.	s.g.	9.9	23.3	50
Grays River Basin				
E.F. Grays R.	o.g.	11.7	7.5	49
N.F. Grays R.	o.g.	16.1	21.9	50
Toutle River Basin				
Eighteen Cr.	s.g.	5.2	5.9	50
Thirteen Cr.	s.g.	6.5	7.9	50
Devils Cr.	s.g.	7.1	16.1	50
Upper Hemlock Cr.	s.g.	7.1	13.5	50
Lower Hemlock Cr.	s.g.	8.4	30.6	50
Tilton River Basin				
M.F. Tilton R.	o.g.	5.9	1.3	50
Otter Cr.	o.g.	9.7	3.8	51
Wallanding Cr.	c.c.	14.2	20.5	50
N.F. Tilton R.	c.c.	23.1	83.7	30

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by University of British Columbia on 01/24/13
For personal use only.

Chapter 4

Habitat Requirements of Salmonids in Streams

T. C. Bjornn and D. W. Reiser

Habitat needs of salmon, trout, and char in streams vary with the season of the year and stage of the life cycle. The major life stages of most salmonid species are associated with different uses of fluvial systems: migration of maturing fish from the ocean (anadromous fishes), lakes, or rivers to natal streams; spawning by adults; incubation of embryos; rearing of juveniles; and downstream migration of juveniles to large-river, lacustrine, or oceanic rearing areas. We present information from the literature and from our own research on the range of habitat conditions for each life stage that allow the various species to exist. When possible, we attempt to define optimum and limiting conditions. Anadromous salmonids of the Pacific drainages of North America are our primary focus, but we have included information on other salmonids to illustrate the ranges of temperature, water velocities, depths, cover, and substrates preferred by salmon, trout, and char in streams. The scientific names of species identified by common names here are listed in the book's front matter.

Upstream Migration of Adults

Adult salmonids returning to their natal streams must reach spawning grounds at the proper time and with sufficient energy reserves to complete their life cycles. Stream discharges, water temperatures, and water quality must be suitable during at least a portion of the migration season. Native stocks of salmon, trout, and char that have evolved in stream systems with fluctuations in flow, turbidity, and temperature have often developed behaviors that enable survival despite the occurrence of temporarily unfavorable conditions. Native salmonids usually have sufficient extra time in their maturation, migration, and spawning schedules to accommodate delays caused by normally occurring low flows, high turbidities, or unsuitable temperatures. When upstream migration is not delayed, the fish in some stocks that migrate long distances arrive in the spawning areas 1–3 months before they spawn. Some stocks of fish that migrate short distances may not move into natal streams until shortly before spawning, but they must often wait in the ocean, lake, or river for flows or temperatures in the spawning streams to become suitable.

The flexibility in maturation and migration schedules observed in many stocks of native salmonids is not unlimited and has evolved for the specific environment

Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats
American Fisheries Society Special Publication 19:83–138, 1991

TABLE 4.1.—Water temperatures (Bell 1986) and depths and velocities (Thompson 1972) that enable upstream migration of adult salmon and trout.

Species of fish	Temperature range (°C)	Minimum depth (m)	Maximum velocity (m/s)
Fall chinook salmon	10.6–19.4	0.24	2.44
Spring chinook salmon	3.3–13.3	0.24	2.44
Summer chinook salmon	13.9–20.0	0.24	2.44
Chum salmon	8.3–15.6	0.18	2.44
Coho salmon	7.2–15.6	0.18	2.44
Pink salmon	7.2–15.6	0.18[a]	2.13
Sockeye salmon	7.2–15.6	0.18	2.13
Steelhead		0.18	2.44
Large trout		0.18	2.44
Trout		0.12	1.22

[a] Estimate based on fish size.

of each stock. Natural or human-caused changes in the environment can be large enough to prevent fish from completing their maturation or migration to spawning areas; the proportion affected depends on the extent of the change. Transplanted stocks of fish may be less successful than native stocks in reproducing themselves if they do not possess the flexibility in migration timing required in their new environment.

Temperature

Salmon and trout respond to stream temperatures during their upstream migrations. Delays in upstream migration because natal streams were too warm have been observed for sockeye salmon (Major and Mighell 1966), chinook salmon (Hallock et al. 1970), and steelhead (Monan et al. 1975). Bell (1986) reported that Pacific salmon and steelhead have migrated upstream at temperatures between 3 and 20°C (Table 4.1).

Streams can be too cold as well as too warm for upstream-migrating salmonids. Cutthroat and rainbow trout have been observed waiting for tributaries to warm in spring before entering them to spawn. Adult steelhead that return from the sea in summer and autumn, and then spend the winter in inland rivers before spawning the following spring, overwinter in larger rivers downstream from their natal streams because the smaller headwater streams are often ice-choked during winter. We believe adult steelhead overwinter in the larger rivers because survival is higher there and the slightly higher temperatures in the rivers enable timely maturation (Reingold 1968).

Stream temperatures can be altered by removal of streambank vegetation, withdrawal and return of water for agricultural irrigation, release of water from deep reservoirs, and cooling of nuclear power plants. Unsuitable temperatures can lead to disease outbreaks in migrating and spawning fish, altered timing of migration, and accelerated or retarded maturation. Most stocks of anadromous salmonids have evolved with the temperature patterns of the streams they use for migration and spawning, and deviations from the normal pattern could adversely affect their survival.

Dissolved Oxygen

Reduced concentrations of dissolved oxygen (DO) can adversely affect the swimming performance of migrating salmonids. Maximum sustained swimming speeds of juvenile and adult coho salmon at temperatures of 10–20°C were reduced when DO dropped below air-saturation levels, and performance declined sharply when DO fell to 6.5–7.0 mg/L, at all temperatures tested (Davis et al. 1963). Swimming performance of brook trout declined similarly (Graham 1949). Low DO may also elicit avoidance reactions (Whitmore et al. 1960; Hallock et al. 1970), and may halt migration. Hallock et al. (1970) observed that adult migration ceased when DO fell below 4.5 mg/L, and did not resume until it exceeded 5 mg/L. Minimum DO recommended for spawning fish (at least 80% of saturation, and not even temporarily less than 5.0 mg/L) should provide the minimum needs of migrating salmonids.

Turbidity

Migrating salmonids avoid waters with high silt loads, or cease migration when such loads are unavoidable (Cordone and Kelley 1961). Bell (1986) cited a study in which salmonids did not move in streams where the suspended sediment concentration exceeded 4,000 mg/L (as a result of a landslide). Timing of arrival at spawning grounds by chinook salmon that migrate upstream during snowmelt runoff can vary by a month or more, depending on the concentration of suspended solids in rivers along their migration route (Bjornn 1978). In the lower Columbia River, the upstream migration of salmon may be retarded when secchi disk readings are less than 0.6 m (Figure 4.1).

High turbidity in rivers may delay migration, but turbidity alone generally does not seem to affect the homing of salmonids very much. In studies after the eruption of Mount St. Helens in 1980, Whitman et al. (1982) found that salmon preferred natal stream water without volcanic ash in an experimental flume, but that they recognized their natal streams despite the ash and attempted to ascend them. Quinn and Fresh (1984) reported that the rate of straying of chinook salmon to the Cowlitz River Hatchery was low and unaffected by the 1980 eruption, but that many coho salmon in the Toutle River, the Cowlitz River tributary most affected by the eruption, did stray to nearby streams in 1980 and 1981. Olfaction is a primary sense salmonids use for homing during upstream migration (Hasler and Larsen 1955; Hasler et al. 1978). Each stream may have a unique bouquet, and the extent to which that bouquet can be altered—by the addition of exotic chemicals, trans-basin diversions, and unnatural suspended sediments—without affecting the homing of salmonids is not known.

Barriers

Waterfalls, debris jams, and excessive water velocities may impede migrating fish. Falls that are insurmountable at one time of the year may be passed by migrating fish at other times when flows have changed. Stuart (1962) determined in laboratory studies that leaping conditions for fish are ideal when the ratio of height of falls to depth of pool below the falls is 1:1.25 (Figure 4.2). Given suitable conditions, salmon and steelhead can get past many obstacles that appear to be barriers. Both Jones (1959) and Stuart (1962) observed salmon jumping over

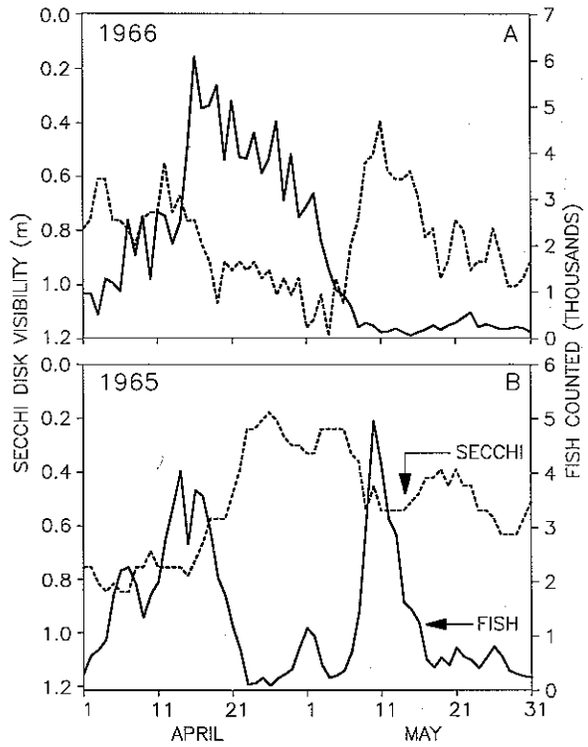


FIGURE 4.1.—Secchi disk visibility (broken line) and number of chinook salmon adults (solid lines) migrating up the Columbia River past Bonneville Dam during April and May of 1965, when high turbid flows interrupted the migration, and of 1966, when turbidities were low and the timing of migration was normal.

obstacles 2–3 m in height. Powers and Orsborn (1985) analyzed barriers to upstream-migrating fish in terms of barrier geometry, stream hydrology, and fish capabilities. They reported the abilities of salmon and trout to pass over barriers depended on the swimming velocity of the fish, the horizontal and vertical distances to be jumped, and the angle to the top of the barrier (Figure 4.3). Reiser and Peacock (1985) computed maximum jumping heights of salmonids on the basis of darting speeds; these heights ranged from 0.8 m for brown trout to more than 3 m for steelhead (Table 4.2).

The swimming abilities of fish are usually described in three categories of speed: cruising speed, the speed a fish can swim for an extended period of time, usually ranging from 2 to 4 body lengths/s; sustained speed, the speed a fish can maintain for a period of several minutes, ranging from 4 to 7 body lengths/s; and darting or burst speed, the speed a fish can swim for a few seconds, ranging from 8 to 12 body lengths/s (Watts 1974; Bell 1986; Table 4.2). According to Bell (1986), cruising speed is used during migration, sustained speed for passage through difficult areas, and darting speed for escape and feeding. Water velocities of 3–4 m/s approach the upper sustained swimming ability of large fish like salmon and steelhead.

Debris jams, whether natural or caused by human activities, can prevent or delay upstream migration. Chapman (1962b) cited a study in which a 75% decrease in number of spawning salmon in one stream was attributed to blockage by debris. On the other hand, many debris jams can be easily passed by fish and they often form pools and provide cover for fish. Removal of debris barriers

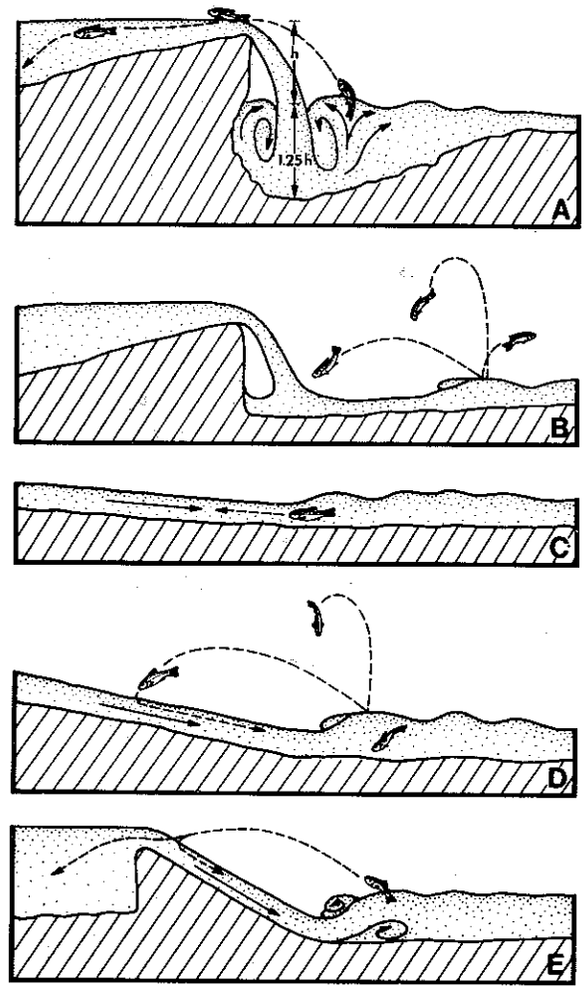


FIGURE 4.2.—Leaping ability of salmonids. (From Eiserman et al. 1975, diagrams drawn after Stuart 1962). (A) Falling water enters the pool at nearly a 90° angle. A standing wave lies close to the waterfall, where fish can use its upward thrust to leap the falls. Plunge-pool depth is 1.25 times the distance (h) from the crest of the waterfall to the water level of the pool. (B) The height of fall is the same as in A, but pool depth is less. The standing wave is formed too far from the ledge to be useful to leaping fish. (C) Flow down a gradual incline is slow enough to allow passage of ascending fish. (D) Flow over an incline steeper than fish can negotiate. Fish may even be repulsed in the standing wave at the foot of the incline. They sometimes leap futilely from the standing wave. (E) A shorter barrier with outflow over a steep incline may be ascended by some fish with difficulty.

should be done with care to avoid sedimentation of downstream spawning and rearing areas and loss of hydraulic stability.

Streamflow

Fish migrating upstream must have streamflows that provide suitable water velocities and depths for successful upstream passage. A variety of techniques have been used to estimate the flows required for migrating fish. Baxter (1961) reported that salmon needed 30–50% of the average annual flow for passage through the lower and middle reaches in Scottish rivers and up to 70% for passage up headwater streams. Thompson (1972) developed a procedure for estimating minimum flows required for migrating fish on the basis of minimum depth and maximum velocity criteria (Table 4.1) and measurements in critical stream reaches, usually shallow riffles. Stream discharges that provide suitable depths and velocities for upstream passage of adults can be estimated by the techniques he described (Thompson 1972):

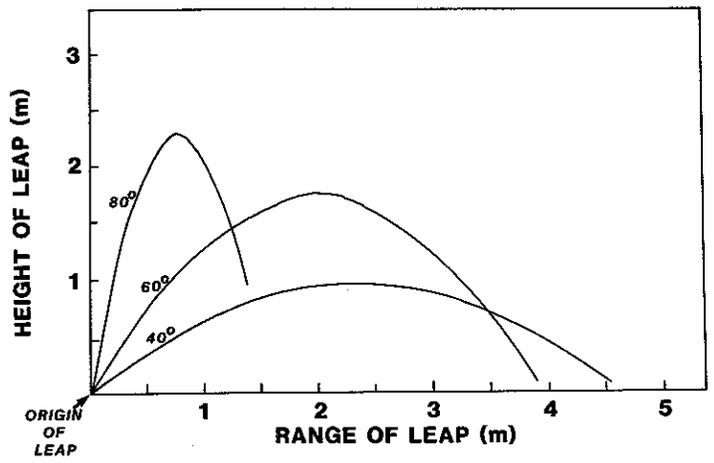


FIGURE 4.3.—Leaping curves for chinook, coho, and sockeye salmon swimming with a maximum burst speed of 6.8 m/s and jumping at various angles. (Adapted from Powers and Orsborn 1985.)

> . . . shallow bars most critical to passage of adult fish are located and a linear transect marked which follows the shallowest course from bank to bank. At each of several flows, the total width and longest continuous portion of the transect meeting minimum depth and maximum velocity criteria are measured. For each transect, the flow is selected that meets the criteria on at least 25% of the total transect width and a continuous portion equaling at least 10% of its total width.

The mean selected flow from all transects is recommended as the minimum flow for passage.

Sautner et al. (1984) reported that passage of chum salmon spawners through sloughs and side channels of the Susitna River, Alaska, depended primarily on water depth, length of the critical stream reach, and size of substrate particles. Fish could successfully pass any stream reach of reasonable length if the depth was greater than 0.12 m when substrate particles averaged larger than 7.6 cm in diameter, or if the depth was greater than 0.09 m when particles were less than 7.6 cm.

TABLE 4.2.—Swimming (Bell 1986) and jumping abilities (Reiser and Peacock 1985) of average-size adult salmonids.

Taxon	Swimming speed (m/s)			Maximum jumping height (m)
	Cruising	Sustained	Darting	
Chinook salmon	0–1.04	1.04–3.29	3.29–6.83	2.4
Coho salmon	0–1.04	1.04–3.23	3.23–6.55	2.2
Sockeye salmon	0–0.98	0.98–3.11	3.11–6.28	2.1
Steelhead	0–1.40	1.40–4.18	4.18–8.08	3.4
Trout	0–0.61	0.61–1.95	1.95–4.11	
Brown trout	0–0.67	0.67–1.89	1.89–3.87	0.8

Spawning

Substrate composition, cover, water quality, and water quantity are important habitat elements for salmonids before and during spawning. The number of spawners that can be accommodated in a stream is a function of the area suitable for spawning (suitable substrate, water depth, and velocity), area required for each redd, suitability of cover for the fish, and behavior of the spawners. Cover is important for species that spend several weeks maturing near spawning areas.

The amount of suitable stream substrate for spawning varies with the size (order) of the stream and species of salmonid using it, as Boehne and House (1983) learned from study of two coastal and two Cascade Range watersheds in Oregon. First-order streams (small headwater streams without tributaries) were not used by salmonids. Less than half the second-order streams (streams resulting from the junction of two or more first-order streams) were used by salmonids; those that were contained nonanadromous cutthroat trout. Most of the third-order streams (steams resulting from the junction of two or more second-order streams) in the coastal watersheds, but only 37% of those in the Cascade Range drainages, were used by cutthroat trout. The larger anadromous steelhead, coho salmon, and chinook salmon spawned in a few third-order streams, but most were found in fourth- and fifth-order streams. As stream order increased, gradient decreased but stream length, width, and depth increased. The amount of spawning gravel per kilometer of stream was greatest in fourth-order coastal watersheds and fifth-order Cascade Range watersheds. Platts (1979b) found similar relations between stream size (order) and use of the streams by fish in an Idaho drainage.

Streamflow

Streamflow regulates the amount of spawning area available in any stream by regulating the area covered by water and the velocities and depths of water over the gravel beds. D. H. Fry (in Hooper 1973) summarized the effect of discharge on the amount of spawning area in a stream.

> As flows increase, more and more gravel is covered and becomes suitable for spawning. As flows continue to increase, velocities in some places become too high for spawning, thus cancelling out the benefit of increases in usable spawning area near the edges of the stream. Eventually, as flows increase, the losses begin to outweigh the gains, and the actual spawning capacity of the stream starts to decrease. If spawning area is plotted against streamflow, the curve will usually show a rise to a relatively wide plateau followed by a gradual decline.

Relations between flow and amount of suitable spawning area have been assessed or predicted by methods based primarily on measurements of water depths and velocities in areas with suitable substrate. Collings (1972, 1974) used a process of depth and velocity contouring to determine the area suitable for spawning at a given discharge. Thompson (1972) quantified the width of the stream at cross-channel transects on spawning bars that met minimum criteria of depth (18 cm) and velocity (0.3–3.0 m/s) at different flows. When measurements have been taken over a wide range of flows, a graph can be plotted of flow versus suitable spawning areas (Figure 4.4) or usable width (Figure 4.5). A method

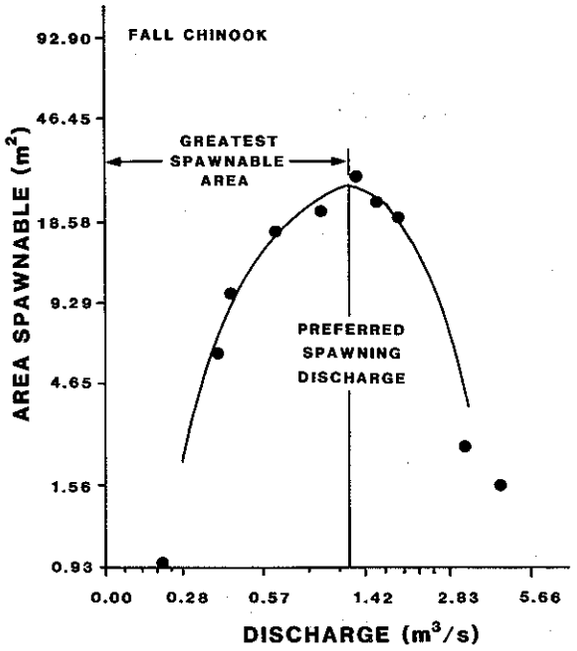


FIGURE 4.4.—Usable-area technique for selecting preferred spawning discharge, North Nemah River. (From Collings 1972.)

similar to that used by Waters (1976), termed the instream flow incremental methodology (IFIM), was developed by U.S. Fish and Wildlife Service personnel to estimate the amount of suitable habitat (for spawning, in this instance); the method relates variations in a stream's water velocity, depth, substrate, and other variables to use of the stream by fishes (Stalnaker and Arnette 1976b; Bovee 1978, 1982, 1986; Bovee and Milhous 1978; Trihey and Wegner 1981). An IFIM analysis results in an index of suitable habitat (weighted usable area, WUA) for a range of streamflows (Figure 4.6). Wesche and Rechard (1980) and EA Engineering, Science and Technology, Inc. (1986) reviewed and evaluated a variety of methods that could be used for estimating the quantity and quality of spawning habitat for salmonids.

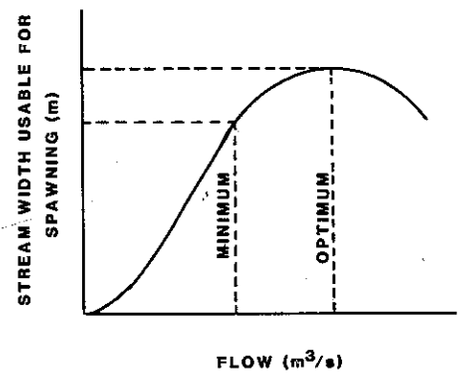


FIGURE 4.5.—Usable-width technique for determining spawning flow. (From Thompson 1972.)

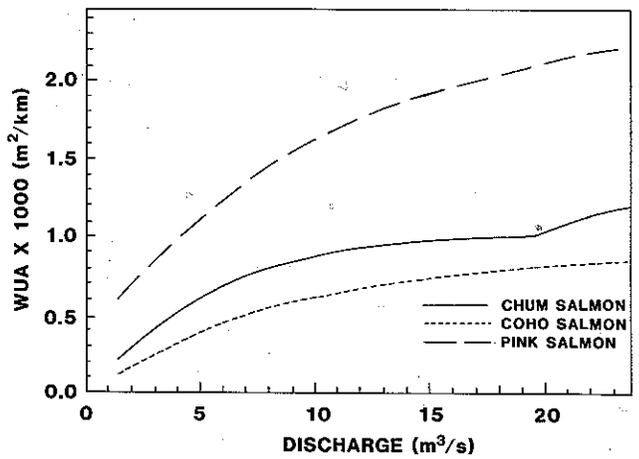


FIGURE 4.6.—Relation of available chum, coho, and pink salmon spawning habitat (weighted usable area, WUA) to streamflow, Upper Tunnel Creek. (From Reiser and Ramey 1984.)

Temperature

Timing of salmonid spawning has likely evolved in response to water temperatures in each stream before, during, and after spawning, and, in some streams, to the occurrence of flows that allow upstream migration of maturing adults. Salmonids have spawned when water temperatures have ranged from 1.0 to 20.0°C, but the favorable range of temperatures for spawning is much narrower (Table 4.3). In British Columbia (Shepherd et al. 1986b), salmon were observed spawning over a wide range of temperatures, but most of the pink, chum, and

TABLE 4.3.—Recommended temperatures for spawning and incubation of salmonid fishes (Bell 1986).

Species	Temperature (°C)	
	Spawning	Incubation[a]
Fall chinook salmon	5.6–13.9	5.0–14.4
Spring chinook salmon	5.6–13.9	5.0–14.4
Summer chinook salmon	5.6–13.9	5.0–14.4
Chum salmon	7.2–12.8	4.4–13.3
Coho salmon	4.4–9.4	4.4–13.3
Pink salmon	7.2–12.8	4.4–13.3
Sockeye salmon	10.6–12.2	4.4–13.3
Kokanee	5.0–12.8	
Steelhead	3.9–9.4	
Rainbow trout	2.2–20.0	
Cutthroat trout	6.1–17.2	
Brown trout	7.2–12.8[b]	

[a] The higher and lower values are threshold temperatures beyond which mortality increases. Eggs survive and develop normally at lower temperatures than indicated, provided initial development of the embryo has progressed to a stage that is tolerant of cold water.

[b] From Hunter (1973).

sockeye salmon spawned in water of 8–13°C, chinook salmon in water of 10–17°C, and coho salmon in water of less than 10°C (mode, 5–6°C).

Each native fish stock appears to have a unique time and temperature for spawning that theoretically maximizes the survival of their offspring. Temperatures before and during spawning must allow the spawners to survive and deposit their eggs, but temperatures during incubation of the embryos (which regulates timing of juvenile emergence from the redd) may be the primary evolutionary factor that has determined the time of spawning (Heggberget 1988). In the case of fall spawners, newly spawned embryos must reach a critical stage of development before the water becomes too cold (Brannon 1965), and emergence of fry must occur at a suitable time during the following spring (Sheridan 1962a; Miller and Brannon 1982; Godin 1982; Burger et al. 1985; Heggberget 1988). Spring spawners must not spawn before the water has warmed sufficiently to permit normal development of embryos, but there may be a survival advantage for the fish to spawn as early as possible to allow the offspring to emerge and grow before the onset of winter. Support for the latter hypothesis can be found in Idaho streams, where steelhead usually spawn before the peak of the snowmelt runoff in spring (thereby risking destruction of their redds by the high flows) rather than after the peak, which would delay the emergence of their offspring until late summer.

Areas with upwelling groundwater have been selected as spawning areas by salmonids such as chum salmon, brown trout, and brook trout (Benson 1953; Bakkala 1970; Witzel and MacCrimmon 1983; Vining et al. 1985). Use of areas with groundwater flow may have survival advantages if the water quality (suitable temperatures and dissolved gases, and lack of damaging heavy metals and sediments) in such areas is more suitable than in areas without groundwater.

Space

The amount of space required by salmonids for spawning depends on the size and behavior of the spawners and the quality of the spawning area. Large fish make large redds; tolerance of nearby fish varies by species; and poor-quality spawning areas may force females to make several redds. Redds range in size from 0.6 m^2 to more than 10 m^2 for anadromous salmonids, and from 0.09 m^2 to 0.9 m^2 for smaller nonanadromous trout and salmon (Table 4.4).

Many salmonids prefer to spawn in the transitional area between pools and riffles (Hazzard 1932; Hobbs 1937; Smith 1941; Briggs 1953; Stuart 1953). Tautz and Groot (1975) reported that chum salmon spawned in an accelerating flow, such as that found at a pool–riffle transition. By placing crystals of potassium permanganate on the gravel surface, Stuart (1953) demonstrated the presence of downwelling currents in these transitional areas (Figure 4.7) and noted that the gravel there was easy to excavate and relatively free of silt and debris. Vaux (1962, 1968) reported that downwelling currents normally occurred in areas where the streambed was convex (such as the pool–riffle transition), and upwelling currents occurred in concave areas (such as the downstream end of a riffle).

The density of redds in streams depends on the amount of stream area suitable for spawning, the number and size of spawners, and the area required for each redd. In two Lake Michigan tributaries with alternating pool–riffle habitat, the densities of spawning chinook salmon ranged from about 80 to 250 fish per hectare of stream area (Carl 1984). The average velocities at the preferred spawning sites in the two streams

TABLE 4.4.—Average area of salmonid redds and area recommended per spawning pair of fish in channels.

Species	Average area of redd (m^2)	Area recommended per spawning pair[a] (m^2)	Source
Chinook salmon	9.1–10.0		Neilson and Banford (1983)
Spring chinook salmon	3.3	13.4	Burner (1951)
Spring chinook salmon	6.0		Reiser and White (1981a)
Fall chinook salmon	5.1	20.1	Burner (1951)
Summer chinook salmon	5.1	20.1	Burner (1951)
Summer chinook salmon	9.4		Reiser and White (1981a)
Coho salmon	2.8	11.7	Burner (1951)
Chum salmon	2.3	9.2	Burner (1951)
Sockeye salmon	1.8	6.7	Burner (1951)
Pink salmon	0.6	0.6	Hourston and MacKinnon (1957)
Pink salmon	0.6–0.9		Wells and McNeil (1970)
Steelhead	5.4		Orcutt et al. (1968)
Steelhead	4.4		Hunter (1973)
Steelhead	4.4		Reiser and White (1981a)
Rainbow trout	0.2		Hunter (1973)
Cutthroat trout	0.09–0.9		Hunter (1973)
Brown trout	0.5		Reiser and Wesche (1977)

[a] Modified from Clay (1961).

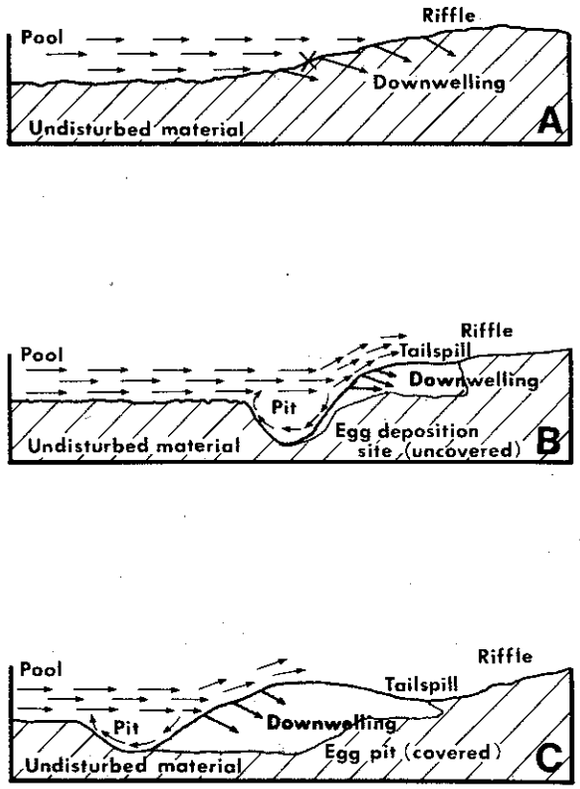


FIGURE 4.7.—Longitudinal sections of a spawning area. (From Reiser and Wesche 1977.) (A) Convexity of the substrate at the pool–riffle transition induces downwelling of water into the gravel. The area likely to be used for spawning is marked with a ×. (B) Redd construction results in negligible currents in the pit (facilitating egg deposition) and increased currents over and through (downwelling) the tailspill. (C) Egg-covering activity results in the formation of a second pit upstream, which may also be used for spawning. Increased permeability and the convexity of the tailspill substrate induces downwelling of water into the gravel, creating a current past eggs. The current brings oxygen to the eggs and removes metabolic wastes.

were 0.42 m/s and 0.50 m/s—similar to those reported by Burner (1951) in the Toutle River, Washington. In the Nechako River, British Columbia, Neilson and Banford (1983) reported that the area of chinook salmon redds averaged 9.1 and 10.0 m^2 and that densities were 1 redd per 235 m^2 and 1 per 112 m^2 in two areas with water depths of at least 0.45 m (the shallowest water in which redd construction was seen). Water depth in the deepest part (pit) of 47 completed redds was 0.46–1.20 m (mean, 0.87 m). Water velocity over the pit of the redds was 15–100 cm/s (mean, 56 cm/s). In a small Oregon coastal tributary, coho salmon constructed 1.7 redds per female and produced a density of 194 redds per hectare of stream (R. A. House, U.S. Bureau of Land Management, unpublished data).

The number of redds that can be built in a stream depends on the amount of suitable spawning habitat and the area required per spawning pair of fish (Reiser and Ramey 1984, 1987; IEC Beak 1984; Reiser 1986). The area suitable for spawning (defined by water depth, velocity, and size of substrate) is usually less than the total area of gravel substrate in the stream, and spatial requirements for each spawning pair may exceed the area of a completed redd. Surface areas of redds can be readily measured, but the spatial requirement for each spawning pair may require additional information such as area of suitable spawning habitat, number of spawners in a given area, and the size and behavior of spawners. Burner (1951) suggested that a conservative estimate of the number of salmon a stream could accommodate could be obtained by dividing the area suitable for spawning by four times the average area of a redd.

In an Oregon stream, gravel substrate made up 25% of the total stream area, but only 30% of that gravel substrate was suitable for spawning by coho salmon (R. A. House, unpublished data). The main stem of the Tucannon River in southeastern Washington contained nearly 200,000 m^2 of gravel substrate (D. W. Kelley and Associates 1982); however, only a small fraction of the river bed was suitable for anadromous fish spawning in the judgment of one of us (T.C.B.), who surveyed 9,000 linear meters of the river and estimated that 3,200 salmon or steelhead redds could be constructed without serious superimposition of redds. If the total area of gravel substrate in the stream (200,000 m^2) had been divided by the average size of salmon or steelhead redds (about 5 m^2), the capacity of the river would have been erroneously estimated to be about 40,000 redds. If Burner's (1951) formula (four times the average redd area) had been used, the estimate would be about 10,000 redds. Much of the river was unsuitable for spawning because water depths and velocities were outside the range acceptable to spawning salmon.

Water Depth and Velocity

Preferred water depths and velocities for various spawning salmonids have been determined from measurements of water depth and velocity at redds (Cope 1957; Sams and Pearson 1963; Orcutt et al. 1968; Thompson 1972; Hooper 1973; Hunter 1973; Smith 1973; Reiser and Wesche 1977; Reiser and White 1981a; Neilson and Banford 1983; Shepherd et al. 1986b). Water depths measured at redd sites varied with species and size of fish and ranged from 6 to 300 cm. In general, the water was at least deep enough to cover the fish during spawning; large salmon required 15–35 cm and smaller trout 6–10 cm (Table 4.5). Many fish spawned in water deeper than necessary to submerge them, but it is not known if the fish preferred the greater depths or were merely using what was available. Water

TABLE 4.5.—Water depth, velocity, and substrate size criteria for anadromous and other salmonid spawning areas.

Species	Depth (cm)	Velocity (cm/s)	Substrate size (cm)	Source
Fall chinook salmon	≥24	30–91	1.3–10.2[a]	Thompson (1972)
Spring chinook salmon	≥24	30–91	1.3–10.2[a]	Thompson (1972)
Summer chinook salmon	≥30	32–109	1.3–10.2[a]	Reiser and White (1981a)
Chum salmon	≥18	46–101	1.3–10.2[a]	Smith (1973)
Coho salmon	≥18	30–91	1.3–10.2[b]	Thompson (1972)
Pink salmon	≥15	21–101	1.3–10.2[a]	Collings (1974)
Sockeye salmon	≥15	21–101[b]	1.3–10.2[a]	[b]
Atlantic salmon	≥25	25–90		Beland et al. (1982)
Kokanee	≥6	15–73		Smith (1973)
Steelhead	≥24	40–91	0.6–10.2[c]	Smith (1973)
Rainbow trout	≥18	48–91	0.6–5.2	Smith (1973)
Cutthroat trout	≥6	11–72	0.6–10.2	Hunter (1973)
Brown trout	≥24	21–64	0.6–7.6[c]	Thompson (1972)

[a] From Bell (1986).
[b] Estimated from criteria for other species.
[c] From Hunter (1973).

velocities at the redd sites ranged from 3 to 152 cm/s, but most were from 20 to 100 cm/s (Table 4.5).

Measurements of depth and velocity were usually taken at the upstream edge of the redd because that point most closely approximated conditions before the redd was constructed and reflected the depths and velocities selected by the fish. Two locations in the water column have been used for making estimates of preferred velocity: 0.6 × depth from the surface to the streambed, and nose velocity (which approximates the location of the fish close to the bed surface). Most velocity criteria have been developed for 0.6 × depth. The ranges of preferred depths and velocities have been defined in a variety of ways. Thompson (1972) used the depths and velocities within a 90–95% confidence interval. Hunter (1973) used the middle 80–90% of the measurements. Smith (1973) used a two-sided tolerance limit within which there was 95% confidence that 80% of the measurements would occur within a normal distribution. Others have simply listed the ranges of depth and velocity measured.

More recently, investigators have developed a series of index curves to depict the suitability of selected variables for different species of fish and life history stages (Figure 4.8). Such curves, used primarily in IFIM, have usually been developed from empirical measurements of depth, velocity, and substrate at the redd site. The curves were based on the assumption that fish select areas in a stream with optimal combinations of physical and hydraulic conditions. The development and limitations of these types of curves were discussed by various investigators (Bovee and Cochnauer 1977; Waters 1976; Baldridge and Amos 1982; Bovee 1982, 1986; Theilke 1985; EA Engineering, Science and Technology, Inc. 1986).

Substrate

The suitability of gravel substrate for spawning depends mostly on fish size; large fish can use larger substrate materials than can small fish. Bell (1986) stated that substrate for anadromous salmon and trout should range from 1.3 to 10.2 cm

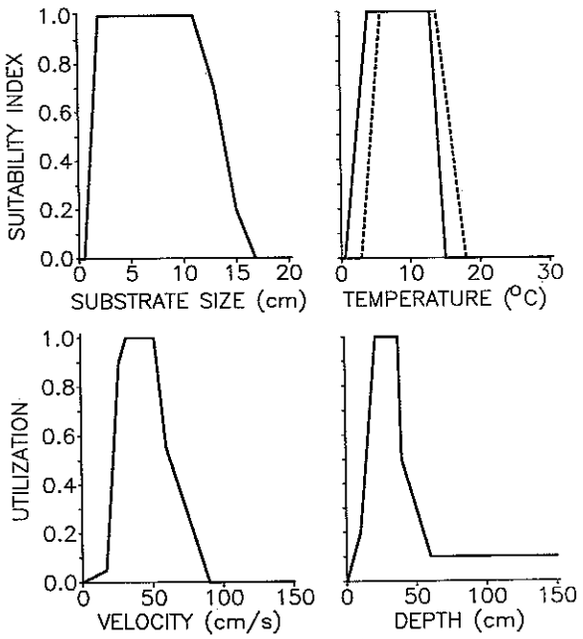


FIGURE 4.8.—Suitability index curves for average substrate particle size and temperature, and use curves for mean current velocity in the water column and water depth, in a spawning area used by chinook salmon. Solid line indicates spawning, dashed line incubation. (Redrawn from Raleigh et al. 1986.)

in diameter (Table 4.5). For smaller fish, other investigators have recommended that the materials not exceed 5.2 or 7.6 cm, depending on size of the fish. The criteria presented above are in general agreement with the sizes of substrate particles found in redds (Orcutt et al. 1968; Hooper 1973; Hunter 1973; Smith 1973; Reiser and Wesche 1977). Salmon have been observed spawning in areas with substrate particles larger than 30 cm, but most often in areas where the majority of particles were smaller than 15 cm (Shepherd et al. 1986b).

To determine the composition of substrate used by salmonids, investigators have collected substrate samples from active redds or known spawning areas and graded them through a series of sieves (Burner 1951; Cope 1957; Warner 1963; Orcutt et al. 1968; Hunter 1973; Reiser and Wesche 1977; Tagart 1976; Corley and Burmeister 1979; Huntington 1985). In such studies, various techniques have been used for the collection of substrate materials (McNeil and Ahnell 1964; Tagart 1976; Walkotten 1976; Platts and Penton 1980; Lotspeich and Everest 1981) and for their characterization (Platts et al. 1979b; Lotspeich and Everest 1981; Shirazi and Seim 1981; Tappel and Bjornn 1983). The particle makeup of redds or spawning areas has been characterized by the proportions within specified size ranges (Tappel and Bjornn 1983), the geometric mean particle diameter (dg: Shirazi and Seim 1981), and the Fredle index (Fi: Lotspeich and Everest 1981).

Substrates used in artificial spawning channels represent the particle sizes best suited for selected species in the judgment of those who designed the channels. Gravel from 2 to 10 cm in diameter was used in the Robertson Creek (British Columbia) spawning channels for pink, coho, and chinook salmon (Lucas 1960). Gravel from 0.6 to 3.8 cm was used in the Jones Creek (British Columbia) spawning channel for anadromous fish (MacKinnon et al. 1961). The Tehama–Colusa spawning channels in California, designed primarily for chinook salmon,

contained gravel 1.9–15.2 cm in diameter (Pollock 1969). Bell (1986) stated that, in general, up to 80% of the substrate in artificial spawning channels should be gravel with diameters of 1.3–3.8 cm; the balance should be of sizes up to 10.2 cm.

Cover

Cover for salmonids waiting to spawn or in the process of spawning can be provided by overhanging vegetation, undercut banks, submerged vegetation, submerged objects such as logs and rocks, floating debris, deep water, turbulence, and turbidity (Giger 1973). Cover can protect fish from disturbance and predation and also can provide shade. Some anadromous fish—chinook salmon and steelhead, for example—enter freshwater streams and arrive at the spawning grounds weeks or even months before they spawn. If the holding and spawning areas have little cover, such fish are vulnerable to disturbance and predation over a long period. Nearness of cover to spawning areas may be a factor in the selection of spawning sites by some species. In three studies, for example, brown trout selected spawning areas that were adjacent to undercut banks and overhanging vegetation (Johnson et al. 1966; Reiser and Wesche 1977; Witzel and MacCrimmon 1983).

Incubation

Although incubation is inextricably tied to spawning, the habitat requirements of embryos during incubation are different from those of spawning adults and thus warrant a separate discussion. When an adult fish selects a spawning site, it is also selecting the incubation environment. Successful incubation of embryos and emergence of fry, however, depend on many extragravel and intragravel chemical, physical, and hydraulic variables: DO, water temperature, biochemical oxygen demand (BOD) of material carried in the water and deposited in the redd, substrate size (including the amount of fine sediment), channel gradient, channel configuration, water depth (head) above the redd, surface water discharge and velocity, permeability and porosity of gravel in the redd and surrounding streambed, and velocity of water through the redd. Chapman (1988) reviewed the literature and discussed the primary factors involved in the incubation of salmonid embryos.

The relations between number of spawners, eggs deposited in redds, and juveniles that emerge from the redds take a variety of forms, depending on the species, life history, stream, and incubation conditions. The number of eggs deposited may increase linearly with the number of spawners as long as the amount of suitable spawning area is not limiting, but level off when suitable habitat becomes in short supply. Usually the number of fry emerging is directly related to the number of eggs deposited; if these two numbers are plotted against each other, differences in the linear slope between areas or streams probably reflect differing qualities of the incubation environment. Some species such as pink or chum salmon occasionally aggregate in extraordinarily large numbers on limited spawning grounds; if redds are superimposed and high egg densities result in oxygen depletion and poor incubation conditions, the number of emerging fry could be inversely related to the number of spawners.

Substrate

Streambed particles in the redd at the end of spawning, and organic and inorganic particles that settle into the redd and surrounding substrate during incubation, affect the rate of water interchange between the stream and the redd, the amount of oxygen available to the embryos, the concentration of embryo wastes, and the movement of alevins (especially when they are ready to emerge from the redd). During redd construction and spawning, the spawners displace streambed particles, deposit eggs and sperm in one or several pockets (Hawke 1978; Chapman 1988), and then cover the embryos with hydraulically displaced particles. During this process, fine sediments and organic materials in the stream substrate tend to be washed downstream; consequently the redd environment is as favorable for the embryos immediately after construction as it will ever be. Conditions for embryos within redds may change little or greatly during incubation depending on weather, streamflows, spawning by other fish in the same area at a later time, and fine sediments and organic materials transported in the stream.

Redds may be disturbed by late-spawning fish constructing redds, or by floods that displace the streambed containing the redd. Redds that remain intact during incubation may become less suitable for embryos if inorganic fine sediments (Figure 4.9) and organic materials are deposited in the interstitial spaces between the larger particles. The fine particles impede the movement of water and alevins in the redd, and the organic material (or the microbe community on it) consumes oxygen during decomposition; if the oxygen is consumed faster than the reduced intragravel water flow can replace it, the embryos or alevins will asphyxiate.

The redd construction process reduces the amounts of fine sediments and organic matter in the pockets where eggs are deposited (McNeil and Ahnell 1964; Ringler 1970; Everest et al. 1987a). If fine sediments are being transported in a stream either as bedload or in suspension, some of them are likely to be deposited in the redd. The amount of fine sediment deposited and the depth to which it intrudes depend on the size of substrate in the redd, flow conditions in the stream, and the amount and size of sediment being transported (Cooper 1965; Beschta and Jackson 1979). In general, intrusion into the redd increases as particle size decreases. When fine sediments are large relative to the spaces (pores) between gravel particles in the redd, they may only settle into the surface layer of the redd, where they can block other sediments from the deeper egg pockets (Hobbs 1937; Beschta and Jackson 1979; Chapman 1988). Under certain conditions, a layer of fine sediments may form above the egg pocket during redd construction or later. Such a layer can be beneficial (if it prevents deposition of fine organic or inorganic materials in the pocket), detrimental (if it impedes emergence of the alevins), or both. Deposition of fine sediments in redds may reduce survival more if it occurs early rather than late in the incubation period (Wickett 1954) because young embryos take up oxygen less efficiently than advanced embryos (Shaw and Maga 1943; Reiser and White 1988).

Depth of the egg pockets below the surface of the streambed varies with the size of fish and the size of streambed material. Large fish like chinook salmon may dig as deep as 43 cm below the streambed surface, but average pocket depths are in the 20- to 30-cm range (Hobbs 1937; Hawke 1978; Chapman 1988). The egg pockets of smaller fish tend to be closer to the streambed surface. Hawke (1978)

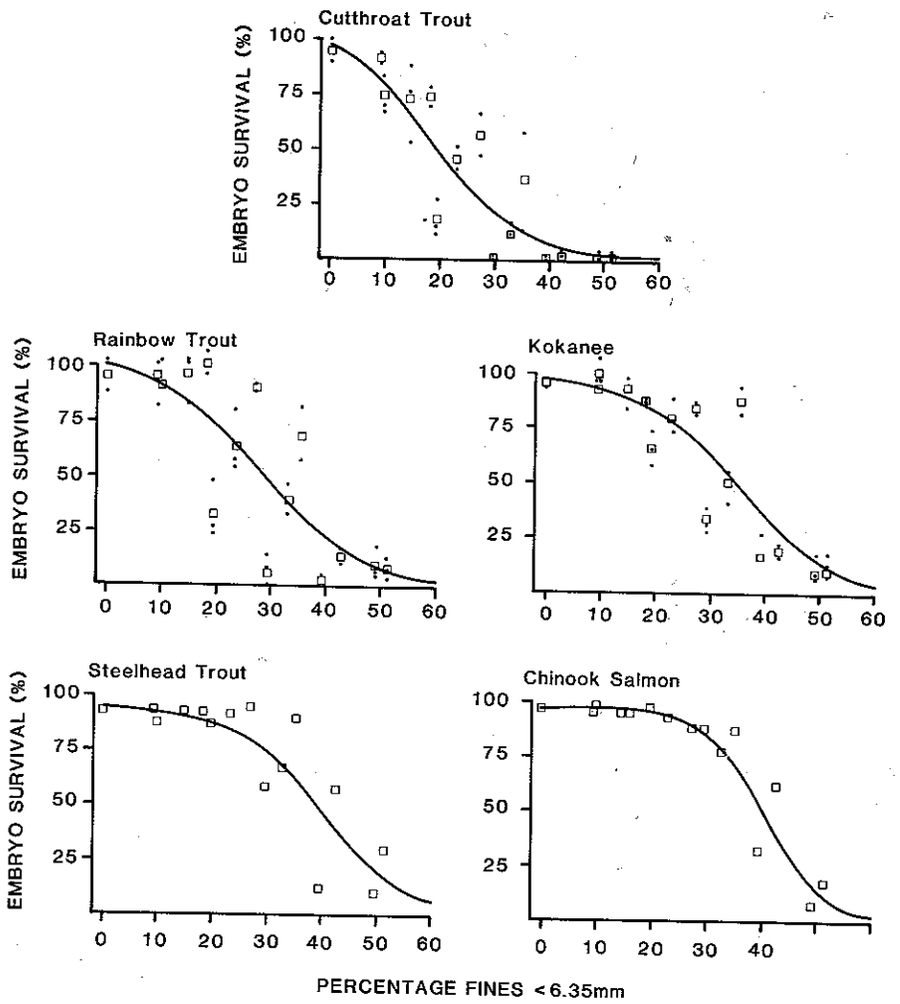


FIGURE 4.9.—Relation between embryo survival and percentage of substrate particles smaller than 6.35 mm for several salmonid species. Chinook salmon and steelhead data are from Tappel and Bjornn (1983); the others are from Irving and Bjornn (1984). Curves were fitted to the data by exponential equations. Squares indicate mean values and dots denote individual replicates.

and Everest et al. (1987a) found that the eggs tended to be near the bottom of the pocket and adjacent to the undisturbed streambed at the bottom of the redd.

During incubation, sufficient water must circulate through the redd as deep as the egg pocket to supply the embryos with oxygen and carry away waste products. Circulation of water through redds is a function of the porosity (ratio of pore space to total volume of redd) of the particles in the redd, hydraulic gradient at the redd, and temperature of the water. Porosity is highest in newly constructed redds and declines during the incubation period as the interstitial spaces acquire fine sediments. The hydraulic gradient through a redd is enhanced by the mounded tailspill created during construction (Figure 4.7). Permeability (ability of

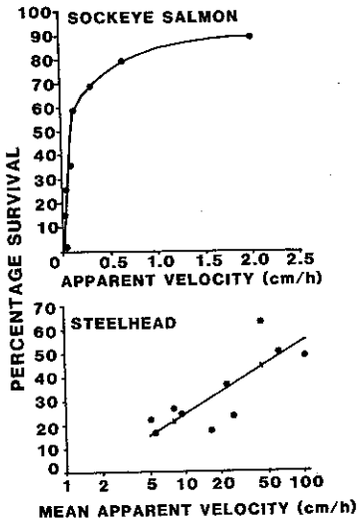


FIGURE 4.10.—Relations between rate of flow of water through a gravel bed and the survival of eyed sockeye salmon eggs (redrawn from Cooper 1965) and steelhead embryos (from Coble 1961).

particles in the redd to transmit water per unit of time) and apparent velocity (volume of water passing through a given area of redd per unit of time) are two commonly used measures of the suitability of a redd for successful incubation of salmonid embryos (Wickett 1954, 1958; Pollard 1955; Terhune 1958; Coble 1961; Vaux 1968). When the permeability and apparent velocity of water in the redd have been too low, reduced embryo survival has been measured for sockeye salmon (Pyper in Cooper 1965), steelhead (Coble 1961), chinook salmon (Gangmark and Bakkala 1960), pink salmon (Wickett 1958), and coho salmon and steelhead (Phillips and Campbell 1961). Survival of embryos decreases as apparent velocities (an indication of the amount of DO reaching the embryos) decrease (Figure 4.10).

Interchange of water between a stream and its streambed particles (Figure 4.7) has been repeatedly demonstrated (Stuart 1953; Sheridan 1962b; Vaux 1962; Cooper 1965). Sheridan (1962b) showed that groundwater in salmon spawning areas in southeast Alaska contains little oxygen, and that the oxygen content of intragravel water decreases with gravel depth. He concluded that the major source of oxygen in intragravel water was the interchange of that water with the surface flow. Cooper (1965) used dyes to demonstrate the influence of streambed configuration on intragravel flow patterns (Figure 4.11). Wells and McNeil (1970) attributed the high intragravel DO in Alaskan pink salmon spawning beds to high permeability of the substrate and to stream gradient. McNeil and Ahnell (1964) reported high permeabilities (>24,000 cm/h) in salmon spawning areas when sands and silts smaller than 0.84 mm made up less than 5% of the particles, and lower permeabilities (<1,300 cm/h) when they made up more than 15%. In sloughs of the Susitna River in central Alaska, Vining et al. (1985) noted that DO concentrations in intragravel water were consistently lower than in surface waters; in the main channel, however, differences in DO concentrations between surface and intragravel waters were slight.

Apparent velocity of water in redds may increase or decrease with the depth (and quantity) of the surface water (Reiser and White 1981a). Early evidence of

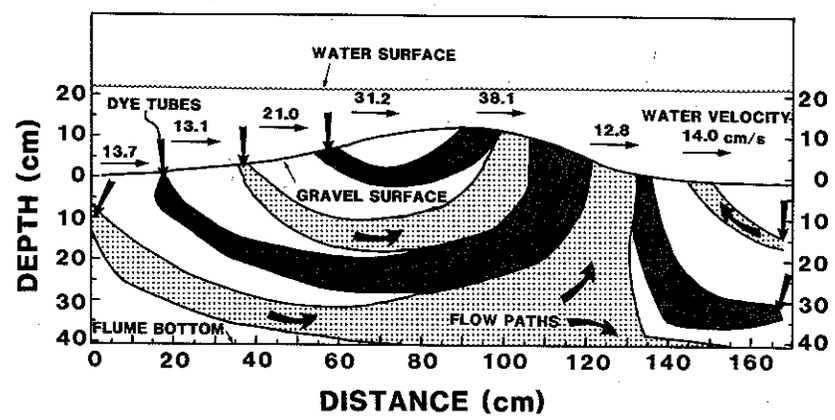


FIGURE 4.11.—Water flow through homogeneous gravel in a flume with a surface similar to that of a new salmon redd. Shadings indicate dispersions of injected dyes. (Redrawn from Cooper 1965.)

this was reported by Wickett (1954), who found a direct relation between gage-height readings in a stream and subsurface flow. Chapman et al. (1982) also observed decreases in apparent velocity when flow decreased from 1,982 to 1,019 m^3/s in the Columbia River.

Salmonid embryos have survived dewatering of redds when the dewatering occurred before hatching, temperatures were kept within a suitable range, fine sediment concentrations did not impede air flow, and humidity was maintained near 100% in the redds (Reiser and White 1981b, 1983; Becker et al. 1982; Stober et al. 1982; Becker and Neitzel 1985; Neitzel and Becker 1985). In a moist environment, unhatched embryos are able to get the oxygen they need from air in the redds (Figure 4.12). Several examples have been reported. Hobbs (1937) found that 80% of the brown trout eggs he observed were still alive in redds that had had no surface flow for 5 weeks, and Hardy (1963) found similar results in brown trout redds after 2–5 weeks of dewatering. Chinook salmon embryos survived in redds that had been dewatered for 3 weeks (Hawke 1978). Steelhead and chinook salmon embryos tolerated 1–5 weeks of dewatering (water flowed through the gravel 10 cm below the eggs) with no significant reduction in survival to hatching, alevin quality, growth rate, or quality of emerged fry (Reiser and White 1983). Survival through hatching of dewatered eggs of chinook, chum, pink, and coho salmon and steelhead was high during a study by Stober et al. (1982). Chinook salmon embryos survived 24 h of dewatering when relative humidity was kept at 100%, but all died if humidity was lowered to 90% (Neitzel and Becker 1985).

In streams with substantial groundwater inflows, DO concentrations and flow patterns of intragravel water may not relate in the usual way to substrate composition and permeability (Hansen 1975; Sowden and Power 1985). Upwelling areas are reportedly favored for spawning by chum, sockeye (Lister et al. 1980; Wilson 1984; Vining et al. 1985), and pink salmon (Krueger 1981). Embryo incubation is improved because upwelling reduces the chances that embryos will become dewatered or frozen, provides a stable incubation environment, and increases the water exchange rate past the embryos, thereby enhancing the

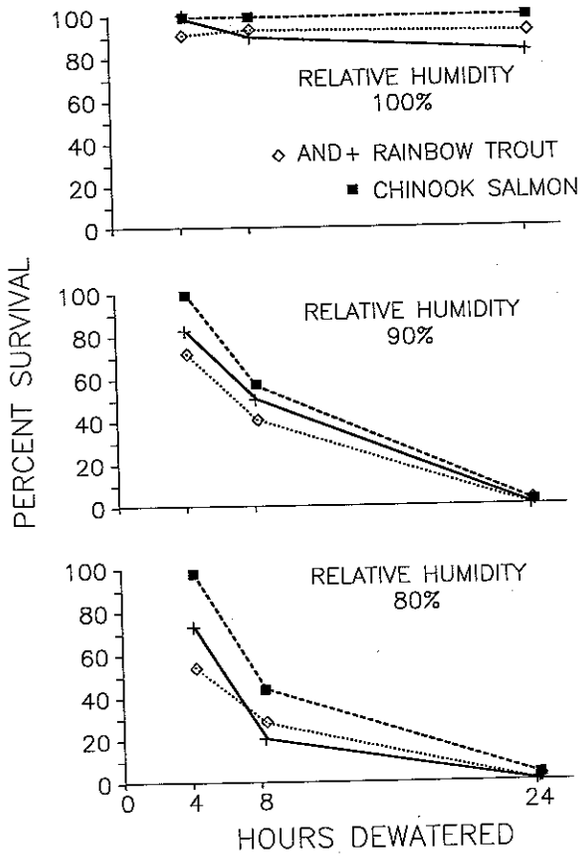


FIGURE 4.12.—Percent survival for dewatered embryos of rainbow trout and chinook salmon under conditions of reduced relative humidity. (From Becker et al. 1986.)

replenishment of DO (if the upwelling water has sufficient amounts) and removal of metabolic waste (Vining et al. 1985).

Egg densities in natural redds are relatively low compared to those in artificial culture facilities; they typically do not affect embryo and alevin survival unless the incubation environment is of marginal quality. If a large chinook salmon deposited 5,000 eggs in a single redd that covered 10 m^2, the density in that redd would be 500 eggs/m^2. However, the density in the actual egg pocket or pockets would be higher, perhaps as high as 2,000–5,000 eggs/m^2 if most of the eggs were deposited in one or two pockets. McNeil (1969) reported that production of pink salmon fry approached 500 fry/m^2 of spawning area when egg deposition was 2,000–3,000 eggs/m^2. In shallow matrix incubators, Kapuscinski and Lannan (1983) found that chum salmon could be incubated at densities as high as 43,000 eggs/m^2 without sacrificing quality of the fry produced.

Once incubation is complete and the alevins are ready to emerge from the redd and begin life in the stream, they must move from the egg pocket up through interstitial spaces to the surface of the streambed. Nunan and Noakes (1985) concluded that emergence of salmonid alevins was a response primarily to gravitational cues rather than to light or intragravel water flow. Emergence can be a problem if the interstitial spaces are not large enough to permit passage of the alevins. In laboratory studies, alevins of chinook salmon and steelhead (Bjornn

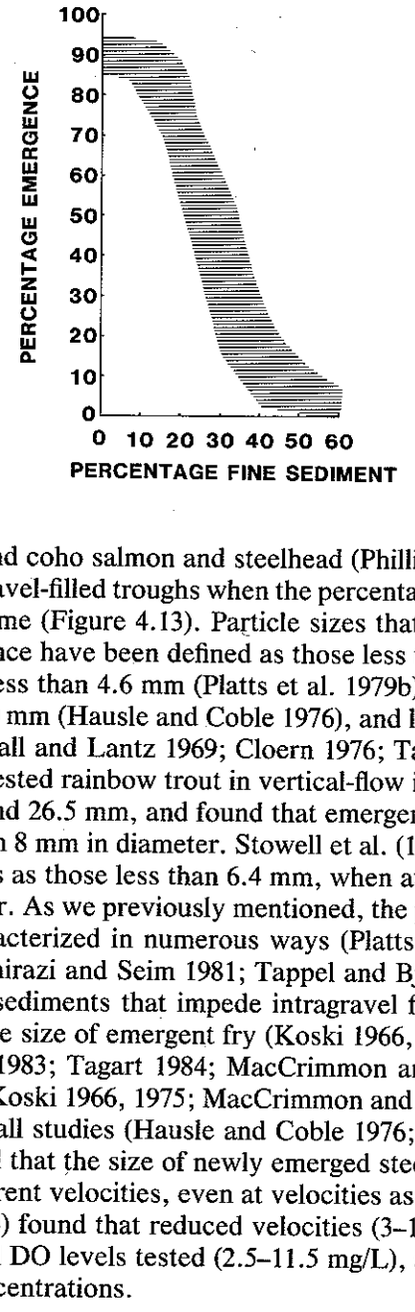


FIGURE 4.13.—Percentage emergence of swim-up fry placed in gravel–sand mixtures in relation to the percentage of sediment smaller than 2–6.4 mm in studies by Bjornn (1968), Phillips et al. (1975), Hausle and Coble (1976), and McCuddin (1977). The stipled area includes data from eight tests on brook trout, steelhead, and chinook and coho salmon.

1968) and coho salmon and steelhead (Phillips et al. 1975) had difficulty emerging from gravel-filled troughs when the percentage of fine sediments exceeded 30–40% by volume (Figure 4.13). Particle sizes that reduce embryo survival and impede emergence have been defined as those less than 6.4 mm (Bjornn 1968; McCuddin 1977), less than 4.6 mm (Platts et al. 1979b), less than 3.3 mm (Koski 1966), less than 2.0 mm (Hausle and Coble 1976), and less than 0.84 mm (McNeil and Ahnell 1964; Hall and Lantz 1969; Cloern 1976; Tagart 1976). Witzel and MacCrimmon (1981) tested rainbow trout in vertical-flow incubators filled with particles of 2, 4, 8, 16, and 26.5 mm, and found that emergence was impeded when particles were less than 8 mm in diameter. Stowell et al. (1983) defined the harmful size range of particles as those less than 6.4 mm, when at least 20% were less than 0.84 mm in diameter. As we previously mentioned, the particle size composition of redds can be characterized in numerous ways (Platts et al. 1979b; Lotspeich and Everest 1981; Shirazi and Seim 1981; Tappel and Bjornn 1983).

Fine sediments that impede intragravel flow and alevin movements may also affect the size of emergent fry (Koski 1966, 1981; Phillips et al. 1975; Tappel and Bjornn 1983; Tagart 1984; MacCrimmon and Gots 1986) and the time of emergence (Koski 1966, 1975; MacCrimmon and Gots 1986), but such effects were not seen in all studies (Hausle and Coble 1976; McCuddin 1977). Silver et al. (1963) reported that the size of newly emerged steelhead and chinook salmon depended on apparent velocities, even at velocities as high as 740–1,350 cm/h. Shumway et al. (1964) found that reduced velocities (3–10 cm/h) resulted in decreased size of fry at all DO levels tested (2.5–11.5 mg/L), and that hatching was delayed at low DO concentrations.

Dissolved Oxygen

Critical concentrations of DO that barely satisfy respiratory demands have been experimentally determined for salmonid embryos at different developmental stages (Table 4.6). Alderdice et al. (1958) found that embryos generally were most sensitive to hypoxial conditions during the early stages of development, when they had received 200–390 temperature units (a temperature unit is one degree

TABLE 4.6.—Critical levels of dissolved oxygen (DO; minimum that satisfies respiratory demand) for salmonid embryos at various stages of development.

Species	Stage of development	Age (d)	Critical DO (mg/L)
Chum salmon (Wickett 1954)	Pre-eyed	0	0.72
	Pre-eyed	5	1.67
	Pre-eyed	12	1.14
	Faintly eyed	85	3.70
Chum salmon (Alderdice et al. 1958)		<1	0.72[a]
		<1	1.67[a]
		4	1.14[a]
		12	3.96
		16	3.70[a]
		27	5.66
		35	6.60
	Nearly hatching	45	7.19
Atlantic salmon (Lindroth 1942)	Died		0.76
	Nearly hatching		5.80
	Hatching		10.00
Atlantic salmon (Hayes et al. 1951)	Eyed	25	3.1
	Hatching	50	7.1

[a] From Wickett (1954).

above zero for one day). Wickett (1954) showed that larval development during the early stage of development depended wholly on diffusion for satisfying oxygen requirements. Once the circulatory system is functional, oxygen transfer to the embryo becomes more efficient.

Embryos may survive when DO concentrations are below saturation (but above the critical level), but their development often deviates from normal. Doudoroff and Warren (1965) found that when DO was below saturation throughout development, embryos were smaller than usual and that hatching was either delayed or premature. Alderdice et al. (1958) showed that low DO concentrations in the early stages of development of chum salmon delayed hatching and increased

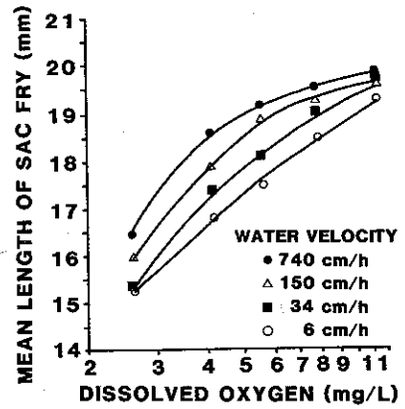


FIGURE 4.14.—Relation between mean length of steelhead sac fry when hatched and dissolved oxygen concentration at which the embryos were incubated, for several water velocities during incubation and a temperature of 9.5°C. (From Silver et al. 1963.)

TABLE 4.7.—Characteristics of sockeye salmon alevins at hatching after embryos were incubated in water at three oxygen concentrations. (From Brannon 1965.)

Characteristic	O_2 concentration (mg/L)		
	3.0	6.0	11.9
Temperature units[a] to 50% hatching	670	670	670
Length (mm)	16.3	18.6	19.7
Yolk-sac shape	Spherical	Longitudinal	Longitudinal
Pigmentation	Lightly on head	On head and starting on back	On head and back
Visibility of the dorsal and anal fin rays	Not visible	Distinguishable	Readily visible
Caudal fin development	Forming	Forming	Well advanced

[a] Degree-days above 0°C.

the incidence of morphological anomalies. Silver et al. (1963) reported that newly hatched steelhead and chinook salmon alevins were smaller and weaker when they had been incubated as embryos at low and intermediate DO concentrations than when they were incubated at higher concentrations (Figure 4.14). Shumway et al. (1964) found that reduced DO lengthened the incubation period of coho salmon embryos, which hatched into smaller alevins than normal. Brannon (1965) found differences in length and other anatomical features among newly hatched sockeye salmon fry that had developed at three DO levels (Table 4.7); however, weights of the emergent fry were similar among treatment groups.

In field studies, survival of steelhead embryos (Coble 1961) and coho salmon embryos (Phillips and Campbell 1961) was positively correlated with intragravel DO in redds (Figure 4.15). Phillips and Campbell (1961) concluded that intragravel DO must average 8 mg/L for embryos and alevins to survive well. Stober et al. (1982) and Fast and Stober (1984) reported that newly hatched alevins in the gravel are able to detect oxygen gradients and migrate to areas containing more DO.

Intragravel DO concentrations are functions of many factors: water temperature, surface and intragravel water interchange, apparent velocity of water flow in

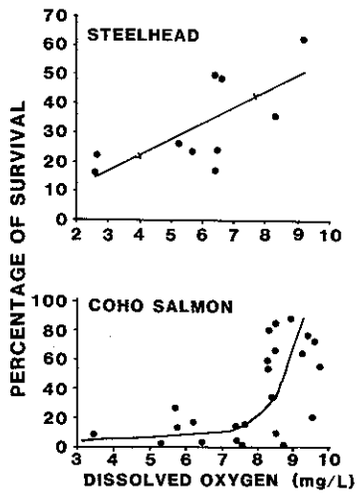


FIGURE 4.15.—Relation between dissolved oxygen concentration and survival of steelhead embryos (from Coble 1961) and coho salmon embryos (Phillips and Campbell 1961) in natural redds.

the redd, permeability of the substrate, and oxygen demand of organic material in the redd, among others. Hall and Lantz (1969), Ringler and Hall (1975), and Moring (1975a) reported that intragravel DO concentrations were reduced in some Oregon streams after adjacent areas had been logged. They attributed such reductions to elevated stream temperatures after removal of the riparian canopy and to increased concentrations of fine sediment that reduced substrate permeability and apparent velocity. Tagart (1976) and Reiser and White (1981b) found direct relations between DO and permeability and inverse relations between DO and percentage of fines in stream substrates. Coble (1961) generalized his experience with this subject by stating that when apparent water velocities are low, DO is low; when they are high, DO is usually high.

All streams transport particulate and dissolved organic matter. The amount transported and the timing of transport varies with the productivity of the stream, the source and type of organic matter, and streamflow (Fisher and Likens 1973; Hobbie and Likens 1973; Liaw and MacCrimmon 1977; Naiman and Sibert 1978; Bilby and Likens 1979; Dance et al. 1979; Naiman and Sedell 1979). Organic matter that settles into redds can reduce the DO concentration as it decomposes; the extent of oxygen depletion depends on the amount and type of organic debris (Hargrave 1972) and the chemical, physical, and hydraulic characteristics (DO content, temperature, permeability, and reaeration capability) of the stream and its substrate. Excessive recruitment of organic material to a stream can result in reduced DO concentrations and intragravel water flow, leading to reduced survival of incubating embryos (Olssen and Persson 1986).

Although DO concentrations required for successful incubation depend on both species and developmental stage, we recommend that concentrations should be at or near saturation, and that temporary reductions should drop to no lower than 5.0 mg/L, for anadromous salmonids. Apparent velocities of water flowing through redds also must be maintained at acceptable rates because high DO alone does not guarantee optimum embryo development. In redds with similar DO concentrations, but different apparent velocities, embryonic development may be better in the redds with the higher rate of water exchange (Coble 1961). Mathematical models have been developed to estimate apparent velocity in redds (Bovee and Cochnauer 1977) and to assess transfer of DO between the stream and substrate (Chevalier and Carson 1985), concentrations of intragravel DO (Chevalier and Murphy 1985), salmonid egg respiration (Carson 1985), and fry emergence (Miller 1985).

Temperature

Water temperature during incubation affects the rate of embryo and alevin development and the capacity of water for dissolved oxygen, and (beyond certain limits) survival of the young fish. There are upper and lower temperature limits (thresholds) for successful incubation of salmonid eggs (Table 4.3). In general, the higher the temperature (within the acceptable range), the faster the rate of development and the shorter the incubation period and time to emergence. The amount of time required for embryos to hatch and for alevins to emerge from redds varies by species and perhaps by location. For example, time to 50% hatch for Pacific salmon species ranges from 115 to 150 d at 4°C and from 35 to 60 d at 12°C; coho salmon require the least time and sockeye salmon the most (Alderdice

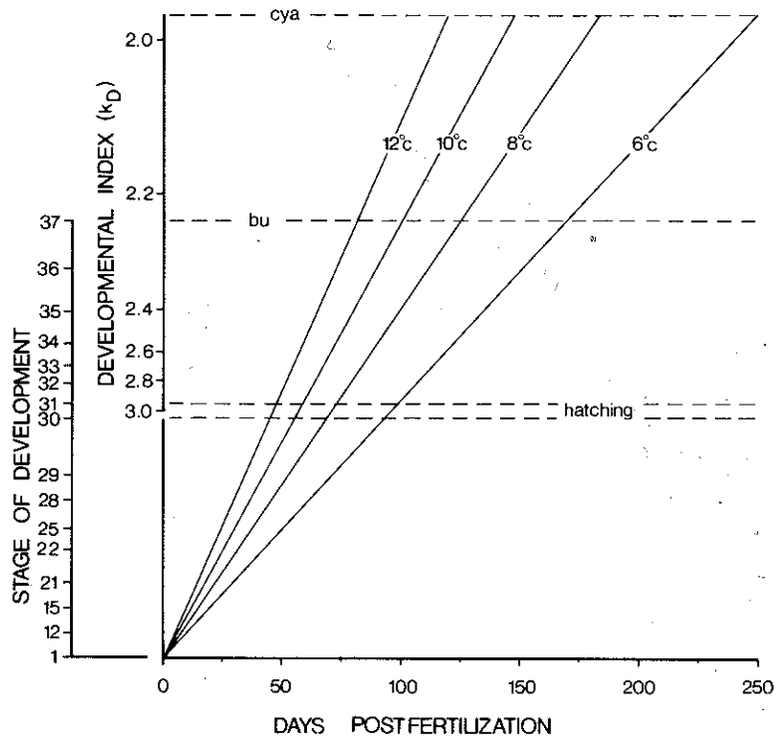


FIGURE 4.16.—Effect of temperature on the development of chinook salmon according to Vernier's (1969) stages of development and Bams's (1970) developmental index (k_D) in a graph from Heming (1982). In the graph, bu = button-up stage of development and cya = complete yolk absorption.

and Velsen 1978; Tang et al. 1987; Velsen 1987). Steelhead and rainbow trout require about 85 d at 4°C and 26 d at 12°C to reach 50% hatch. Heming (1982) graphed stage of development against time (Figure 4.16) for chinook salmon raised experimentally at several temperatures; from these graphs, he estimated emergence at 192 d at 6°C and 85 d at 12°C, about twice the time to 50% hatch. In field studies on the Columbia River, Chapman et al. (1982) found that Heming's curves were reasonable predictors of the time chinook salmon fry emerge. Time to hatch for lake trout is similar to that of chinook salmon, 80–90 d at 6°C (Dwyer 1987).

In many streams in which salmonids spawn, winter temperatures are lower than the 4.4°C minimum recommended for incubation in Table 4.3, but the eggs develop normally because spawning and initial embryo development occur when temperatures are within the suitable range. Combs and Burrows (1957) and Combs (1965) reported that pink and chinook salmon embryos could tolerate long periods of low temperature if the initial temperature was above 6.0°C and embryogenesis had proceeded to a critical developmental stage before the onset of lower water temperatures. Combs and Burrows (1957) believed that salmon produced from eggs deposited in water colder than 4.5°C would be less viable than fish produced from eggs spawned in warmer water. Wangaard and Burger (1983) reported 3.4°C as the temperature below which some newly spawned chum and pink salmon

embryos would be killed. Bailey and Evans (1971) defined the lower threshold temperature for pink salmon embryos as 4.5°C. In a summarization of available data, Velsen (1987) reported high mortalities for all Pacific salmon and steelhead when water temperatures were lower than 2–3°C after fertilization. Jungwirth and Winkler (1984) reported that embryos of fall-spawning fishes develop more slowly at any temperature, and have lower upper lethal incubation temperatures, than progeny of spring spawners. Incubation temperatures can also affect the size of newly hatched alevins. When Beacham and Murray (1985) incubated chum salmon eggs at temperatures of 4, 8, and 12°C, the newly hatched alevins incubated at 4°C were the longest, and those at 12°C were the heaviest, but there was no difference in size at emergence. Reiser and White (1981b) observed similar early differences among chinook salmon, which then reached equivalent sizes after 57 d of rearing.

Intragravel water temperatures are influenced by temperatures of the surface water, the thermal mass of the substrate, and the interchange rate of surface and intragravel water. Ringler and Hall (1975) observed that temperatures of intragravel water reached diurnal maxima 2–6 h after those of surface waters in an Oregon stream. Chapman et al. (1982) observed temperature lags of 2–8 h between surface and intragravel waters. There are seasonal as well as daily differences: intragravel water temperatures often are lower than surface water temperatures during summer, and higher during winter (Shepherd et al. 1986a). When salmonids spawn in areas close to groundwater inflows (Hansen 1975; Witzel and MacCrimmon 1983; Wilson 1984; Vining et al. 1985), embryos experience reduced extremes in water temperatures than they would otherwise.

Incubating embryos and alevins can be killed when frazil or anchor ice forms in streams and reduces water interchange between the stream and the redd. Anchor ice normally forms in shallow water typical of spawning areas and may completely blanket the substrate. Ice dams may impede flow or even dewater spawning areas. When such dams melt, the released water may, floodlike, displace the streambed and scour the redds. In an experiment by Reiser and Wesche (1977), eggs placed in plastic-mesh boxes 15 cm below the surface of the streambed completely froze even though the stream above was more than 13 cm deep. Anchor ice had formed at least twice during the incubation period. Neave (1953) and McNeil (1966b) also reported that embryo survival was poor at freezing temperatures.

Rearing in Fresh Water

The abundance of juvenile salmon, trout, and char in streams is a function of many factors, including abundance of newly emerged fry, quantity and quality of suitable habitat, abundance and composition of food, and interactions with other fish, birds, and mammals. Fausch et al. (1988) reviewed many of the models developed in recent years to predict the abundance of fish in streams from habitat variables. We next discuss variables of habitat quantity and quality, and where possible, list the preferences of juvenile salmonids.

The abundance of older fish generally increases as the abundance of juveniles increases until an upper limit (here termed carrying capacity) is reached. We believe that the relation between the seeding level—the number of young fish emplaced in a stream by adult fish or humans—and the abundance of older fish is

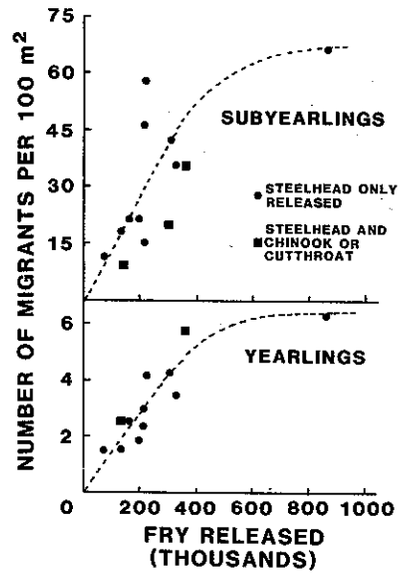


FIGURE 4.17.—Relation between the number of steelhead fry released in Big Springs Creek, Idaho, and the number of subyearling and yearling rainbow trout and steelhead per 100 m^2 that migrated from the stream. Each point represents one of the 1962–1974 year-classes (1962–1973 for yearlings); curves were fitted by inspection. (From Bjornn 1978.)

asymptotic for most salmonids that spend an extended period in streams. At relatively low seeding levels, environmental conditions that set the carrying capacity of a stream for a given age group of fish will place little constraint on the abundance of juveniles and older fish. As spawner abundance (or stocking) approaches that needed for full seeding, the biotic or physical factors that set the carrying capacity come into full play. Habitat variables we discuss here may set the carrying capacity of streams for salmonid fishes, but interactions among many of the relevant physical and biotic variables have not been well defined. In addition, variables that are important in one stream or season may be relatively unimportant in another.

Changes in spawner abundance and variation in the success of incubation and emergence affect the number of young fish entering a stream. Changes in the abundance of newly emerged fry can result in large or insignificant changes in abundance of older fish, depending on the shape of the reproduction curve and actual fry abundance. In two productive Idaho streams, the abundance of older steelhead was primarily a function of the number of newly emerged juveniles placed in the stream at seeding rates up to about 6 fish/m^2 (Bjornn 1978) (Figure 4.17). When steelhead were stocked at a rate of 12/m^2 in Big Springs Creek (right-most point in Figure 4.17), no more subyearlings or yearlings were produced than when 6/m^2 were stocked—evidence that the carrying capacity had been reached. In the Lemhi River, about the same number of steelhead smolts were produced (75,000–80,000) from releases of 2.5 and 4.6 million newly emerged juveniles—additional evidence that carrying capacity had been achieved. The carrying capacity for chinook salmon in the Lemhi River was not reached during 12 years of study in which natural egg-deposition rates ranged from 2 to 8/m^2 (Figure 4.18).

In less-productive Idaho streams, seeding rate (abundance of spawners) was the main factor regulating the abundance of juvenile steelhead (Figure 4.19) and chinook salmon when spawner abundance was relatively low. In Marsh Creek,

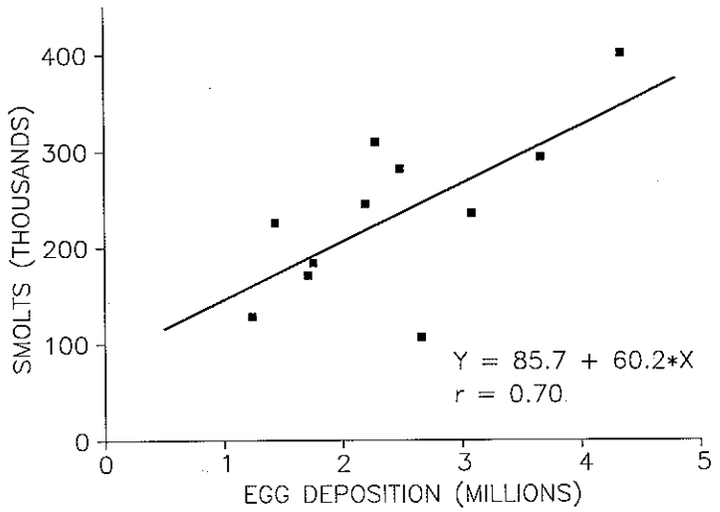


FIGURE 4.18.—Egg deposition *(X)* by adult chinook salmon in the upper Lemhi River, Idaho, and number of smolt-sized fish *(Y)* that later migrated past the Lemhi River weir during fall, winter, and spring, 1963–1973. (From Bjornn 1978.)

one of the relatively unproductive streams, the density of juvenile chinook salmon, monitored irregularly over 12 years, was related to spawner abundance over a nearly 20-fold range (Figure 4.20). Sekulich (1980) presented evidence that the summer carrying capacity for naturally produced salmon in the relatively unproductive streams was 2–3 g/m^2, lower than the carrying capacity of at least 13 g/m^2 in the relatively productive Lemhi River (Bjornn 1978). In Pacific coast streams, the biomass of coho salmon averaged 2–3 g/m^2 in several studies (Cederholm and Reid 1987).

The number of chinook salmon smolts produced in two Lake Michigan tributaries with alternating pool–riffle habitats was independent of the threefold difference in spawner densities that occurred in 2 years of study (Carl 1984). Even at their lower density, spawners apparently seeded the rearing area fully (about 80 spawners per hectare, 0.7–2.9 newly emerged fish per square meter).

For a given level of seeding, what factors in the stream environment regulate abundance or set the carrying capacity for juvenile salmonids? Density-independent environmental factors (amount of suitable habitat, quality of cover, productivity of the stream, and certain types of predation) set an upper limit on the abundance of juveniles, and the population is held to that level by interactions that function in a density-dependent fashion (competition and some types of predation). Carrying capacity, and hence fish production, may vary yearly if controlling habitat components, such as streamflow, vary widely from year to year at critical periods such as late summer (Smoker 1955). The carrying capacity of a stream may also vary with the season, differing, for example, between winter and summer (Bjornn 1978), and it may differ for the various life stages of fish.

Environmental factors can affect the distribution and abundance of juvenile salmonids throughout a stream or drainage or within specific segments of streams.

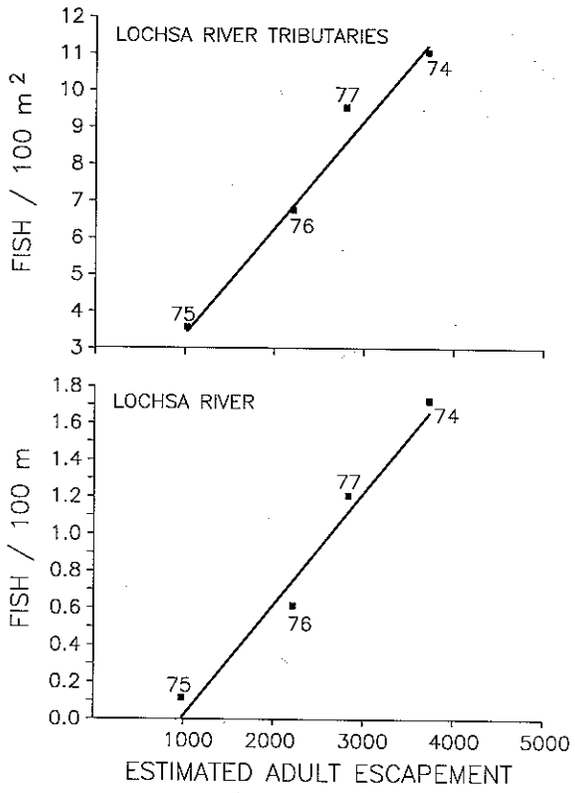


FIGURE 4.19.—Observed density of age-1 steelhead in relation to estimated number of adults returning to the Lochsa River and its tributaries, Idaho, 1974–1977. (Redrawn from Mabbott 1982.)

Temperature, productivity, suitable space, and water quality (turbidity, DO, etc.) are examples of variables that regulate the general distribution and abundance of fish within a stream or drainage. Factors to which fish respond at specific locations in a stream are velocity, depth, substrate, cover, predators, and competitors. Fish often spawn in limited parts of a drainage (sometimes in ephemeral streams), but

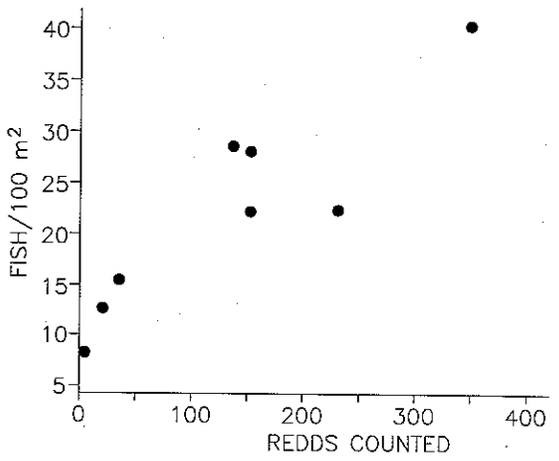


FIGURE 4.20.—Relation between chinook salmon redds counted and density of age-0 juveniles the following summer in an Idaho stream. (Authors' original data.)

the juveniles spread out and occupy most of the areas that are suitable and accessible (Everest 1973; Leider et al. 1986).

All of the general factors must be within suitable ranges for salmonids during the time they use a stream segment; otherwise, no fish will be present and there will be no concern about site-specific factors. Rarely, if ever, are most factors optimum for salmonid production. Often some factors may be near optimum while others are suboptimum but still in a suitable range.

Temperature

Salmonids are coldwater fish with definite temperature requirements during rearing. Water temperature influences the metabolism, behavior, and mortality of fish and the other organisms in their environment (Mihursky and Kennedy 1967). Although fish may survive at temperatures near the extremes of the suitable range, growth is reduced at low temperatures—because all metabolic processes are slowed—and at high temperatures—because most or all food must be used for maintenance. Many salmonids change behavior with increases or decreases in temperature.

Normal water temperatures in salmonid streams vary daily, seasonally, annually, and spatially. Humans have altered temperature patterns by changing riparian zone vegetation, diverting water, building reservoirs, and discharging hot water from power plants. Alterations of natural light and temperature patterns in streams can be beneficial or detrimental, depending on the situation, but the consequences of marked changes in the temperature regime of a stream are not fully understood. Small streams in dense forests of the Pacific Northwest, for example, might be too cold in summer for maximum growth of salmonids (Chapman and Knudsen 1980), but warming the stream by altering the riparian vegetation (Gray and Edington 1969; Narver 1972a; Moring 1975a; Moring and Lantz 1975; Murphy et al. 1981; Johnson et al. 1986; Murphy et al. 1986; Beschta et al. 1987) might not enhance growth unless food abundance can satisfy the increase in fish metabolism and other needs of the fish are met (Brett et al. 1969; Hughes and Davis 1986; Hartman et al. 1987; Holtby 1988a). Care must be taken to avoid unwanted warming of downstream waters and excessive loss of cover (both overhead bank and instream) that may be important in winter as well as in summer (Murphy et al. 1986). In many large streams, temperatures become too warm for salmonids in summer for a variety of reasons, including excessive exposure to the sun.

Temperatures that can be tolerated by fishes have been defined and determined in two ways (Brett 1952; Becker and Genoway 1979): slow heating of fish (to reveal the critical thermal maximum, CTM), and abrupt transfer of fish between waters of different temperature (to show the incipient lethal temperature, ILT). In general, upper lethal temperatures determined by the CTM procedure tend to be higher than those established with the ILT technique. The upper ILT for anadromous Pacific salmon, Atlantic salmon, trout, and char range from about 23 to 29°C, depending on species and acclimation temperature (selected examples are in Table 4.8). Half of the upper lethal values presented in Table 4.8 were taken from Brett (1952), who acclimated fish at 20°C and used 50% mortality at 1,000 min as the end point. Lee and Rinne (1980) reported CTM values of 29–30°C for hatchery stocks of rainbow, brown, and brook trout stocked in Arizona and two

TABLE 4.8.—Lower lethal, upper lethal, and preferred temperatures (°C) for selected species of salmon, trout, and char based on techniques to determine incipient lethal temperatures (ILT) and critical thermal maxima (CTM).

Species	Lethal temperature (°C)		Preferred temperature (°C)	Source	Technique
	Lower lethal[a]	Upper lethal[b]			
Chinook salmon	0.8	26.2	12–14	Brett (1952)	ILT
Coho salmon	1.7	26.0	12–14	Brett (1952)	ILT
		28.8[c]		Becker and Genoway (1979)	CTM
Sockeye salmon	3.1	25.8	12–14	Brett (1952)	ILT
Chum salmon	0.5	25.4	12–14	Brett (1952)	ILT
Steelhead	0.0	23.9	10–13	Bell (1986)	
Rainbow trout		29.4		Lee and Rinne (1980)	CTM
		25.0		Charlon et al. (1970)	ILT
Brown trout		29.9		Lee and Rinne (1980)	CTM
		26.7		Brett (1952)	ILT
Gila trout		29.6		Lee and Rinne (1980)	CTM
Apache trout		29.4		Lee and Rinne (1980)	CTM
Brook trout		29.8		Lee and Rinne (1980)	CTM
		25.8		Brett (1952)	ILT
			14–16	Graham (1949)	
Cutthroat trout	0.6	22.8		Bell (1986)	
Atlantic salmon		27.1		Brett (1952)	ILT
		27.8		Garside (1973)	ILT
Lake trout		25.0		Brett (1952)	ILT

[a] Acclimation temperature was 10°C; no mortality occurred in 5,500 min.
[b] Acclimation temperature was 20°C unless noted otherwise; 50% mortality occurred in 1,000 min.
[c] Acclimation temperature was 15°C.

native trouts (Gila trout and Apache trout) when these fish were acclimated at 20°C and subjected to a temperature change rate of 1.2°C/h. Although some salmonids can survive at relatively high temperatures, most are placed in life-threatening conditions when temperatures exceed 23–25°C, and they usually try to avoid such temperatures by moving to other areas.

Lower lethal temperatures for salmonids depend somewhat on previous acclimation (Brett 1952) but they probably are no lower than −0.1°C (Brett and Alderdice 1958). Temperatures in the range of 1 to 4°C can be lethal if fish acclimated in warmer water are transferred abruptly into the cold water. Under natural conditions, fish are not subjected to cold water (<4°C) without prior acclimation in gradually decreasing temperatures, and thus lower lethal temperatures for most species are near 0°C.

Daily summer temperatures can fluctuate more than 15°C in small streams with flows less than 1 m^3/s and little or no shade (Meehan 1970; Bjornn 1978).

Temperatures can increase rapidly in a short distance under direct sunlight: 6°C in 1,000 m within a stream flowing at about 1.4 m^3/s in central Idaho, for example (Bjornn et al. 1968). As stream size and water mass increase, daily temperatures of streams fluctuate less and tend to reflect the local climate near the stream.

Many populations of native salmonids respond to natural temperature patterns in streams by moving upstream or downstream when water temperatures become unsuitable. Fish may use a section of stream during one season of the year, but move to other sections at other seasons because temperatures become unsuitable. Salmonids may not always avoid unsuitable temperatures, however, especially if the temperatures change rapidly and are not part of the normal pattern in which the fish evolved. Munson et al. (1980) found that rainbow trout accustomed to feeding in a certain location continued to enter the area after temperatures had been changed to a lethal level.

In small streams where daily maximum temperatures approach upper incipient lethal values, salmonids can thrive if the temperature is high for only a short time and then declines well into the optimum range. In an Idaho stream with daily maximum temperatures up to 24°C that lasted less than 1 h and minimums of 8–12°C, juvenile chinook salmon and steelhead maintained high densities and grew normally (Bjornn 1978). In larger Idaho streams where summer maximum temperatures were 24–26°C, but the minimums were relatively high (15–16°C), most young salmon and trout moved upstream or into tributaries where temperatures were lower (Mabbott 1982).

As water temperatures in temperate-zone streams decline in autumn, salmonids change behavior from mostly feeding and defending territory to hiding and schooling. The winter behavior patterns appear to us to be motivated by security. Fish that were curious and easily approached by divers in summer become wary and often dart from view in winter. Winter water temperatures in streams can range from freezing to relatively moderate, according to geographic and groundwater influences. Temperatures in coastal streams often are moderated by maritime climates. Inland, streams can become filled with flow ice, anchor ice, and ice jams during extreme cold spells. The temperature at which the change in behavior occurs apparently varies by species. Chapman and Bjornn (1969) reported that most of the steelhead and chinook salmon juveniles they tested in winter were visible above the substrate at 6°C but hid at 4°C (Figure 4.21). In a British Columbia stream, juvenile coho salmon and steelhead began shifting to winter positions at about 7°C (Bustard and Narver 1975a). Gibson (1978) found that Atlantic salmon began entering the interstitial spaces of rubble substrate in autumn when water temperatures dropped to 10°C, and most had disappeared at 9°C.

The response of salmonids to the lower temperatures that occur in autumn and winter in temperate streams can vary by species and size of fish. Small fish (<15–20 cm) tend to hide in interstitial spaces in the substrate of streams, or in other forms of cover if available, and may move to shallower water (Bustard and Narver 1975a; Gibson 1978), whereas larger fish may join together in schools and move long distances to find suitable winter habitat. In the Lemhi River drainage, Idaho, a large fraction of the young chinook salmon and steelhead moved downstream from rearing areas after their first summer (Bjornn 1971). The chinook salmon moved down into the Salmon River and even the Snake River

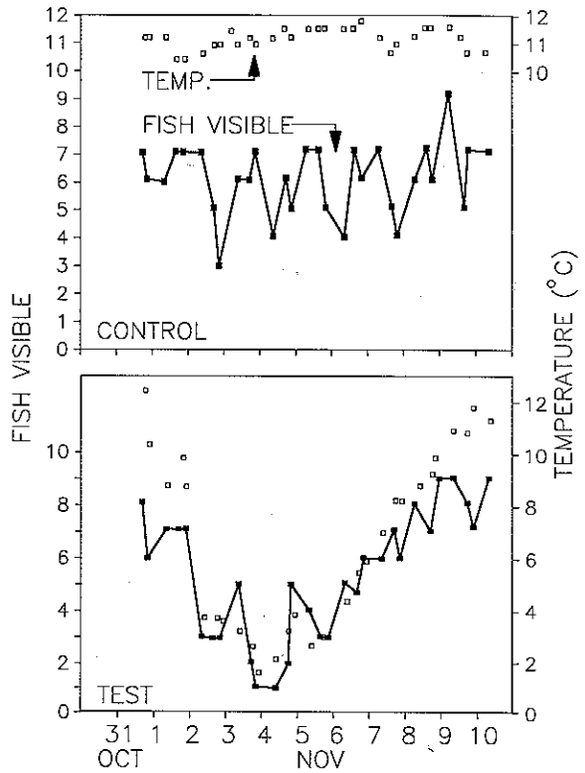


FIGURE 4.21.—Water temperature and number of age-0 steelhead visible above the substrate in test and control vats. (From Chapman and Bjornn 1969.)

(50–200 km) to spend the winter before continuing to the ocean as smolts the following spring. The steelhead moved downstream out of a tributary with a high summer carrying capacity (at least 12 g/m^2) but a lower winter carrying capacity, and spent the winter, the next summer, and the following winter in the larger stream before going to the ocean the following spring. Both the chinook salmon and steelhead moved downstream in response to low winter temperatures and a lack of winter cover. Fish migrating downstream in the fall ceased moving when placed in channels with large rock piles (which contained interstitial spaces used in winter) but continued moving downstream when placed in channels without the rock piles (Bjornn and Morrill 1972). In contrast, few juvenile cutthroat trout moved downstream in autumn in tributaries of other Idaho streams where densities were lower (2.1 g/m^2) and adequate amounts of suitable winter cover were apparently present (Mauser 1972). On sunny autumn days, the cutthroat trout could be seen in the stream in the afternoon when temperatures approached the daily high (8–10°C), but were not visible in the morning when temperatures were low (3–5°C).

Larger fish that may not be able to use voids in the substrate to hide in winter have been observed joining together in large schools (600 fish) and in some cases moving long distances in fall and spring. In the Coeur d'Alene River of Idaho, Lewynsky (1986) counted fish along transects throughout the summer, fall, and winter; in winter, larger (>20 cm) cutthroat trout moved from dispersed summer feeding stations throughout the river to a few large pools, where they became

much more wary and difficult to approach. The extent of seasonal movements of fish in response to temperature is illustrated by migrations of cutthroat and bull trout more than 100 km downstream in autumn and back upstream in spring and early summer in the Salmon River, Idaho (Bjornn and Mallet 1964). Winter temperatures and ice conditions apparently were unsuitable in the upper portions of the Middle Fork drainage and most of the fish larger than 15 cm moved. Temperatures in the main-stem rivers became marginal in summer for salmonids.

Temperature is one of the factors that contribute to quality of habitat for fish. If temperature is in a tolerable range for the fish, the question of optimum temperature becomes pertinent. Optimum temperature could be defined in relation to a variety of population or individual variables, including temperature preference, growth, efficiency of converting food to tissue, standing crops, and swimming performance. When Brett (1952) placed five species of Pacific salmon in a vertical temperature gradient, they all tended to congregate in the 12–14°C stratum.

Optimum temperatures, measured in terms of fish growth rate and food conversion efficiency, vary with the amount of food available. Brett et al. (1969) reported that growth of yearling sockeye salmon was highest at about 5°C when the daily ration (percent of body weight) available was 1.5%, but shifted to about 15°C when the ration was 6%. At highest temperatures, the growth rate declined regardless of food abundance. Food conversion efficiency peaked at 8–11°C (Brett et al. 1969)—lower than the 15°C associated with maximum growth, optimum metabolic scope for activity, greatest tolerance of oxygen debt, and maximum sustained swimming speed (Brett 1964). After tests with Atlantic salmon, Dwyer and Piper (1987) reported that maximum growth with unlimited food was attained at 16–19°C, but that growth efficiency was highest at 10–16°C.

Similar relations—with variations in the optimum temperature or temperature range—probably exist for other species. The optimum temperature for brook trout, for example, appears to be 14–16°C. Graham (1949), as reported in Mihursky and Kennedy (1967), listed 14–16°C as the temperature preferendum for brook trout, and Beamish (1964) gave 15°C as the temperature for maximum spontaneous activity. Dwyer et al. (1983) reported that brook trout grew most efficiently at 10 and 13°C. Jensen and Johnsen (1986) presented evidence that stocks of fish may be able to adapt to temperatures that might otherwise make their existence unlikely.

Brett et al. (1958) reported that the optimum temperature for sustained swimming was 15°C for sockeye and 20°C for coho salmon (Figure 4.22), and that maximum sustained swimming speeds at these temperatures were 35 and 30 cm/s, respectively. Sustained swimming performance was reduced to about 12 cm/s for sockeye salmon and to 6 cm/s for coho salmon at temperatures near 0°C. Davis et al. (1963) also found that the maximum sustained swimming speed of underyearling coho salmon was higher at 20°C than at 15 or 10°C. In a study of the critical swimming speeds of yearling rainbow trout as a measure of temperature preference, Schneider and Connors (1982) found no significant differences at 10, 15, or 20°C, but swimming performance was reduced at 25°C. The 25°C test temperature was 2°C less than the ILT measured for rainbow trout by Charlon et al. (1970).

The effect of water temperature on fish behavior and the regulation of densities in streams is not well understood, but there is some evidence that densities or

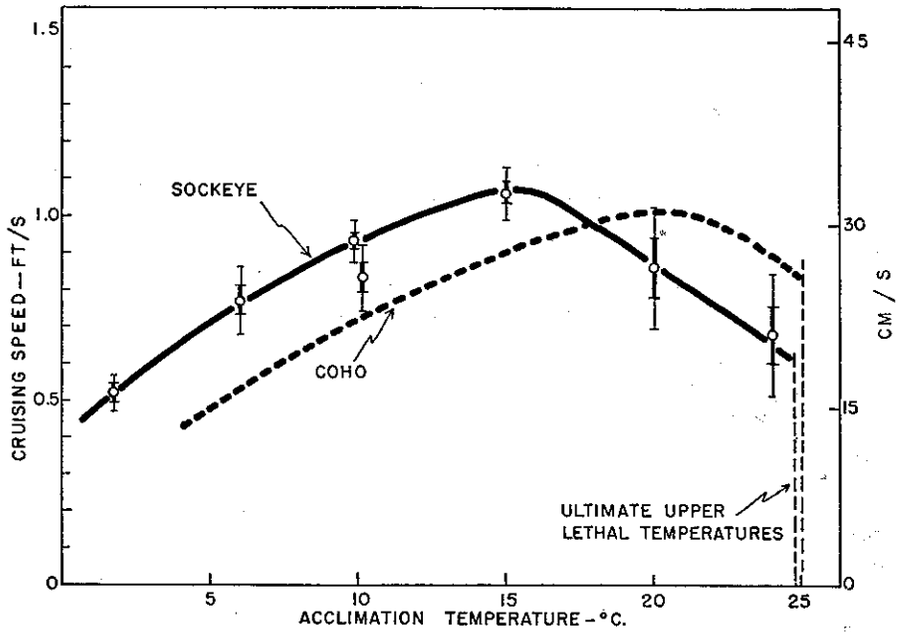


FIGURE 4.22.—Variation in cruising speed among temperature-acclimated underyearling sockeye and coho salmon, adjusted to common mean lengths of 6.9 cm and 5.4 cm, respectively. The fish were cultured under similar conditions and were 4 to 6 months of age. The sockeye salmon data are means (circles), standard errors (heavy vertical bars), and standard deviations. (From Brett et al. 1958.)

even production of fish may be less at high (but suitable) temperatures than at lower ones. In laboratory stream studies, Hahn (1977) found that twice as many steelhead fry remained in channels with daily temperature fluctuations of 8–19°C or a constant temperature of 13.5°C than in a channel held at a constant 18.5°C. At constant 8.5°C, the density of fish was twice that found in channels held at 13.5°C. Hughes and Davis (1986), who studied coho salmon and steelhead in laboratory streams, concluded that a moderate (4°C) increase in temperature could decrease the productivity of streams for those species when food is limiting. Glova (1986) found that habitat use by juvenile coho salmon and cutthroat trout in summer, when temperatures were 13°C, was different from that in winter, when temperatures were colder. When tested separately in summer, most fish of both species took up residence in pools, but, when tested together, most of the coho salmon stayed in pools and cutthroat trout remained in riffles. In winter at temperatures of 3°C, both species, whether together or separate, preferred pools and overhead cover.

Changes in water temperatures resulting from land and water use may affect fish indirectly as well as directly. In a small Vancouver Island stream, coho salmon emerged earlier when winter water temperatures became higher after logging, and detrimental downstream movement of the newly emerged fish occurred when freshets took place soon after emergence (Scrivener and Andersen 1984). Growth rate of coho salmon juveniles was inversely related to density in the stream, and the fish were larger in autumn after logging than before because of the earlier

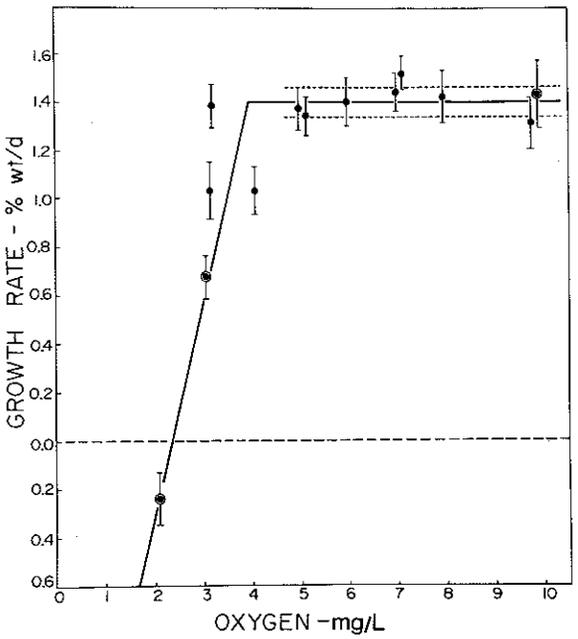


FIGURE 4.23.—Specific growth rate (percent of body weight per day ± SE) of fingerling coho salmon (5–10 g) in relation to oxygen concentration at 15°C. (From Brett and Blackburn 1981.) Dotted lines are 95% confidence limits for values with dissolved oxygen above 6 mg/L. Sloped line (fitted by eye) defines the zone of dependence of growth on dissolved oxygen.

emergence and longer period of growth. A dam on the Rogue River, Oregon, altered flows and temperatures in both summer and winter, and changed the timing of salmon and steelhead fry emergence, adult migration, fish distribution in the river, and adult mortality (Cramer et al. 1985).

Dissolved Oxygen

The waters of most natural salmonid streams have enough DO for juveniles, although concentrations in small streams may be reduced by large amounts of organic debris when temperatures are high and flows low (Hall and Lantz 1969). Streams downstream from deep, productive reservoirs may have marginally low DO concentrations at times if the discharge comes from the hypolimnion. The DO must be above a critical level for salmonids to exist in streams. Rainbow trout have survived laboratory tests at DO concentrations of less than 2 mg/L (Alabaster et al. 1957), and the survival threshold concentration for Atlantic salmon smolts is about 3.3 mg/L (Alabaster et al. 1979), but growth rate (Figure 4.23) and food conversion efficiency (Figure 4.24) are probably limited by concentrations less than 5 mg/L. Davis (1975), who reviewed information on incipient DO response thresholds and developed oxygen criteria related to concentration, water temperature, and percent saturation (Table 4.9), concluded that salmonids would not be impaired at concentrations near 8 mg/L (76–93% saturation), and that initial symptoms of DO deprivation would occur at about 6 mg/L (57–72% saturation). Davis et al. (1963) and Dahlberg et al. (1968) found the maximum sustained swimming performances of coho and chinook salmon decreased when DO concentrations were much below air-saturation levels (about 8–9 mg/L at 20°C).

In summary, salmonids may be able to survive when DO concentrations are relatively low (<5 mg/L), but growth, food conversion efficiency, and swimming

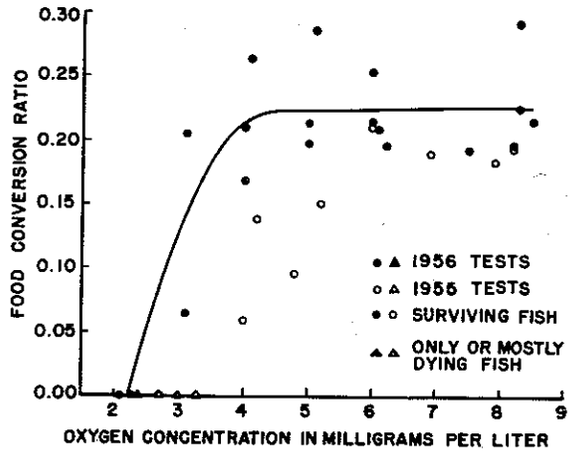


FIGURE 4.24.—Food conversion ratio (weight gained by fish/weight of food consumed) for frequently fed age-0 coho salmon in relation to dissolved oxygen concentration. A food conversion ratio of zero (not a negative ratio) has been assigned to each group of fish that lost weight. The curve has been fitted only to the 1956 data. (From Herrmann et al. 1962.)

performance will be adversely affected. High water temperature, which reduces oxygen solubility, can compound the stress on fish caused by marginal DO concentrations.

Most data on the oxygen requirements of salmonids come from laboratory studies. Brett and Blackburn (1981) appropriately urged caution when such data are extrapolated to fish in natural streams. Water qualities and the biological activities necessary for survival may differ between laboratory and field environments.

Turbidity

In most streams, there are periods when the water is relatively turbid and contains variable amounts of suspended sediments. Larger juvenile and adult salmon and trout appear to be little affected by ephemerally high concentrations of suspended sediments that occur during most storms and episodes of snowmelt (Cordone and Kelley 1961; Sorenson et al. 1977). Bisson and Bilby (1982) reported, however, that juvenile coho salmon avoided water with turbidities that exceeded 70 NTU (nephelometric turbidity units), which may occur in certain types of watersheds and with severe erosion. Berg and Northcote (1985) reported that feeding and territorial behavior of juvenile coho salmon were disrupted by short-term exposures (2.5–4.5 d) to turbid water (up to 60 NTU).

Newly emerged fry appear to be more susceptible to even moderate turbidities than are older fish. Turbidities in the 25–50-NTU range (equivalent to 125–275 mg/L of bentonite clay) reduced growth and caused more young coho salmon and steelhead to emigrate from laboratory streams than did clear water (Sigler et al.

TABLE 4.9.—Response of freshwater salmonid populations to three concentrations of dissolved oxygen. (Modified from Davis 1975.)

Response	Dissolved oxygen (mg/L)	Percent saturation at temperature (°C)					
		0	5	10	15	20	25
Function without impairment	7.75	76	76	76	76	85	93
Initial distress symptoms	6.00	57	57	57	59	65	72
Most fish affected by lack of oxygen	4.25	38	38	38	42	46	51

1984). Juvenile salmonids tend to avoid streams that are chronically turbid, such as glacial streams or those disturbed by human activities (Lloyd et al. 1987), except when the fish have to traverse them along migration routes.

Productivity of Streams

Streams vary in productivity due largely to the nutrients and energy available. The rates of primary and secondary production largely determine the amount of food available to fish. A detailed discussion of energy sources and processes is presented by Murphy and Meehan (1991, this volume).

The amount of food available to fish is one of the factors that set the salmonid carrying capacity of streams. In many infertile streams, summer fish production appears to be food-limited. A change in fish production, density, or growth when food availability increases or decreases is proof of food limitation. More coho salmon could be produced in a small Vancouver Island stream during summer when Mason (1976) increased the amount of food available. In another Vancouver Island stream, Slaney et al. (1986) added inorganic fertilizers (phosphorus and nitrogen) to a 29-km section and found large increases in primary production, no significant changes in invertebrate abundance and fish density, and significant increases in trout growth. The increased growth allowed steelhead to become smolts at a younger age; because this period of juvenile mortality was reduced, the stream produced more smolts.

Positive correlations between stream productivity and production, standing crops, and growth of brown trout were observed by McFadden and Cooper (1962). In Idaho streams that differed in conductivity by a factor of 10 (40 to 400 $\mu S/cm^3$), the production and standing crop of age-0 chinook salmon differed by a similar factor (T. C. Bjornn, unpublished data). Konopacky (1984) found juvenile chinook salmon and steelhead lost weight and eventually left laboratory streams when no food was supplied; he also found proportionate increases in production, but not in density, in response to two levels of daily ration. Wilzbach (1985) reported that most cutthroat trout left laboratory channels when they were given a daily ration of frozen brine shrimp equal to only 5% of their body weight, whether cover was provided or not, but they stayed when given a 15% ration.

Brett et al. (1969) defined the daily rations needed for maximum growth of sockeye salmon at various temperatures. If this relation is similar for other species of salmon and trout, a yearling salmonid in a stream with daily mean temperature of 10°C would need a daily food supply equivalent to 6–7% of its body weight to attain maximum growth. In streams that are food-limited, maximum growth rates may not be achieved by the fish because that may not be the most efficient use of resources. The social interactions that fish use to regulate densities and respond to food abundance may result in more fish growing at less-than-maximum rates, rather than fewer fish growing at maximum rates.

Juvenile salmonids can consume a large fraction of the invertebrates drifting during daylight in the streams they occupy (Allan 1982; Wilzbach et al. 1986), but fish do not appear to regulate the abundance of benthic or drifting invertebrates in streams except in very limited situations of time and space (Allan 1983). Production of aquatic invertebrates that juvenile salmonids eat depends on the amount of organic material available in streams. Bilby and Likens (1980) showed the importance of debris dams in small streams for the accumulation of coarse particulate organic matter. Nearly 75% of the organic matter deposited in first-order streams was associated with the dams, versus 58% in second-order streams and 20% in third-order streams. Fish also eat terrestrial invertebrates that are associated with vegetation surrounding streams.

Space

Space suitable for occupancy by salmonids in streams is a function of streamflow, channel morphometry, gradient, and (in many instances) various forms of instream or riparian cover. Suitable space for each salmonid life stage has water of sufficient depth and quality flowing at appropriate velocities. The addition of cover (extra depth, preferred substrates, woody debris, etc.) increases the complexity of the space and usually the carrying capacity. The addition of certain types of cover (overhead, for example) may make some areas in streams suitable for fish that would not otherwise be used.

The space an individual fish needs and uses—in some instances a territory—is a part of the total suitable space available. Food abundance (Chapman 1966), the competitors (Fausch and White 1981, 1986) and predators present, and the complexity of the habitat determine what part of the available suitable space an individual fish uses.

Fish densities in streams provide a measure of the spatial requirements of juvenile salmonids, but the wide variation in observed densities illustrates the diversity of habitat quantity and quality and other factors that regulate fish abundance. In a productive Idaho stream, end-of-summer densities of age-0 chinook salmon (9.6 g mean weight) have been as high as 1.35 fish/m^2 and 12.9 g/m^2 (Bjornn 1978). With the age-0 steelhead (4.5 g) also produced in the stream, the combined densities were 2.05 fish/m^2 and 16.1 g/m^2. These salmonids were not uniformly distributed throughout the length of the stream and densities in some sections were as high as 3.4 fish/m^2 (21.8 g/m^2). Total salmonid density, including the age-1 and older fish, has been as high as 3.5 fish/m^2 and 27.0 g/m^2. Spring-to-fall production (tissue elaborated) by age-0 chinook salmon and steelhead has been measured at rates as high as 20.3 g/m^2.

In less productive third- and fourth-order streams in Idaho, age-0 chinook salmon were less dense (usually <0.8 fish/m^2), the fish grew slower (end-of-summer weight, about 5 g), biomass standing crops were only 1–3 g/m^2, and few fish of other species were produced. Summer production was 1–2 g/m^2 (T. C. Bjornn, unpublished data). In coastal and inland British Columbia streams, Shepherd et al. (1986b) reported overall maximum densities of 0.14 age-0 chinook salmon/m^2 (five streams) and 0.41 age-0 and age-1 coho salmon/m^2 (nine streams).

Salmonids, especially the juveniles, also use the space available in side channels for rearing. Mundie and Traber (1983) found higher densities of steelhead (0.66 smolts/m^2 and 9.94 g/m^2) and coho salmon (0.85 smolts/m^2 and 12.8 g/m^2) in side-channel pools than are commonly found in the main channels of Pacific coastal streams. Peterson (1982a, 1982b) reported coho salmon moving into side-channel pools for the winter.

The amount of space needed by fish increases with age and size. Allen (1969) assembled data on densities for a variety of salmonids and found a positive relation between area per fish in streams and age (Figure 4.25) or length. For the streams he evaluated, 7–10-cm fish (which had completed the first year of life)

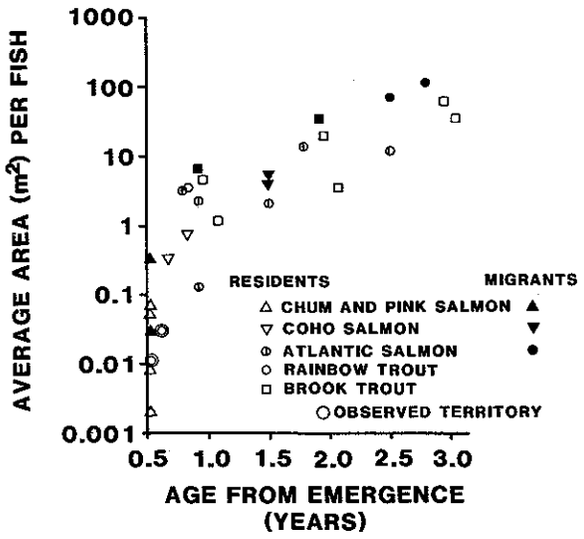


FIGURE 4.25.—Average area per fish (on a logarithmic scale) versus age for several salmonids in streams. (Redrawn from Allen 1969.)

were found at densities of 0.1 to 1.0 fish/m^2 (10-cm fish averaged 0.17 fish/m^2 and 1.7 g/m^2). Densities of larger and older fish were usually less than 0.1 fish/m^2.

Based on the foregoing, the summer space requirements of juvenile salmonids during their first year in streams probably range from 0.25 to 10 m^2 of stream per fish, depending on such things as the species and age composition of fish present, stream productivity, and quality of the space. The space required in winter has not been as well defined.

The presence of abundant space does not necessarily mean there will be large numbers of fish. The space must be in the right context with other needs of the fish. For example, the abundance of age-0 chinook salmon in some infertile Idaho nursery streams appeared to be asymptotically related to the size of pools (Figure 4.26). In pools up to about 200 m^2 in area (volume, 150 m^3), the number (or biomass) of fish observed was directly related to size of the pools. In larger pools, however, much of the space in the downstream portions was unused, despite the presence of suitable depths and velocities. Fish abundance was probably food-limited in these streams and thus the fish were concentrated in the upper portions of each pool, close to the incoming food supply.

The effect of reducing space available to fish in small pools of third-order streams was illustrated by Bjornn et al. (1977) in a stream sedimentation experiment. When sand was added to a natural pool, reducing pool volume by half and surface area of water deeper than 0.3 m by two-thirds, fish numbers declined by two-thirds.

Streamflow.—Streamflow, one of the basic determinants of the amount of space available for fish, varies seasonally in ways that depend on geography and climate. In coastal streams, flows are often high in winter because of heavy rain and snowfall. In inland areas, flows are most often high in spring as a result of snowmelt, but rain-on-snow events occasionally cause high flows in winter. In most unregulated salmonid streams of North America, flows are usually lowest in late summer, fall, or winter (Stalnaker and Arnette 1976a). Diversion of water

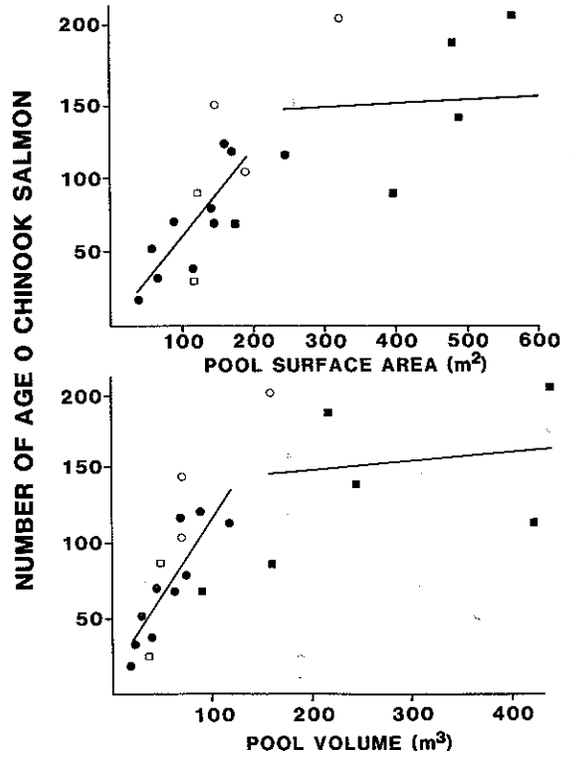


FIGURE 4.26.—Relation between pool surface area or volume in several Idaho streams (denoted by different symbols) and number of juvenile chinook salmon per pool. (Redrawn from Konopacky 1984.)

from streams and storage of water for municipal, agricultural, flood control, and hydropower uses usually lead to altered streamflows and potential changes in the carrying capacity of streams for salmonid fishes. The relation between streamflow and carrying capacity could vary with channel geometry and surrounding land forms; it probably differs, for example, between streams consisting mostly of riffles in a V-shaped canyon and streams with alternating pools and riffles in a broad valley. In general, the relation must start at the origin (no flow, no fish), increase (perhaps not uniformly) with increases in flow up to a point, and then level off or decline if flows become excessive. The relation between flow and carrying capacity is difficult to assess directly in natural streams, however, and there are few studies for reference. The roles of flow magnitude and seasonality in setting the carrying capacity of a stream have not been well defined.

Kraft (1972) diverted water from a 520-m section of natural stream channel in Montana for 3 months in summer and found that both physical stream characteristics and resident brook trout were more affected in runs than in pools. After a 90% reduction from normal summer flows (about 1.0 m^3/s), depth in runs decreased 38%, average water velocity decreased 73%, and cover decreased 50%; decreases were smaller in pools. The response of brook trout to the 90% flow reduction was variable, but many fish in the dewatered section moved from runs into pools; the number of fish decreased an average 62% in dewatered runs compared with 20% in runs that were not dewatered (Figure 4.27).

In an Oregon flume studied by White et al. (1981), water velocities, depths, wetted perimeters, and surface areas in runs declined with decreases in flow, as

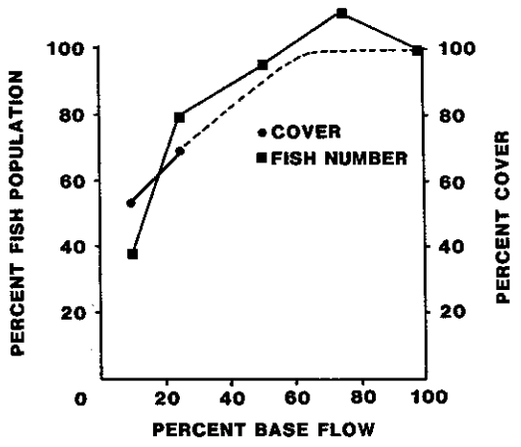


FIGURE 4.27.—Relations of fish number and cover to reductions in summer base flow in three runs in Blacktail Creek, Montana. (Data from Kraft 1968, as plotted by White 1976.)

did the abundance of wild steelhead juveniles, but the researchers were unable to determine the relative influences of the physical features on fish abundance. The authors also calculated an index (weighted usable area, WUA) of the amount of suitable habitat in the flumes for juvenile steelhead, based on IFIM. Their estimates of WUA from suitability curves for velocity and depth did not correspond closely with the number of fish remaining at each flow.

The IFIM, although controversial and incompletely validated, is a modeling procedure designed to help evaluate the importance of differing streamflows to the production of fish. The procedure generates a relation between WUA and flow. Typically, WUA increases asymptotically with flow (Figure 4.28), but the estimates can vary widely depending on the velocity and depth suitability indexes used. In an Idaho stream, WUA estimates for age-0 chinook salmon were highest at flows that occurred near the end of summer, and decreased when flows were higher or lower. The WUA values based on velocity and depth were highest for pools, followed by runs, and then riffles.

For IFIM models to be useful, there must be a definable relation between WUA index values and the standing crop or production of fish in a stream. Such relations can exist only if the physical variables included in the model (velocity, depth, substrate, cover, etc.) are the factors that regulate abundance. Stalnaker (1979) found that standing crop of brown trout was strongly correlated with WUA in 19 sections of 8 Wyoming streams. Orth and Maughan (1982) and Conder and Annear (1987) had less success in relating WUA index values to standing crops of fish or to another habitat quality index. Conder and Annear (1987) discussed the use of the IFIM to estimate changes in fish production in streams as related to streamflow. Nickelson et al. (1979) reported on studies of models that could be used to evaluate streamflow requirements of salmonids in Oregon streams. After several years of study, they recommended use of the IFIM with the addition of variables for pool volume and cover.

Smoker (1955) found a correlation between the commercial catch of coho salmon and annual runoff, summer flow, and lowest monthly flow in 21 western Washington drainages 2 years previously; the data covered the years 1935–1954. In the last two decades, hatchery production of coho salmon smolts has increased markedly and made such comparisons more difficult, but Mathews and Olson (1980) analyzed data

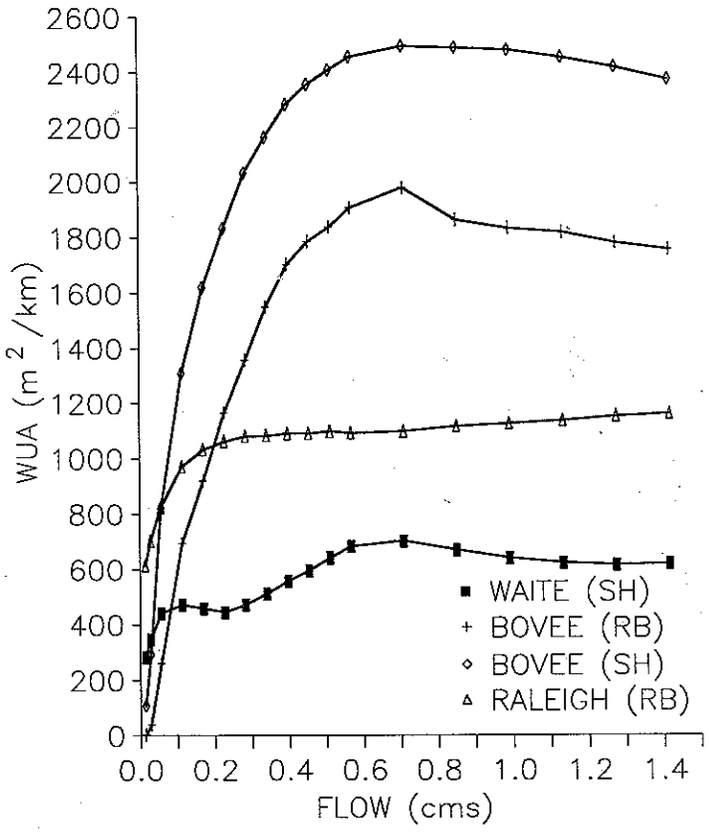


FIGURE 4.28.—Indices of suitable area (weighted usable area, WUA) versus flow (cubic meters per second) for juvenile steelhead (SH) and rainbow trout (RB) in a California stream based on different probability-of-use curves devised by Waite, Bovee, and Raleigh. (Ian Waite, unpublished data.)

from Washington for the years 1952–1977 and found that summer streamflow still had an important influence on total coho salmon production in Puget Sound area streams. Scarnecchia (1981) found that the coho salmon catch off the Oregon coast for the years 1942–1962 was correlated with total flow in five coastal rivers during the salmon's freshwater existence; however, the catch was poorly correlated with the 60-d period of lowest flow in these rivers. Nickelson (1986), in an analysis of coho salmon survival from smolt to adult off the Oregon–California coast, concluded that survival at sea was variable (related to upwelling), but density independent. The implication of the above studies is that the abundance of adult coho salmon is a function of the number of smolts produced, which is in turn related to streamflow and the other factors that regulate the production of smolts.

Velocity.—Given flow in a stream, velocity is probably the next most important factor in determining the amount of suitable space for rearing salmonids (Chapman 1966; deGraaf and Bain 1986); if the velocities are unsuitable, no fish will be present. Natural streams contain a diversity of velocities (Figure 4.29) and depths,

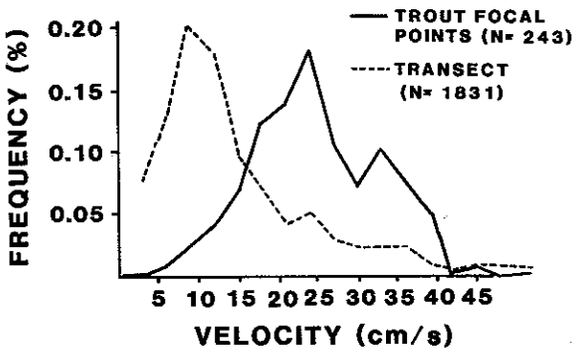


FIGURE 4.29.—Frequency of velocities at sites (focal points) occupied by trout in three sections of Uvas Creek, California, and frequency of velocities measured along transects in the stream. (From Smith and Li 1983.)

some of which are suitable for most salmonids. The velocities required and used by juvenile salmonids vary with size of fish, and sometimes with species. Some juvenile salmonids, as they grow, select sites in streams with increasingly faster velocities (Chapman and Bjornn 1969; Everest and Chapman 1972; Rimmer et al. 1984; Moyle and Baltz 1985), presumably to gain access to more abundant food (Chapman and Bjornn 1969; Fausch 1984). Sites used for feeding over long periods and the size of food items eaten may be selected largely to maximize net energy gain (Bachman 1984).

Water velocities required by fish of various sizes have been estimated from studies of the sites fish occupy in streams and of the swimming performance of fish in laboratories. Use of data from so-called field microhabitat studies to establish velocity and depth requirements has limitations because the sites selected by fish in natural streams are influenced by factors other than their velocity and depth preferences. Interactions with other fishes and the presence and location of cover alter sites selected by fish (Fausch and White 1981, 1986). Wild brown trout placed in a flume shifted position to stay within a suitable velocity range when flows were increased (Baldes and Vincent 1969). In a study by Shirvell and Dungey (1983), velocity was the most important factor determining the preferred sites of large brown trout (42 cm), but the fish often chose compromise positions to be close to food or cover.

Velocity and depth preferences may change seasonally. Chisholm et al. (1987) noted that brook trout selected areas of lower velocity (<15 cm/s) and deeper water (>30 cm) in winter than in summer, but showed no preference for substrate. Tschaplinski and Hartman (1983) noted similar shifts by coho salmon in winter to

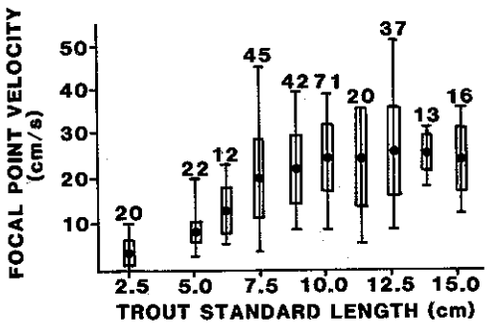


FIGURE 4.30.—Water velocities at focal points (means, ranges, and 95% confidence intervals) for trout of different standard lengths in a California stream. Numbers above data points are sample sizes. (From Smith and Li 1983.)

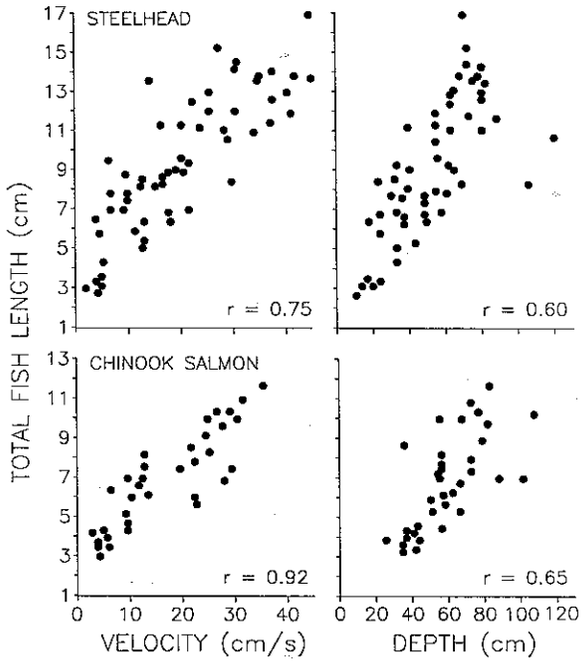


FIGURE 4.31.—Correlations between length of juvenile steelhead and chinook salmon and velocity and depth of water at sites (focal points) used by the fish in two Idaho streams. (Redrawn from Everest and Chapman 1972.)

sites (deep pools, undercuts, debris jams, side sloughs) with low velocity (<30 cm/s) but good cover.

Newly emerged fry (20–35 mm long) of salmon, trout, and char require velocities of less than 10 cm/s, based on studies of sites selected by the fish in streams (Chapman and Bjornn 1969; Everest and Chapman 1972; Griffith 1972; Hanson 1977; Smith and Li 1983; Konopacky 1984; Pratt 1984; Bugert 1985; Moyle and Baltz 1985; Sheppard and Johnson 1985). Larger fish (4–18 cm long) usually occupy sites with velocities up to about 40 cm/s (Figures 4.30, 4.31, 4.32; Table 4.10). Velocities at the sites occupied (focal points) by juvenile steelhead in a California stream were higher than the modal velocities in the stream (Figure 4.29), increased asymptotically with fish length (Figure 4.30), increased with temperature, and were less than the velocities at their usual feeding sites (Smith and Li 1983). Because invertebrate drift abundance increased with velocity across a stream section, there was a potential energetic benefit from feeding in the fastest water possible. In Idaho streams, young chinook salmon and steelhead occupied deeper and faster water as they increased in size (Figure 4.31), presumably to gain better access to food. By the end of summer, young chinook salmon (4–10 cm long) were found in the full range of available depths, but in velocities that were on the low end of those available (Figure 4.32).

Swimming performance as measured in the laboratory provides a measure of the ability of a fish to swim under specified conditions, but may not reveal velocities preferred by the fish. Brett et al. (1958) reported cruising speeds (speeds a fish could maintain for at least 1 h under stimulation) of juvenile coho salmon increased with fish size and temperature (Figure 4.33). At 10°C, cruising speeds

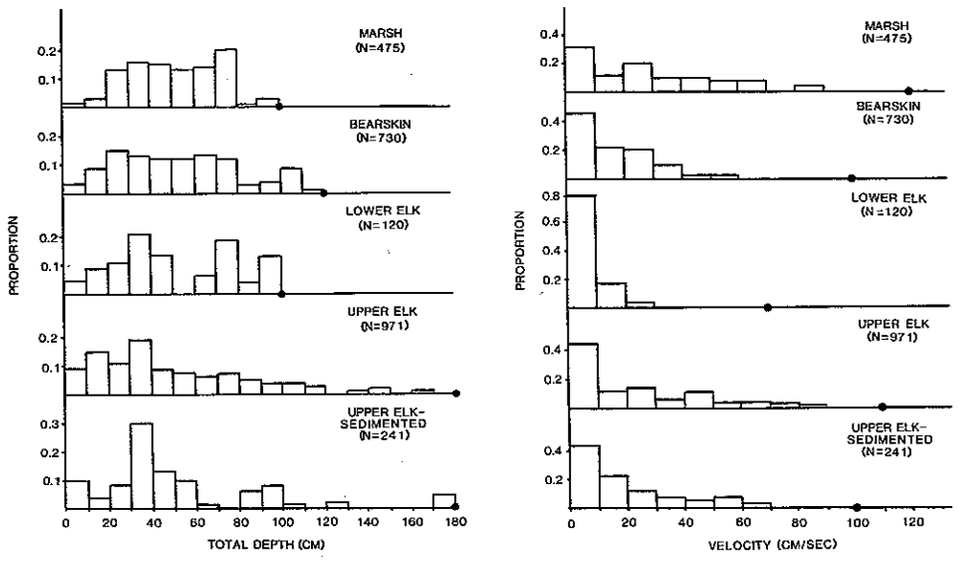


FIGURE 4.32.—Distribution of age-0 chinook salmon (77–89 mm mean total length) relative to water depth and velocity in pools of Idaho streams in August 1979. Dots indicate maximum water depth or velocity observed in the pools surveyed. (From Konopacky 1984.)

were 20–25 cm/s for 5-cm coho salmon and 35–40 cm/s for 9-cm fish; at 20°C, the speeds were 5–6 cm/s faster. Cruising speeds of fish are lower than speeds at which fish can swim for short bursts, but may be higher than water velocities observed at focal points selected by fish in streams. In a southeast Alaska stream, the mean velocity at focal points selected by age-0 (<7 cm long) and yearling (up to 12 cm long) coho salmon averaged 13–14 cm/s (T. C. Bjornn, unpublished data). Brett (1967) reported that juvenile sockeye salmon (136 mm mean length) could swim for 300 min in velocities up to about 37 cm/s (at 15°C) without becoming fatigued; at increasingly higher velocities, all fish eventually became fatigued (Figure 4.34). Velocities that did not produce fatigue in 300 min (<37 cm/s) were about half the cruising speed for fish of a given size.

Depth.—The depth of water juvenile salmonids use depends on what is available, the amounts and type of cover present, and the perceived threat from predators and competitors. Young trout and salmon have been seen in water barely deep enough to cover them and in water more than a meter deep. Densities (fish/m^2) of some salmonids are often higher in pools than in other habitat types (runs, riffles, pocket waters; Figure 4.35), but that may reflect the space available (there is more volume in pools per unit of surface) rather than a preference for deep water, especially for smaller fish (<15 cm long).

Fish usually are not uniformly distributed at all depths in a stream. Raleigh et al. (1986) presented index curves for chinook salmon in which suitabilities for newly emerged fry and juveniles were highest at depths of 25–60 cm. The curves were constructed from observations of fish distributions in streams. Everest and Chapman (1972) found significant correlations between size of fish and total water

TABLE 4.10.—Depths and velocities at sites used by salmonids in streams.

Species and source	Age[a] or size	Depth (cm)	Velocity (cm/s)
Steelhead			
Bugert (1985)	31–44 mm	24	40
Everest and Chapman (1972)	0	<15	<15
	1	60–75	15–30
Hanson (1977)	1	51 mean	10 mean
	2	58 mean	15 mean
	3	60 mean	15 mean
Moyle and Baltz (1985)	0	35	7.3
	Juvenile	63	19.4
	Adult	82	28.6
Sheppard and Johnson (1985)	37 mm	<30	<25
Smith and Li (1983)	25 mm		4
	50 mm		8
	75 mm		18
	100 mm		24
	150 mm		24
Stuehrenberg (1975)	0	<30	14 (range, 3–26)
	1	>15	16 (range, 5–37)
Thompson (1972)	0	18–67	6–49
Chinook salmon			
Everest and Chapman (1972)	0	15–30	<15
Konopacky (1984)	77–89 mm	55–60	12–30
			18 (dawn)
			12 (midday)
			25 (dusk)
Stuehrenberg (1975)	0	<61	9 (range, 0–21)
	1	<61	17 (range, 5–38)
Thompson (1972)	0	30–122	6–24
Steward and Bjornn (1987)	78–81 mm	40–58	8–10
Coho salmon			
Bugert (1985)	40–50 mm	24	39 (flume)
	0		15
	1		18
Nickelson and Reisenbichler (1977)	0	>30	<30
Pearson et al. (1970)	0		9–21
Sheppard and Johnson (1985)	62 mm	30–70	<30
Thompson (1972)	0	30–122	5–24
Cutthroat trout			
Hanson (1977)	1	51 mean	10 mean
	2	56 mean	14 mean
	3	57 mean	20 mean
	4	54 mean	14 mean
Pratt (1984)	<100 mm	32	10
	>100 mm	62	22
Thompson (1972)	0, 1	40–122	6–49
Atlantic salmon			
Rimmer et al. (1984)	40–100 mm		30
	100–150 mm		38
Bull trout			
Pratt (1984)	<100 mm	33	9
	>100 mm	45	12

[a] Ages are in years or life stages, without units.

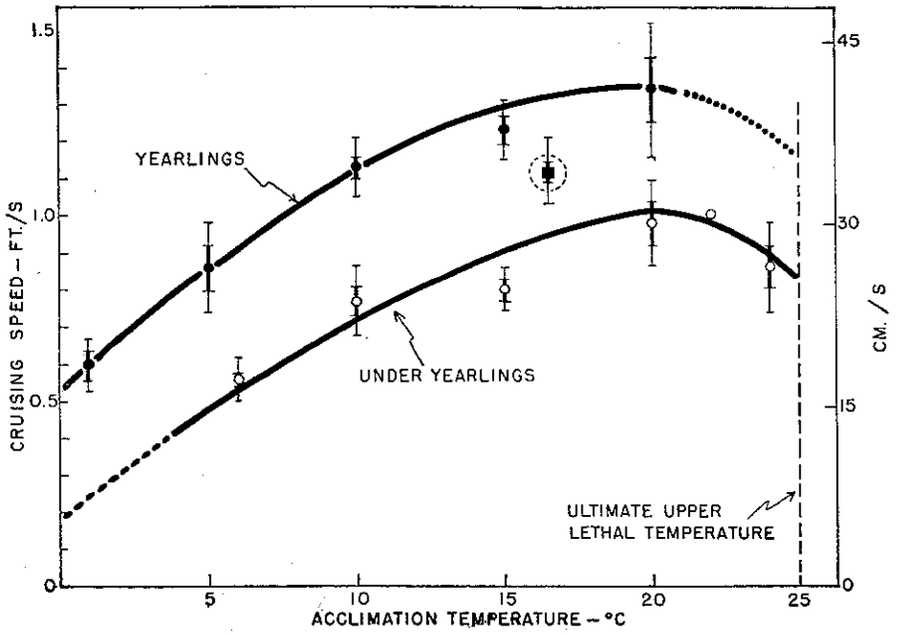


FIGURE 4.33.—Variation in cruising speed for temperature-acclimated underyearling and yearling coho salmon, adjusted in each age group to common mean lengths of 5.4 cm and 8.9 cm, respectively. The circled point between two curves is for exercised underyearling coho salmon acclimated to 16.5°C. Standard deviation (thin vertical bar) and standard error (heavy bar) are indicated for each sample. (From Brett et al. 1958.)

depth at sites (focal points) occupied by juvenile chinook salmon and steelhead (Figure 4.31). Correlations were poor between fish size and distance of focal point from the bottom; most fish, regardless of size, were near the bottom. In two Newfoundland Rivers, water depth was an unimportant factor in site selection by juvenile Atlantic salmon (deGraaf and Bain 1986).

If fish have a preferred depth of water, we believe it is readily subjugated to the needs for suitable velocities, access to food, and security from predators. Sites that fish select in streams must satisfy all the basic needs to enable the fish to survive. In laboratory streams, chinook salmon fry 30–40 mm long occupied a wide variety of

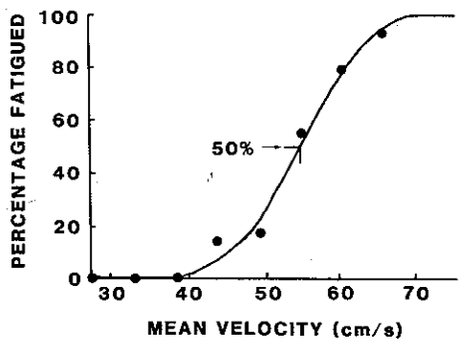


FIGURE 4.34.—Percentage of young sockeye salmon that became fatigued within 300 min at 15°C when forced to swim at the velocity indicated. The mean total length of the 104 fish in the sample was 13.6 cm. (Redrawn from Brett 1967.)

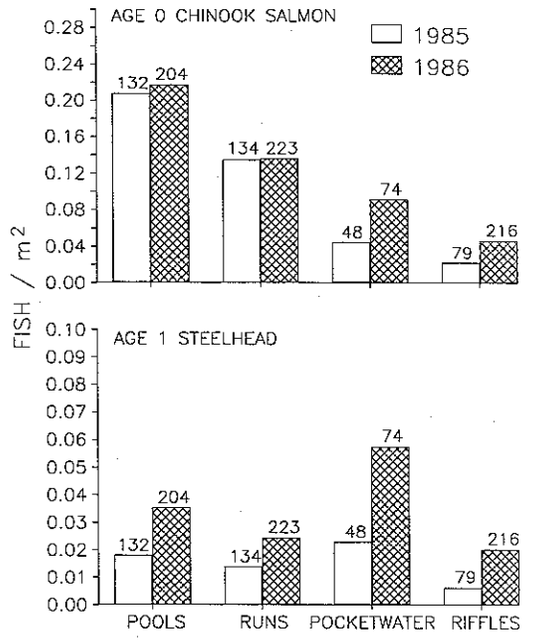


FIGURE 4.35.—Densities of age-0 chinook salmon and age-1 steelhead in various types of habitat in 22 Idaho streams. Numbers above bars represent the number of units of each type of habitat surveyed. (Authors' original data.)

sites (including the deepest water) when they were the only fish present, but only restricted areas when they shared the streams with yearling steelhead 70–120 mm long (T. C. Bjornn, unpublished data). The newly emerged fry were distributed throughout the water in both small pools (0.6 m wide, 1.2 m long, 0.32 m deep) and larger pools (1.5 m wide, 2.5 m long, 1.1 m deep) when no other fish were present and there was no threat of bird predation. The presence of only two yearling steelhead in a 4.8-m section of the smaller stream (two pools, two riffles, one run) changed the behavior of and site selection by the chinook salmon fry: some left the stream and those that remained stayed close to the bottom in the pools or moved into the interstitial spaces of the gravel substrate. When larger numbers of yearling steelhead were present, all chinook salmon fry left the stream or were eaten. In the larger stream, the fry moved to shallow water (<6 cm deep) above a sand bar, left the stream, moved into the substrate, or were eaten when yearling steelhead were present. A simulated kingfisher flight over the sand bar frightened the fry into the pool where they were vulnerable to predation by steelhead.

The relation between water depth in streams and fish numbers has not been empirically defined, but depends on the mixture of fish species and sizes, types and amounts of other cover present, and size of stream. In second- to fourth-order salmon streams, we suspect the relation is asymptotic, fish abundance increasing with increases in depth (more space) up to a point. We see no reason why fish that form schools in pools should become less abundant in extra deep water, but territorial fishes and those that select sites close to the substrate may not be as abundant in deep pools as in shallower types of habitat (runs and pocket water; Figure 4.35).

Substrate.—The substrates of salmonid streams are important habitats for incubating embryos and aquatic invertebrates that provide much of the food of

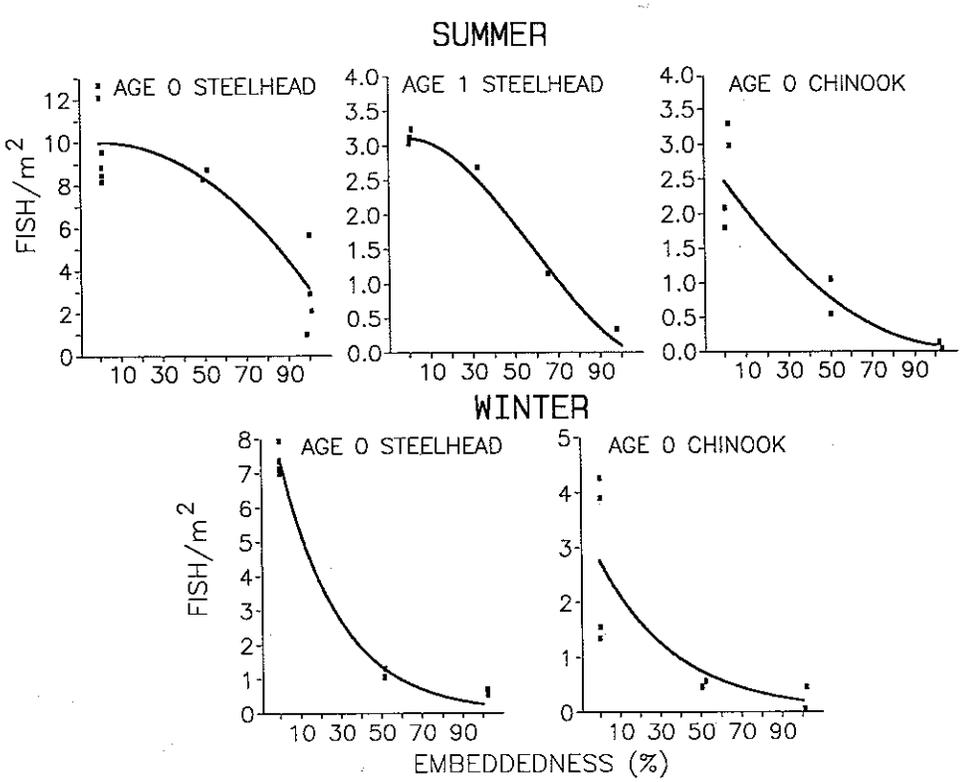


FIGURE 4.36.—Densities of chinook salmon and steelhead juveniles remaining in laboratory stream channels after 5 d during winter and summer tests to evaluate the effects of sedimentation. The channels had alternating pool–riffle configurations; fine sediments (<6 mm) were added to pools and riffles to embed the cobbles and boulders from 0 to 100%. (From Bjornn et al. 1977.)

salmonids, and they provide cover for fish in summer and winter. Silt and sand substrates have little or no value as cover for fish. Larger substrate materials (up to 40 cm in diameter) provide visual isolation and their interstitial spaces are often the primary cover, along with depth and water turbulence, in some streams.

Salmonids will hide in the interstitial spaces in stream substrates, particularly in winter, when the voids are accessible (Chapman and Bjornn 1969; Bjornn and Morrill 1972; Gibson 1978; Rimmer et al. 1984; Hillman et al. 1987). Newly emerged fry can occupy the voids of substrate made up of 2–5-cm diameter rocks, but larger fish need cobble and boulder-size (>7.5-cm diameter) substrates. The summer or winter carrying capacity of the stream for fish declines when fine sediments fill the interstitial spaces of the substrate (Figure 4.36). In a laboratory stream experiment, Crouse et al. (1981) found that production (tissue elaboration) of juvenile coho salmon was related to the amount of fine sediments in the substrate. When large substrate particles (>12 mm in diameter) were covered (embedded) with various amounts of fine sediments (<2 mm in diameter), fish production was reduced in direct proportion to the degree of embeddedness (expressed as a substrate score or geometric mean size of particles). In another laboratory stream study, Bjornn et al. (1977) found that the density of juvenile

steelhead and chinook salmon in summer and winter was reduced by more than half when enough sand was added to fully embed the large cobble substrate (Figure 4.36).

Much of the food eaten by salmonid fishes in streams is produced in the substrate. Particles that make up stream substrates, and thus the habitat of aquatic invertebrates, vary widely from silts and sands to boulders and barely fractured bedrock. Invertebrates differ in their ability to thrive in various types of substrates. Chironomids of various species do well in silts and sands, but the larger ephemeropterans, trichopterans, and plecopterans prefer a mixture of coarse sands and gravels. The addition of fine sediments to stream substrates as a result of watershed disturbances and erosion is worrisome because sedimentation may reduce the abundance of invertebrates. In streams where food is limiting for fish, a reduction in aquatic invertebrate abundance would lead to reduced fish production.

The influence of fine sediments on aquatic invertebrates and ultimately on fish has been investigated, but has not been clearly defined. Cordone and Kelley (1961) reported that fine sediments were detrimental to aquatic organisms. Brusven and Prather (1974) found that invertebrate abundance was reduced when larger streambed particles were fully embedded in fine sediments. Bjornn et al. (1977) found that many ephemeropterans, trichopterans, and simuliids were less abundant in riffles fully embedded with fine granitic sediments than in less-embedded riffle substrates. Hawkins et al. (1983) found decreasing numbers of invertebrates in shaded riffles as the percentage of fine sediments increased, but no such correlation existed in unshaded riffles. In seminatural laboratory streams, benthic and drifting invertebrates (mostly chironomids and ephemeropterans) were more abundant in sections with sand–pebble substrate than in sections with large gravel (Konopacky 1984).

Summer and winter carrying capacities of streams for salmonids may differ markedly because of the substrate present. For example, more than half the steelhead and chinook salmon that reared in two Idaho streams in summer left during fall and winter, but ceased migrating downstream when they encountered areas with larger substrate (Bjornn 1978). In laboratory experiments, fall and winter migrants stopped migrating downstream when placed in channels with large rocks, but continued migrating when put in channels with small gravel (Bjornn and Morrill 1972). After piles of large rock were added to provide cover in sections of a stream with small gravel, more juvenile steelhead stayed there in winter than previously (Chapman and Bjornn 1969). In summer, substrates contribute to a stream's carrying capacity by providing habitat for invertebrates that fish eat and, perhaps less importantly, by providing cover. In winter, the substrate is more important as a source of cover than as a source of food.

Cover

Cover is an important, but difficult to define, aspect of salmonid habitats in streams. Some of the features that may provide cover and increase the carrying capacity of streams for fish are water depth, water turbulence, large-particle substrates, overhanging or undercut banks, overhanging riparian vegetation, woody debris (brush, logs), and aquatic vegetation. Cover provides security from predation for fish and allows them to occupy portions of streams that they might

not use otherwise. The needs of fish for cover may vary diurnally, seasonally, by species, and by size of fish (Kalleberg 1958; Hartman 1963, 1965; Chapman 1966; Ruggles 1966; Butler and Hawthorne 1968; Edmundson et al. 1968; Allen 1969; Chapman and Bjornn 1969; Everest 1969; Lewis 1969; Wesche 1973; Hanson 1977; Cunjak and Power 1986). Cover is usually an important variable in models developed to estimate the standing crop of salmonids that could be expected in streams (Binns and Eiserman 1979; Conder and Annear 1987).

Fish abundance in streams has been correlated with the abundance and quality of cover. Standing crops of cutthroat trout in summer were correlated with the indices of cover (Figure 4.37) and surface area used by Wesche (1974). Juvenile steelhead and chinook salmon responded to various types (Figure 4.38) and amounts (Figure 4.39) of cover in winter by either staying in or leaving outdoor laboratory streams (T. C. Bjornn and C. R. Steward, unpublished data). More fish remained in channel pools with a combination of deep water, undercut bank, large rocks, and a bundle of brush than in pools with less cover. The number of chinook salmon remaining in pools increased with increasing amounts of cover (Figure 4.39).

The addition of structures or large boulders to streams to create pools and cover can increase the abundance of salmonids if the amount of suitable habitat is limiting the fish population. When gabions were added to an Oregon stream after logging, debris removal, and floods, the number, depth, and total volume of pools increased, as did the biomass of salmonids (House and Boehne 1985).

Large woody debris originating from riparian timber is a form of cover in many streams and its importance has become more widely known in recent years (Bisson et al. 1987; Holtby 1988a). For example, coho salmon production declined when woody debris was removed from second-order streams in southeast Alaska (Dolloff 1983). More large woody debris and juvenile coho salmon were found in

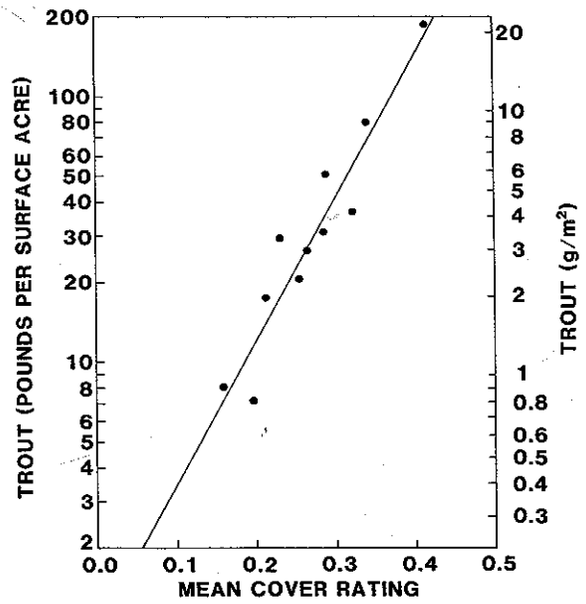


FIGURE 4.37.—Relation between mean trout cover rating and standing crop estimate of trout for 11 study areas. (From Wesche 1974.)

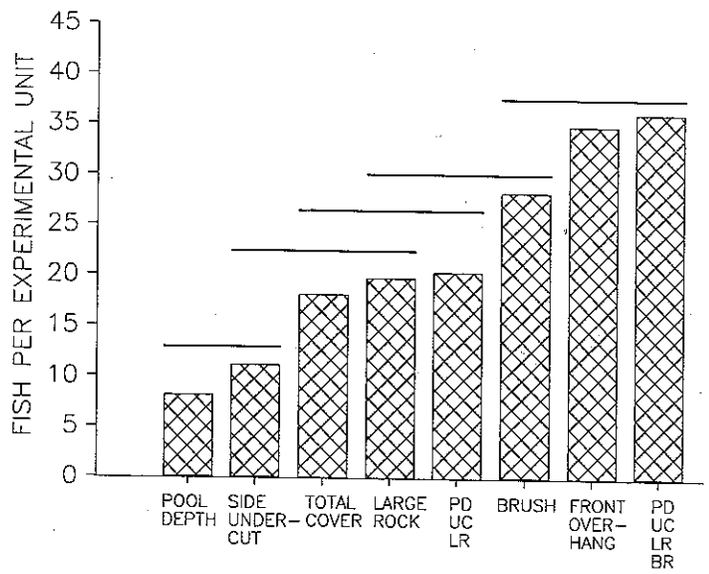


FIGURE 4.38.—Number of yearling steelhead that remained in sections of an outdoor laboratory stream in winter in pools that contained various types of cover. (T. C. Bjornn and C. R. Steward, unpublished data.) Bars not covered by the same horizontal lines were statistically different ($P < 0.05$).

streams surrounded by mature, mixed-conifer forest than in streams lined by red alder that had grown in a 20-year-old clear-cut (House and Boehne 1986). When wood debris was removed from a stream, the surface area, number, and size of pools decreased, water velocity increased, and the biomass of Dolly Varden decreased from 12.5 to 3.9 g/m^2 (Elliott 1986). In another stream, young steelhead were more abundant in clear-cut than in wooded areas in summer but moved to areas with pools and forest canopy in winter (Johnson et al. 1986). Bryant (1983, 1985)

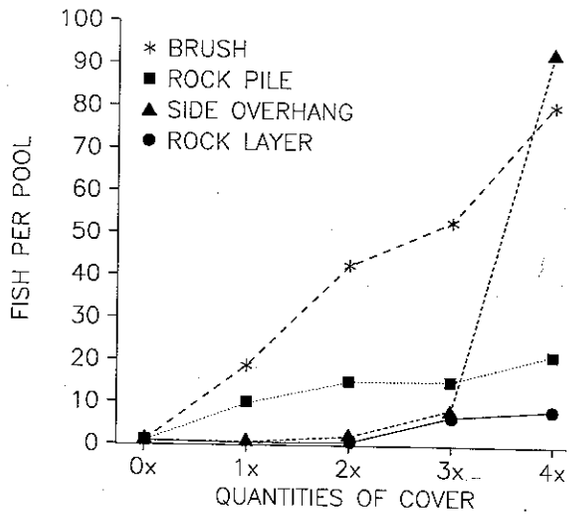


FIGURE 4.39.—Response (number remaining in pools) of yearling chinook salmon to various amounts of different types of cover in an outdoor laboratory stream during winter. (C. R. Steward and T. C. Bjornn, unpublished data.)

proposed guidelines for woody debris management in streams after he found a gradual loss of large debris from streams where riparian timber had been removed.

Overhead cover (including undercut banks, overhanging vegetation, logs, and debris jams) is often an important component of fish habitat in streams. Boussu (1954) reported increases in trout standing crop after the addition of overhanging brush as cover, and decreases when brush and overhanging banks were removed. Overhead bank cover, in association with water depths of at least 15 cm, was the single most important type of cover for brown trout in Wyoming streams (Wesche et al. 1985, 1987). In a small Lake Erie tributary, the distribution of subyearling rainbow trout, brown trout, and coho salmon was related to bank and instream cover (Gordon and MacCrimmon 1982). Brusven et al. (1986) found that 82% of age-0 chinook salmon preferred sections of a small stream channel with one-third overhead cover to sections without such cover. With the same stream channel, Meehan et al. (1987) showed that the fish preferred shade from artificial canopies to open areas, especially in the shallow reaches. Juvenile Atlantic salmon and brook trout were attracted to shaded areas of a shallow flume, but moved to deeper water when given the opportunity (Gibson 1978). Wilzbach et al. (1986), however, found that cutthroat trout foraged more effective on experimentally introduced invertebrate prey in pools within a recently logged area than in forested pools, presumably because light levels were higher in the logged area. Growth of trout was higher in pools of the logged section, but the investigators thought differences in foraging efficiency alone did not fully account for the slower growth in the forested pools.

Use of stream habitat and cover by juvenile salmonids may depend on the presence of other fish. Glova (1986) reported evidence of interactive segregation between juvenile coho salmon and cutthroat trout in summer. When tested separately, most fish of both species were found in pools, but when tested together, most coho salmon were in pools and cutthroat trout were in riffles. In winter, Glova (1986) found that both species, whether together or separate, preferred pools and overhead cover. Similar interactive segregation in summer has been demonstrated for coho salmon and steelhead: salmon used the pools and steelhead the riffles when the species were together in the same streams (Hartman 1965). In southeast Alaska streams, cover affected habitat use by coho salmon, steelhead, and Dolly Varden with respect to depth, position in the water column, and water velocity. Coho salmon and steelhead selected lower positions in the water column in pools without cover than in pools with overhead bank cover or instream cover (Bugert 1985). The presence or absence of Dolly Varden 10–20 cm long in pools caused shifts in habitat use by age-0 steelhead and coho salmon, even when some forms of cover were provided.

Seaward or Lakeward Migration

In some populations of salmonids, the fish spend their entire lives in a limited reach of stream (Miller 1954, 1957; Hunt 1974; Bachman 1984). In many other populations, however, juveniles may live in their natal streams for a few days to more than 3 years and then move to other areas to complete their maturation. Nonanadromous salmon, trout, and char may move downstream into lakes (upstream in some cases) or larger rivers. The anadromous salmonids eventually

migrate to the sea, but in some cases spend extended periods rearing or overwintering in streams (or lakes) other than their natal sites (Bjornn 1978; Leider et al. 1986). Regardless of the destination of the juvenile migrants, flows and water quality must be suitable for the migration to be successful.

The timing of most lakeward or seaward migrations of salmonids that rear for an extended period in steams appears to be regulated primarily by photoperiod, but streamflow, water temperatures, and growth may play a role in some areas. Chinook salmon and steelhead smolts migrated seaward from an Idaho stream at slightly different times, but the timing for each species was similar each year, and was modified only slightly by flow and moon phase (Bjornn 1971); water temperatures were similar each year. In a Norwegian river, water temperature (increase and general temperature in spring) accounted for most of the variation in timing of the seaward migrations of Atlantic salmon (Jonsson and Ruud-Hansen 1985); streamflow, cloudiness, and lunar cycle were not correlated with the migration.

Streamflows are usually adequate in unaltered streams because seaward migration commonly occurs in the spring. Seaward migration has been altered in streams and rivers from which large amounts of water are diverted or along which large reservoirs have been created. Streamflows that were sufficient before construction of dams become inadequate in large reservoirs. There is evidence that smolts depend on river currents during their downstream migration (Fried et al. 1978), and they have difficulty finding their way through large reservoirs with barely perceptible currents. The time required for a smolt to travel the 517 km from the Salmon River in Idaho to The Dalles Dam in the lower Columbia River increased by about 30 d during years with low flows after completion of six intervening dams. The poor success of smolts moving down through large reservoirs with low flows may be due in part to the suppression of some parr-to-smolt physiological processes; Adams et al. (1973) observed this condition when fish were held in relatively high water temperatures (15–20°C). The parr-to-smolt transition is often incomplete when fish begin to migrate and may fail to develop fully if the fish encounter high temperatures and reservoirs without perceptible currents.

Another hazard created at some dams is supersaturation of dissolved gases, particularly nitrogen, which can cause gas bubble disease in both upstream- and downstream-migrating salmonids (Ebel 1970; Ebel and Raymond 1976). Salmon may be more successful than steelhead in sensing and avoiding highly supersaturated waters (Stevens et al. 1980), but most salmonids migrating in the rivers are susceptible to gas bubble disease.

The magnitude of the effect dams and associated reservoirs can have on anadromous fishes is evident in data from the Columbia River drainage. Salmon and steelhead must pass up to nine dams in the Columbia and Snake rivers during their migrations to and from the sea. Smolt-to-adult survival rates declined from more than 4% before 1968 to less than 1.5% in the mid-1970s when all the dams were completed (Raymond 1988). In years with low flows (such as 1973 and 1977), smolt mortality averaged 45% at each dam and reservoir, compared to 15% in years with higher flows. In recent years, smolt-to-adult survival rates of steelhead and chinook salmon from the Snake River have increased to 2–5% with the help of spillway deflectors to reduce gas supersaturation, fish bypasses around

turbines, transportation around dams, and supplemental spills at dams without bypasses (Raymond 1988).

Summary

In the foregoing discussion of habitat variables, each factor was addressed separately, but the reader should keep in mind that fish usually respond to the combined effect of two or more of the physical, chemical, and biological variables in their environment. The fish may respond physiologically (altered growth and health) and behaviorally (site selection and interactions) to the array of environmental features they encounter. In streams where fish live and reproduce, all the important factors are in a suitable (but usually not optimum) range throughout the life of the fish. The mix of environmental factors in any stream sets the carrying capacity of that stream for fish, and the capacity can be changed if one or more of the factors are altered. The importance of specific factors in setting carrying capacity may change with life stage of the fish and season of the year.

Low streamflows, high water temperatures, and excessive turbidities impede adult salmon, trout, and char on their migration to spawning areas. These impediments occur even in pristine environments on occasion, but more often in drainages with irrigation, extensive agriculture, hydropower, surface mining, forest harvesting, and flood control projects. Once in the spawning areas, the amount and suitability of stream substrate and flows in the spawning areas are key factors. During incubation of the embryos and alevins, conditions within the redd dictate the number of young fish that will emerge into the stream. Adequate flows of well-oxygenated water and relatively small amounts of fine sediments (organic and inorganic) will allow a high percentage of the young fish to survive and emerge from the redd.

As soon as the young fish begin rearing in the stream, they become subject to predation by other fish, birds, and mammals, and they interact with the other fish present for choice feeding sites and cover. Given adequate numbers of young fish to use all the available habitat, the number and size of fish that can be produced in a stream is governed by the quantity and quality of space available, productivity of the stream, and the presence of competitors and predators. In summer, juvenile fish are primarily concerned with feeding and they select sites in streams that optimize the opportunity to obtain food, yet provide acceptable security from predation. In winter where water temperatures are low, the fish appear to be primarily concerned with security; they hide in cover or adopt behavior patterns that may have security benefits (such as gathering in large schools) and they are less interested in feeding. Because the requirements of salmonids and their use of habitat in winter are different from those in summer, the carrying capacity of streams or stream reaches may not be the same during both seasons. The changes in carrying capacity that result from alteration of stream features depend on the roles those features play in establishing the carrying capacity—roles that can change with time.

Biological Conservation 169 (2014) 362–371

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Multifunctionality and biodiversity: Ecosystem services in temperate rainforests of the Pacific Northwest, USA

Patric Brandt [a,b,*], David J. Abson [c], Dominick A. DellaSala [d], Robert Feller [b], Henrik von Wehrden [b,c]

[a] Karlsruhe Institute of Technology, Institute of Meteorology and Climate - Atmospheric Environmental Research, Kreuzeckbahnstraße 19, 82467 Garmisch-Partenkirchen, Germany
[b] Leuphana University Lüneburg, Centre for Methods & Institute of Ecology, Faculty of Sustainability, Scharnhorststr. 1, 21335 Lüneburg, Germany
[c] Leuphana University Lüneburg, FuturES Research Center, Scharnhorststr. 1, 21335 Lüneburg, Germany
[d] Geos Institute, 84-4th St., Ashland, OR 97520, USA

ARTICLE INFO

Article history:
Received 1 August 2013
Received in revised form 30 October 2013
Accepted 2 December 2013
Available online xxxx

Keywords:
Biodiversity conservation
Ecosystem management
Ecosystem service diversity
Multifunctional ecosystems
Temperate rainforests

ABSTRACT

Forests produce a myriad of ecosystem related benefits known as ecosystem services. Maximizing the provision of single goods may lead to the overexploitation of ecosystems that negatively affects biodiversity and causes ecosystem degradation. We analyzed the temperate rainforest region of the Pacific Northwest, which offers a multitude of ecosystem services and harbors unique biodiversity, to investigate linkages and trade-offs between ecosystem services and biodiversity. We mapped nine actual and potential ecosystem services, grouped into provision, supporting, regulating and cultural ecosystem service categories, as well as species richness of four taxonomic groups (mammals, birds, trees, and amphibians). We analyzed linkages and tradeoffs between ecosystem services, their overall diversity, and species richness as well as different levels of taxon diversity. We also tested if ecosystem service categories, in addition to climate and land cover parameters, could indicate species richness. We found significant positive linkages between ecosystem service diversity and species richness of all considered taxa. The provision of the majority of ecosystem services was higher in areas of high taxon diversity, indicating both positive relationships and slight trade-offs in maximizing single ecosystem services. In general, ecosystem service categories were a comparable indicator of species richness as climate. Our findings show that multifunctionality largely coincides with high levels of biodiversity within the study region. Hence, an integrative ecosystem management approach that incorporates ecosystem services and biodiversity concerns is needed to both provide diverse ecosystem benefits and conserve biological diversity.
© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Ecosystem services and biodiversity conservation have become the two dominant, and potentially conflicting (Bullock et al., 2011; Marrs et al., 2007; McShane et al., 2011) management aims in conservation science during the last decades. Ecosystem services are the numerous benefits people directly or indirectly appropriate from the functioning of ecological systems and provide the foundations for human well-being (Daily, 1997; Nelson et al., 2009). The ecosystem services concept combines resource use, ecosystem management – including adaptation to impacts of driving forces such as land use and climate change – and the valuation of nature (Maskell et al., 2013), making it a key concept that bridges social and ecological systems (Carpenter et al., 2009). Biodiversity is vital for maintaining ecosystem processes and functioning (Duffy, 2009; Hector and Bagchi, 2007). Its loss has been shown to cause ecosystem degradation (Hooper et al., 2012). Hence, biodiversity is seen as essential requirement for the provisioning of ecosystem services (Diaz et al., 2006). Here it should be noted that as well as an instrumental value related to the provision of ecosystem services, the conservation of biodiversity is also a normative goal in its own right (Mace et al., 2012). Biodiversity conservation is therefore not solely contingent on the instrumental contribution to human well-being it may provide.

The increasing number of studies on the functional relationships between biodiversity and ecosystem services reveal mostly positive patterns (Gamfeldt et al., 2013; Hector and Bagchi, 2007; Maskell et al., 2013). However, many of these diversity-ecosystem services studies focus on a single facet of diversity such as one species group and a single ecosystem service, such as primary productivity (Costanza et al., 2007), pest control (Simon et al., 2010) or agricultural yields (Di Falco and Chavas, 2006). Managing an ecosystem for a single ecosystem service is potentially problematic as it may result in trade-offs in terms of associated biodiversity (Ingram et al., 2012; Ridder, 2008; Rodriguez et al., 2006) and thereby compromises conservation efforts. The interplay between the provision of multiple ecosystem services and biodiversity

* Corresponding author. Tel.: +49 4131 677 1571.
E-mail address: patricbrandt@gmx.de (P. Brandt).

0006-3207/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2013.12.003

represents an important knowledge gap (Geijzendorffer and Roche, 2013; Sircely and Naeem, 2012), potentially limiting our ability to effectively manage multifunctional landscapes for both ecosystem services provision and biodiversity conservation.

In this regard, it becomes vital to analyze ecosystems that are managed for diverse societal needs. Multifunctional ecosystems offer several services simultaneously to satisfy social, cultural, economic and environmental demands (O'Farrell et al., 2010). Hence, a diverse set of ecosystem services needs to be considered when assessing the relations between biodiversity conservation and ecosystem service provision in multifunctional ecosystems (Chan et al., 2006; Tallis and Polasky, 2009). This includes services that cannot be straightforwardly linked to specific ecosystem functions such as cultural services (Hernandez-Morcillo et al., 2013). Potential synergies between ecosystem services and biodiversity are expected, though they might vary across ecosystems and depend on the specific ecosystem services and aspects of biodiversity taken into consideration (Mace et al., 2012).

Forests are of immense global importance in delivering a myriad of benefits to humanity (Bonan, 2008; FAO, 2010; Schwenk et al., 2012). In particular, temperate rainforests represent an ecologically complex, unique ecosystem with high biodiversity importance, subjected to multiple human demands. We analyzed a region along the Pacific coastline of North America harboring the world's largest remaining extents of temperate rainforests (DellaSala, 2011). While currently offering a broad range of goods and services such as salmon (*Oncorhynchus* spp.), timber, water regulation and recreation, these rainforests are threatened by climate and land use changes (DellaSala, 2011; Fitzgerald et al., 2011).

We addressed three key questions to investigate linkages and trade-offs between ecosystem services and biodiversity across the temperate rainforest region of the Pacific Northwest: (1) How is ecosystem service diversity related to species richness across different taxonomic groups? (2) How are ecosystem services and their diversity linked to different diversity levels of the considered taxa? (3) In order to untangle the interrelations among the environment, ecosystem services and species richness we tested if the provision of ecosystem services, grouped by the millennium ecosystem service assessment (MA) categories, alongside environmental variables such as climate and land cover, indicate species richness. Here, we did not seek to explain the functional relations between biodiversity and ecosystem services categories. Rather, we described the patterns (Shmueli, 2010) between the types of ecosystem services provided, their diversity and biodiversity across the temperate rainforest region of the Pacific Northwest and discussed the implications of these patterns for multifunctional landscape management and conservation at a regional scale.

Recent studies focusing on the relationship between ecosystem services and biodiversity have taken a functional perspective and mostly considered limited ecosystem service categories such as provisioning or regulating services (e.g. Balvanera et al., 2006; Costanza et al., 2007; Schwenk et al., 2012) and single species groups such as plant species (e.g. Gamfeldt et al., 2013; Maskell et al., 2013; Tilman et al., 2012). By involving multiple taxa and multiple ecosystem services including supporting and cultural services, we aim to identify more comprehensive patterns relating ecosystem services to biodiversity.

Here we note that the direct quantification of ecosystem services is often problematic and that there might be considerable differences between the ecosystem services that potentially flow from a given ecosystem and the actual services that are appropriated at a given point in time. For example, timber harvest is an indicator for the appropriation of timber but provides limited information regarding the capacity of a given system to sustainably provide timber. Similarly it can be argued that benefits received (i.e. the direct quantification of services) from physically appropriated goods such as timber must be related to how those physical goods contribute to human well-being (Fischer et al., 2009). Given the importance of both the actual appropriation and the potential capacity to supply ecosystem services and the difficulty in directly and accurately quantifying multiple ecosystem services across large spatial and temporal extents, we focus on the mapping of proxy datasets that indicate nine important potential and actual ecosystem services within the temperate rainforest region of the Pacific Northwest. The following proxy data for ecosystem services were modeled: timber harvest, salmon abundance, deer hunting, net primary productivity, carbon storage in vegetation, organic matter in soil, forest importance for drinking water supply, landscape aesthetics, and park visitation. These proxies for ecosystem services were grouped into the MA categories of provision, supporting, regulating, and cultural ecosystem services (MA, 2005). Biodiversity was quantified in terms of spatially explicit species richness data for higher taxa, including mammals, birds, trees and amphibians. Diversity metrics were derived for ecosystem services and the higher taxa. Subsequently, we computed univariate models to reveal the patterns between ecosystem service diversity and species richness. Potential and actual ecosystem services and their diversity were linked to the higher taxon diversity. Multivariate direct gradient analyses were performed to assess if the MA ecosystem service categories are able to indicate species richness in interaction with and untangled from environmental variables such as climate and land cover.

2. Materials and methods

2.1. Study area

The study area was based on the original coastal temperate rainforest extent of the Pacific Northwest region (DellaSala, 2011) that shows an overall high proportion of forest coverage. All US counties that intersect the original coastal rainforest extent, including a buffer of 15 km, were incorporated into the study area of 325,614 km^2. This broad extent was chosen to ensure that climate and land cover gradients are well represented. Due to limited data availability, coastal rainforest regions located in British Columbia and Alaska were excluded from our analyses. All metrics related to species richness, ecosystem services and environmental data were mapped at a resolution of approximately 8 × 8 km – 3997 grid cells in total. It is important to note that the study extent, while dominated by forests, encompasses a spatially heterogeneous matrix of different land uses that in turn create spatially heterogeneous patterns of ecosystem service provision and biodiversity. The study extent comprised 55% forest, 33% scrub- and grassland, 7% cultivated areas and 5% developed/urban regions. Public lands in this region are managed under the Northwest Forest Plan that governs ecosystem management and biodiversity conservation (DellaSala and Williams, 2006). However, non-federal landowners frequently focus on timber management as the primary ecosystem service. ARCGIS 10.1 was used for all geo-processing work.

2.2. Ecosystem service data

The proxy data used refer either to the actual goods or services people appropriate from nature, known as 'ecosystem services', or to the capacity of the ecosystem to deliver those goods and services to society, conceptualized here as 'potential ecosystem services' (Vira and Adams, 2009). The data were based on physical occurrence of actual and potential ecosystem services, rather than the monetary or non-monetary values associated with those services.

All data were gathered from publically available datasets, further processed and linked to spatial data or were readily available in a spatially explicit format. We compiled GIS-layers indicating the nine potential and actual ecosystem services, which were also grouped into MA categories – i.e. provisioning, regulating, supporting, and cultural ecosystem services (MA, 2005). Detailed descriptions of the datasets and data sources can be found in the online appendix (Online appendix, Table A1).

2.2.1. Provisioning services

2.2.1.1. Timber harvest. Timber is one of the most prominent resources derived from forest ecosystems and has been intensively harvested from temperate rainforests in this region. This layer depicts the total volume of timber harvested in 2010 measured in thousands of board feet. Derived tabular data are based on the county level.

2.2.1.2. Salmon abundance. Salmon are an important economic and food resource for the entire coastal rainforest region in North America and they are the key for trophic dynamics and energy transfer (DellaSala, 2011). The salmon abundance data are based on observed (1998–2005) and modeled data at the watershed level (Pinsky et al., 2009). Watershed based data were normalized and then converted into gridded data.

2.2.1.3. Deer hunting. Hunting has been taking place for millennia across the coastal temperate rainforest region of North America (Schoonmaker et al., 1997). Hence, hunting can be considered as a traditional source of local food resources. This layer indicates overall deer hunting successes for 2010 measured in counted deer kills. Census data are obtained and mapped based on hunting management units defined by State Departments of Fish & Wildlife.

2.2.2. Supporting services

2.2.2.1. Net primary productivity. The Pacific coastal rainforests belong to the most productive ecosystems worldwide (DellaSala, 2011), and primary productivity is a key ecological function from which many other, directly used, ecosystem services flow. Gridded information on NPP is derived from NASA's MODIS satellite data in a 10 km^2 grid cell resolution based on monthly values averaged for 2010 in gC m^{-2} day^{-1}.

2.2.3. Regulating services

2.2.3.1. Carbon storage in vegetation. The storage of atmospheric carbon in biomass is essential to climate regulation and climate change mitigation. The coastal temperate rainforests in North America show high carbon densities compared to other forest ecosystems (DellaSala, 2011; Woodbury et al., 2007). Gridded data show total mean carbon content in vegetation for 1961–1990 and originate from outputs of the MC1 dynamic vegetation model (Bachelet et al., 2001a,b) in an 8.8 km^2 grid cell resolution.

2.2.3.2. Organic matter in soil. Organic matter strongly influences soil properties such as water retention, erodibility and fertility (Ontl and Schulte, 2012). Furthermore, soil represents a large carbon pool. The sequestration of atmospheric carbon in soil organic matter contributes to climate change mitigation (Lal, 2004). The data used indicates the total content of organic matter in soil expressed as percent by weight of the 2 mm soil fraction at the watershed level.

2.2.3.3. Forest importance for drinking water supply. Forests are known to serve as important regulators of drinking water, particularly in this region (DellaSala et al., 2011). This layer combines precipitation intensity, proportion of forests and population density per watershed and was derived from the USDA 'forests to faucets' dataset (Barnes et al., 2009). We used these data as proxy for water regulation (Todd and Weidner, 2010).

2.2.4. Cultural services

2.2.4.1. Landscape aesthetics. The possibility to experience landscapes that are largely undisturbed by human pressure is usually accepted as a great benefit that ecological systems may offer in terms of recreation (Gobster et al., 2007). The compiled dataset consists of several spatial layers related to infrastructure such as roads, railroads and settlements, and natural elements such as lakes, rivers and forests that are undisturbed by human influences. All layers were weighted according to their naturalness. Terrain roughness was incorporated as proxy for physical landscape heterogeneity. Each layer was weighted either positively or negatively except for terrain roughness that was weighted based on three states, low roughness as negative, medium roughness as neutral and high roughness as positive. The resulted 'landscape aesthetics' layer is considered as a potential ecosystem service since the quantification of the actual cultural values associated with the landscapes of the study region was beyond the scope of our analysis.

2.2.4.2. Park visitation. State and national parks represent essential recreation areas in the US (Daniel et al., 2012), facilitating environmental education and sustainable tourism. We mapped the tabular park visitation data for 2010 on state and national parks, derived from the PAD-US protected area database (v. 1.2). Subsequently spatial data were aggregated on county level since most of the state parks do not match the working resolution and hence would not have been visible for the analyses. We used this dataset as proxy for the provision of space for recreation and cultural experiences.

All data based on unequally sized areas were normalized based on area. Thus, every layer refers to equal area units. For further analyses all potential and actual ecosystem service layers were transformed to a standardized scale based on their maximum values (Raudsepp-Hearne et al., 2010). Hence, all ecosystem service values range between 0 and 1.

2.3. Species data

Spatially explicit species richness data for higher taxa, including mammals (between 1 and 85 species recorded), birds (88–223 species), trees (1–50 species) and amphibians (2–38 species) were obtained as gridded layer from several resources (Online appendix, Table A2). For tree species, we compiled a richness layer through aggregating range polygon data (Little, 1978). Selected species groups represent major parts of the overall species diversity that exists across the Pacific coastal temperate rainforests and contain numerous species of economic, cultural and conservation importance. Reptiles, as a further terrestrial vertebrate group, were not included into the analyses since they are not well represented, nor particularly abundant, across the Pacific coastal temperate rainforests compared to other regions of their occurrence (Böhm et al., 2013).

2.4. Applied statistical approaches

All statistical analyses were undertaken using R 2.15, including the packages 'raster' (v. 2.1.12) for handling spatial data, 'car' (v. 2.0.16) for building generalized linear models (GLMs), 'spdep' (v. 0.5.56) for correcting autocorrelation patterns, 'vegan' (v. 2.0.6) to obtain diversity indices and to perform principal component analyses (PCAs) as well as redundancy analyses (RDAs).

2.4.1. Simpson diversity metrics

Diversity metrics were derived by using the Simpson diversity index for potential and actual ecosystem services (Raudsepp-Hearne et al., 2010) and higher taxa ranging between 0 (low diversity) and 1 (high diversity). The Simpson index is illustrated by the following formula:

$$D = 1 - \sum_{i=1}^{R} p^2 i$$

R is the richness of taxa/ecosystem services and p_i is the proportion of abundances for the ith taxon/ecosystem service.

The Simpson diversity measure takes abundances into account and equals the probability that two entities taken at random from the dataset represent the same type (Simpson, 1949). The Simpson diversity of higher taxonomic groups was used as biodiversity metric that is comparable to the Simpson diversity of ecosystem services. A color map was compiled illustrating the degree of spatial correspondence between the diversity metrics across the study area.

2.4.2. Univariate linkage modeling: ecosystem service diversity – species richness

In order to model the relationship between ecosystem service diversity and species richness, we chose a univariate model approach using GLMs (Crawley, 2007). Due to the non-normalized distribution of model residuals, we opted for GLMs with Poisson error structure. Species richness data were selected as dependent variables and ecosystem service diversity as independent variable since Poisson-GLMs require real count data. Hence, we follow a descriptive approach rather than explaining the causal relationship between biodiversity and ecosystem services. GLMs also included quadratic terms and were reduced based on the Akaike information criterion (AIC), to avoid overfitting (Sakamoto et al., 1986). Since model residuals revealed patterns of spatial autocorrelation, we applied spatial eigenvector filtering to incorporate spatial autocorrelation structures (Dray et al., 2006; Griffith and Peres-Neto, 2006). Spatial eigenvectors are derived from a neighborhood matrix spanning a distance of 100 km, which was chosen due to highest spatial autocorrelation values within that distance. The number of incorporated spatial eigenvectors was based on Moran's I significance values for each GLM. Eigenvectors were included until they exceeded a significant Moran's I value ($p < 0.05$).

2.4.3. Ordination techniques: ecosystem service categories, land cover and climate – species richness

A multivariate direct gradient analysis was applied to investigate the proportion of species richness variances captured by potential as well as actual ecosystem services grouped into the MA categories and environmental variables. Initial analyses of data distribution and gradient lengths showed that linear models are a correct general assumption for our data. Hence we used a PCA to reduce multicollinearity inherent to the climatic parameters applied and a partially constrained RDA as overall multivariate model (Legendre and Legendre, 2012) to partition the explained variance of four different variable groups, such as potential and actual ecosystem services for each MA category, 'climate', 'land cover' and 'geography'. Species richness data from the considered taxonomic groups served as response variables and were subjected to Hellinger transformations as proposed for analyzing heterogeneous community datasets (Legendre and Gallagher, 2001). Climatic data were derived by performing a PCA, including 19 BIOCLIM variables that were obtained as downscaled spatial grids in a 2.5 arc-min resolution (Hijmans et al., 2005). The PCA scores from the first two principal components were extracted and subsequently used as 'climate' variable group for the RDAs (Hanspach et al., 2011). Land cover data were derived from the USGS land use survey 2006 comprising 16 land cover classes, including developed, forested, cultivated, wetland, herbaceous, scrubland and barren land cover types at a grid cell resolution of 30 meters. The original dataset was spatially downscaled to match the working resolution. To account for spatial autocorrelation effects, we defined latitude and longitude as a further variable group named 'geography'.

3. Results

3.1. Ecosystem service diversity and species richness

The compiled spatial layers of potential as well as actual ecosystem services, the derived Simpson diversity metrics of the considered taxa and ecosystem services varied across the study area (Fig. 1). The diversity of taxa and the diversity of ecosystem services were highly correlated, indicated by Spearman's rho = 0.719 ($p < 0.001$). Species richness maps for mammals, birds, trees and amphibians are shown in online appendix (Fig. A1).

Ecosystem service diversity showed significant positive interactions with the richness of mammal, bird, tree, and amphibian

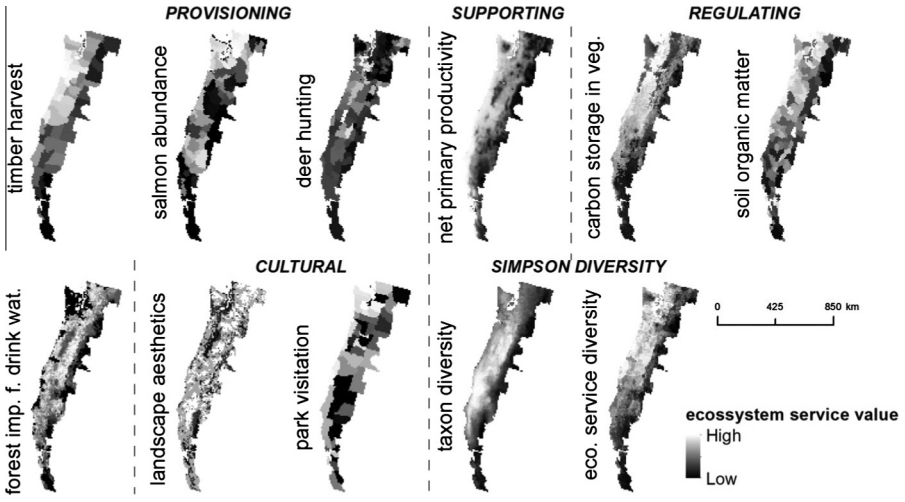


Fig. 1. Spatial distribution of nine potential and actual ecosystem services as well as the Simpson diversity of considered taxa and ecosystem services across the coastal temperate rainforest region of the Pacific Northwest, USA.

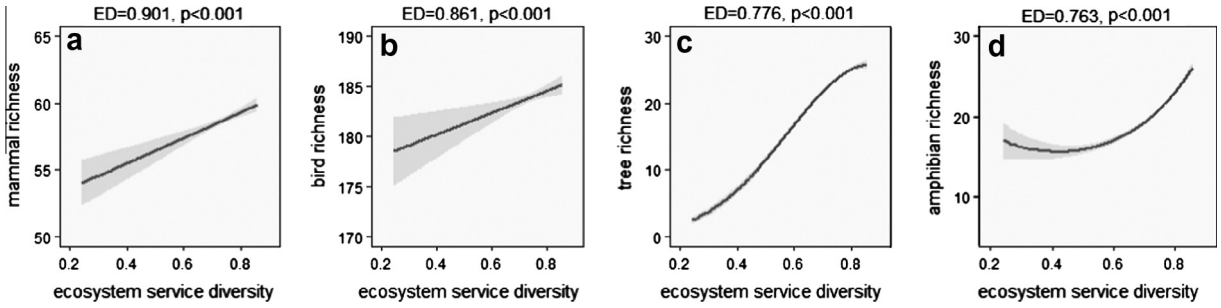


Fig. 2. GLM results for linkages between ecosystem service diversity and mammal, bird, tree, and amphibian richness. Incorporated spatial eigenvectors were kept at mean level. Light gray areas indicate the 95% confidence intervals of prediction errors (ED = explained deviance).

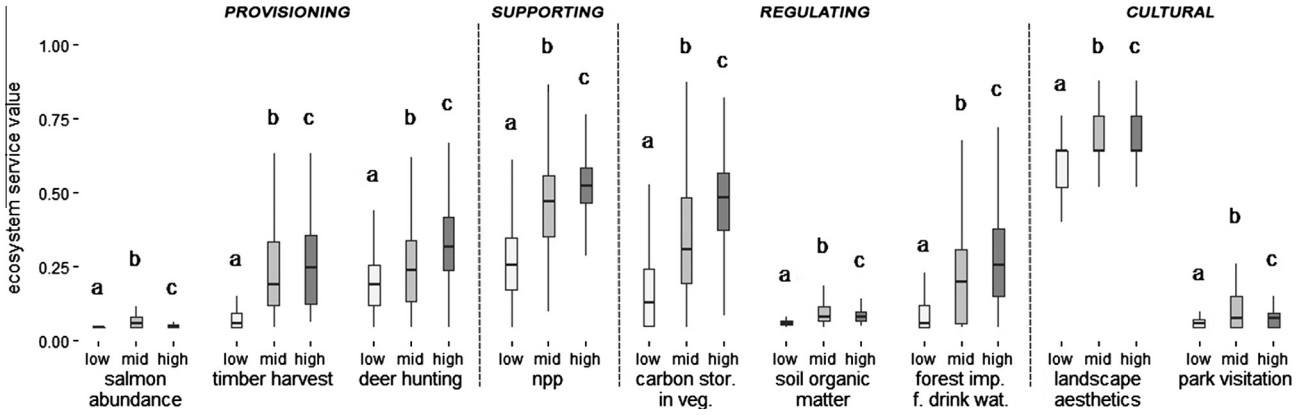


Fig. 3. Potential and actual ecosystem services for three levels of overall Simpson diversity of considered taxa (low = 0.335–0.514, mid = 0.514–0.573, high = 0.573–0.634). Grouping maintained equal sample sizes within each level. A Wilcoxon rank sum test was performed to assess the mean differences between Simpson diversity levels ($p < 0.001$). *P*-values were Bonferroni corrected to account for multiple testing.

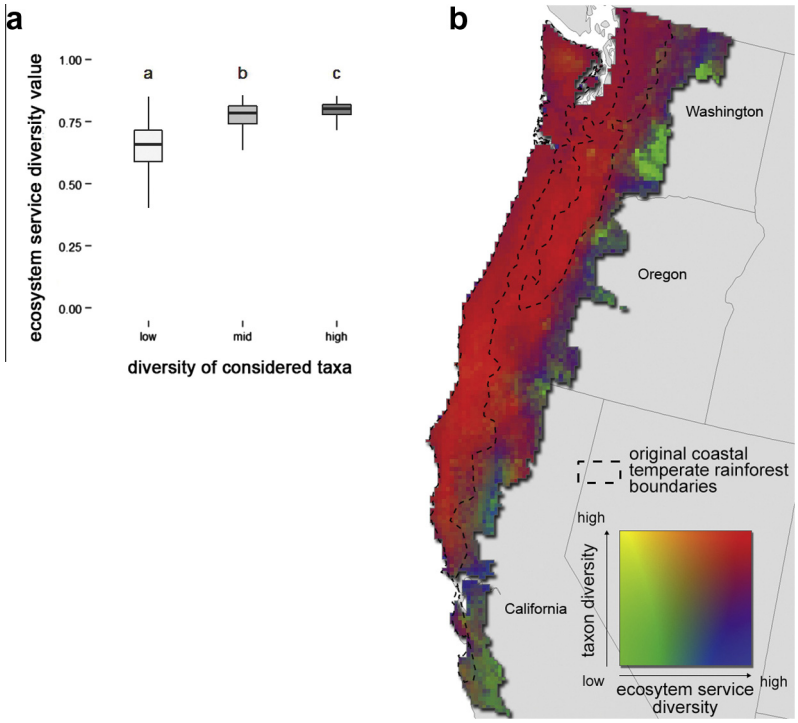


Fig. 4. (a) Ecosystem service diversity for three levels of overall Simpson diversity of the four considered taxonomic groups (low = 0.335–0.514, mid = 0.514–0.573, high = 0.573–0.634). Grouping maintained equal sample sizes within each level. A Wilcoxon rank sum test was performed to assess the mean differences between Simpson diversity levels ($p < 0.001$). *P*-values were Bonferroni corrected to account for multiple testing. (b) Spatial correspondence between ecosystem service diversity and diversity of considered taxa. Mapped pixel colors were assigned based on a RGB color space defined by ecosystem service diversity on the *x*-axis and diversity of four considered taxa on the *y*-axis.

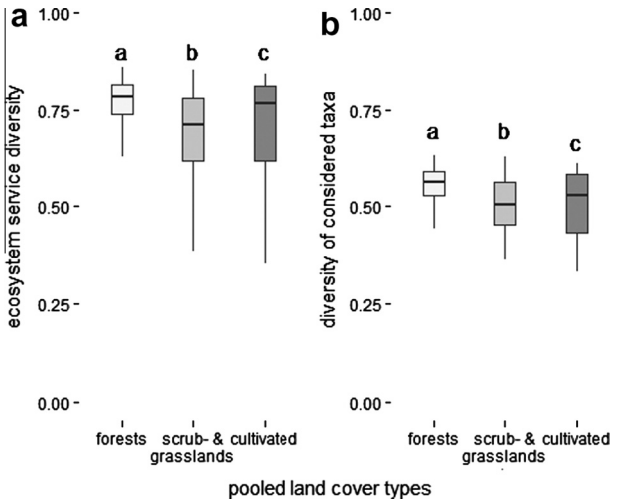


Fig. 5. Ecosystem service diversity (a) and diversity of considered taxa (b) for three pooled land cover types: forests, scrub- and grasslands, and cultivated areas. Developed land cover types were excluded due to minor relevance for the provisioning of analyzed ecosystem services.

species (Fig. 2, $p < 0.001$). Mammal and bird species richness increased linearly with higher ecosystem service diversity (Fig. 2a and b), tree richness showed a sigmoidal relationship indicating a saturation effect of tree species richness at the highest levels of ecosystem service diversity (Fig. 2c). Amphibian richness increased steeply with elevated ecosystem service diversity (Fig. 2d). The GLM on mammal richness had the highest model fit expressed as explained deviance (ED = 0.901), the model that considered amphibian richness the lowest (ED = 0.763).

3.2. Ecosystem services and taxon diversity

Higher values of ecosystem services were related to higher levels of the overall Simpson taxon diversity for most of the applied potential and actual ecosystem services across all MA categories (Fig. 3). However, salmon abundance, soil organic matter and park visitation differed from that pattern, indicating trade-offs between maxima of single ecosystem services and diversity of involved taxa. No pronounced ecosystem service gradient could be detected based on a PCA, including all modeled ecosystem services (not shown). The first two PCA axes together explained 46% of the overall variance.

Higher ecosystem service diversity was significantly linked to elevated taxon diversity (Fig. 4a, $p < 0.001$). However, less pronounced differences between medium and high levels of taxon diversity suggested a nonlinear relationship resulting in a saturation effect for ecosystem service diversity in areas of high taxon diversity. High spatial correspondence between ecosystem service diversity and the diversity of included taxa was shown within coastal temperate rainforest regions throughout most of the Pacific Northwest (Fig. 4b).

3.3. Ecosystem service categories as indicators for species richness

To assess both the distribution of ecosystem service diversity and the diversity of higher taxa for major land cover types, we pooled the detailed land cover types into three groups, namely, 'forests', 'scrub- and grasslands', and 'cultivated areas'. Highest diversity values for ecosystem services as well as considered taxa were significantly higher for forests (Fig. 5a and b, $p < 0.05$). Groups differed significantly as assessed through a one-way analysis of

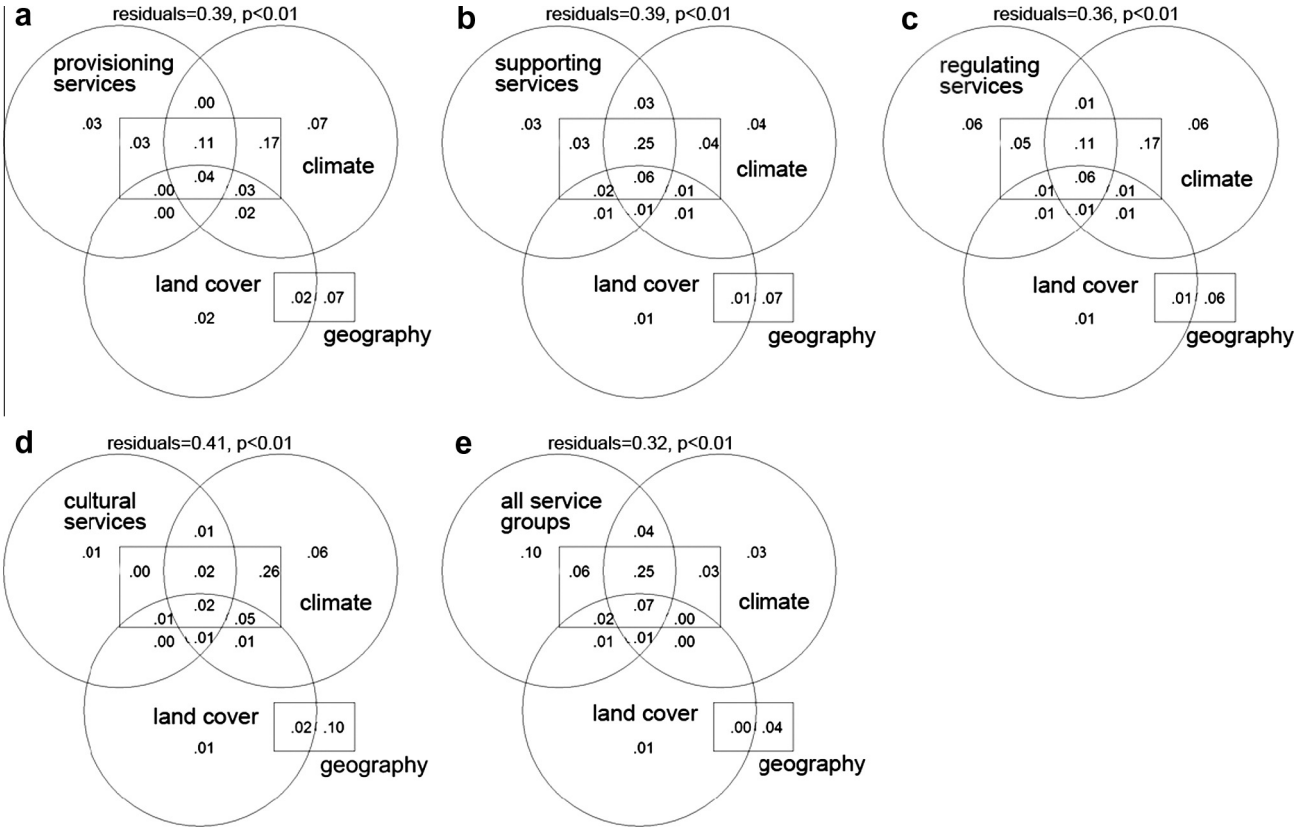


Fig. 6. RDA variance partitioning results for species richness including mammals, birds, trees and amphibians separately indicated by different ecosystem service categories: (a) provisioning, (b) supporting, (c) regulating, (d) cultural and (e) all potential and actual ecosystem services, climate, land cover (circles) and geography (rectangle). Displayed values show captured variances as adjusted R^2 for all single (non-overlapping parts of circles and the rectangle) and combined effects (overlapping parts of circles and the rectangle).

variance and a subsequent paired t-test ($p < 0.05$). P-values were Bonferroni corrected to account for multiple testing.

Constrained RDAs revealed that ecosystem service categories significantly indicated species richness in a comparable magnitude of land cover and climate (Fig. 6, $p < 0.001$). Among the RDAs that were fitted with single ecosystem service categories, the RDA with regulating services showed the lowest model error (Fig. 6c, residuals = 0.36) and the one that included cultural services the highest error (Fig. 6d, residuals = 0.41). The RDA incorporating the entire set of potential and actual ecosystem services as variable group showed the lowest model error among all RDAs (Fig. 6e, residuals = 0.32). However, for the majority of RDAs the climatic space was, after geography, the variable group that captured most of the species richness variances. This reflected both the prevailing climatic gradient that shapes diversity patterns across the temperate rainforests of the Pacific Northwest and an inherent autocorrelation pattern. Focusing on interactions between variable groups the climate-geography interactions showed the strongest effects followed by the ecosystem service category–climate interactions.

4. Discussion

4.1. Ecosystem service diversity and species richness

We found broad, positive relationships between ecosystem service diversity and species richness. Such a pattern confirms the findings of Egoh et al. (2009) who illustrated a spatial congruency between ecosystem services and biological diversity in South Africa. No trade-offs were observed in our study between ecosystem service diversity and species richness. Other studies reported both trade-offs and concordances between ecosystem service hotspots and biodiversity or its conservation (Chan et al., 2006; Turner et al., 2007). Our results clearly show that high levels of biodiversity are found in areas that provide diverse actual and potential ecosystem services across the coastal temperate rainforest region of the Pacific Northwest. This pattern was also apparent when all considered taxa were combined to one diversity index, particularly within the original coastal temperate rainforest boundaries. Though, some minor areas showed a contrasting pattern of low biodiversity but high ecosystem service diversity. These scattered areas were mostly distributed at the inland edges of our study region indicating transition zones to other ecosystems that might start to harbor different species inventories not included in our study.

Saturation effects were revealed for tree species and overall taxon diversity suggesting that further ecosystem service increases in regions of highly diverse ecosystem service provision coincide with marginally higher biodiversity levels. This might relate to redundancies of present species in terms of the necessary ecosystem functions that are required to maintain considered ecosystem services (Duffy, 2009; Hector and Bagchi, 2007). Notwithstanding, including more services and thus more ecosystem functions would probably incorporate more biodiversity needed to sustain these functions (Gamfeldt et al., 2008). Moreover, biodiversity reduces the vulnerability of ecosystems to disturbances, serving both as a backup for functional degradation and to ensure diverse and fast responses to perturbations hence improving overall ecosystem resilience (Mori et al., 2013).

4.2. Ecosystem services and their diversity for different levels of taxon diversity

The majority of our results indicate positive relationships between single ecosystem services included and the overall diversity of the considered taxa. Similar patterns are found in recent studies (Balvanera et al., 2006; Schneiders et al., 2012), in particular for productivity and biodiversity (Gamfeldt et al., 2013; Tilman et al., 2012) – though Costanza et al. (2007) found a temperature dependent relationship. The relation between timber harvest and taxon diversity was most surprising and probably, in part, resulted from a scale artifact inherent to the data used. It is important to note here that the established relationships do not imply causality. Yet, intense forest management is usually considered to have negative impacts on biodiversity (Bengtsson et al., 2000). The data used in our study did not include any information on how the forests are managed for timber harvest on a local scale. Hence, it is beyond the scope of our analyses to assess the effects of forest practices on biodiversity patterns.

Despite the largely positive patterns found, a few trade-offs were noticeable in our results. Salmon abundance, soil organic matter and park visitation were highest in areas with moderate levels of taxon diversity. Non-supporting patterns or trade-offs among ecosystem services are postulated (Bennett et al., 2009) and reported on a regional (Raudsepp-Hearne et al., 2010), continental (Haines-Young et al., 2012) and global scale (Naidoo et al., 2008). Though, in our case, no clear trade-offs among the studied ecosystem services could be detected.

4.3. Ecosystem service categories as indicators for species richness

Both, ecosystem service diversity and taxon diversity were highest in forested extents within the study region. Although the differences among land cover types were only marginal, it suggests that forests provide conditions most suited for supplying ecosystem services and biodiversity.

Using a multivariate approach, including the nine actual and potential ecosystem services grouped into MA categories as well as environmental variables showed that the different MA ecosystem service categories indicated species richness of the four different taxa in a comparable magnitude to climate and land cover. The capability of all ecosystem service categories, in interaction with climate, to indicate species richness illustrates that a management focusing on multiple ecosystem-based benefits and the current climatic conditions are synergistic for both ecosystem services and biodiversity. These findings support the idea that the ecosystem service approach could be used to monitor and manage biodiversity (Egoh et al., 2009). However, cultural services showed an overall weak link, probably due to the most indirect relationship to richness for instance compared to the considered regulating ecosystem services. Nevertheless, the management of ecosystems based on providing a diversity of ecosystem services might have co-benefits in terms of biodiversity conservation.

4.4. Ecosystem service approach and multifunctional ecosystems

Temperate rainforests of the Pacific Northwest simultaneously offer a multitude of ecosystem-based benefits. We were able to show that such a multifunctional ecosystem might serve as indicator of biodiversity and its conservation while delivering important goods and services to society. Our results are restricted to one region and spatial scale as well as one point in time. Thus, extrapolating these results to other regions featuring different ecosystem properties and species should be done with considerable caution. However, high biodiversity levels in multifunctional landscapes also have been shown before for areas with heterogeneous land use or agricultural regions (O'Farrell et al., 2010; Schneiders et al., 2012; Sircely and Naeem, 2012). Managing for multiple ecosystem services may also create conditions for higher levels of biodiversity. Given the co-occurrence of biodiversity and diverse ecosystem service provision, we suggest that biodiversity conservation should be integrated into the management of

multifunctional ecosystems and not only take place in areas explicitly designated for conservation.

4.5. Threats to ecosystem services and biodiversity: land use and climate change

North America's temperate rainforests are fragmented by logging, road building, and other human disturbances (DellaSala, 2011). Coinciding biodiversity loss and the degradation of ecosystem functions are expected due to habitat fragmentation and increasing land use intensity (Foley et al., 2005). However, sustainable trajectories of land use changes and restoration efforts have been positively linked to ecosystem service provision and biodiversity conservation (Nelson et al., 2009; Rey Benayas et al., 2009).

Ecosystem services in this region are threatened by a changing climate regime and projected vegetation shifts in Western North America (Wang et al., 2012). Dominant tree species and vegetation types in our study area are predicted to shift substantially until the end of the 21st century (Coops and Waring, 2011; Gonzalez et al., 2010; McKenney et al., 2007), probably detrimentally affecting both current ecosystem service and biodiversity patterns. Hence, an adaptive ecosystem management approach is needed to mitigate estimated impacts.

5. Conclusions

Our results confirm that multifunctional landscapes, here largely covered by temperate rainforests, co-occur with high levels of biodiversity. Thus, the management of ecosystem services should not substitute, but rather incorporate, biodiversity conservation since the two concepts are interdependently related through maintaining the functioning of ecosystems on the one hand and the management for goods and services on the other hand (Ingram et al., 2012; Mace et al., 2012). Based on our results, we derive the following management and research recommendations for the coastal temperate rainforest region across the Pacific Northwest.

1. The concepts of ecosystem services and biodiversity are not only linked, they act in concert. Based on our analysis, an integrative approach of ecosystem management that incorporates both ecosystem services and biodiversity is indeed beneficial in providing goods and services to society while maintaining biodiversity. We therefore support the perspective that multifunctional ecosystems should become a key for sustainable ecosystem management in this region, particularly in a way that optimizes land-use and strives for compatibility in management among different ecosystem services.
2. Our findings generally show that land managers who are interested in the provisioning of diverse ecosystem services are also able to maintain biodiversity. For instance, large landscape level management efforts inherent to the Northwest Forest Plan (DellaSala and Williams, 2006) represent approaches in which ecosystem management and biodiversity conservation on public lands are capable to produce multiple ecosystem benefits and, hence, help to maintain multifunctionality.
3. Research at finer spatial scales, incorporating time series data and information on how local forest management practices determine possible relationships between timber harvest, other ecosystem services and biodiversity would be useful for our study region. Standardized surveys and sampling protocols are required and data on socio-economical dynamics and ecosystem service valuations should be linked to assess the compatibility of (potentially competing) provisioning ecosystem services at the local and regional scale. Scenario driven analyses (Carpenter et al., 2006; Nelson et al., 2009) that consider climate and land-use changes are necessary since they may offer valuable insights about possible future trajectories of biodiversity and ecosystem service patterns in this region.

Acknowledgements

We thank the Leuphana University Lüneburg for providing the project fund. We are also very grateful to all governmental and non-governmental organizations that made available the data needed for our analyses. Finally we thank Pascal Fust for his contribution to the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.12.003.

References

Bachelet, D., Lenihan, J.M., Daly, C., Neilson, R.P., Ojima, D.S., Parton, W.J., 2001a. MC1: A Dynamic Vegetation Model for Estimating the Distribution of Vegetation and Associated Ecosystem Fluxes of Carbon, Nutrients, and Water. Technical Documentation. Version 1.0.

Bachelet, D., Neilson, R.P., Lenihan, J.M., Drapek, R.J., 2001b. Climate change effects on vegetation distribution and carbon budget in the United States. Ecosystems 4, 164–185.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol. Lett. 9, 1146–1156.

Barnes, M., Todd, A., Whitney, L.R., Barten, P., 2009. Forests, Water and People: Drinking water supply and forest lands in the Northeast and Midwest United States.

Benayas, J.M.R., Newton, A.C., Diaz, A., Bullock, J.M., 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325, 1121–1124.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. For. Ecol. Manage. 132, 39–50.

Bennett, E.M., Peterson, G.D., Gordon, L.J., 2009. Understanding relationships among multiple ecosystem services. Ecol. Lett. 12, 1394–1404.

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., Rhodin, A.G.J., Stuart, S.N., van Dijk, P.P., Young, B.E., Afuang, L.E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., Akarsu, F., Alencar, L.R.V., Allison, A., Ananjeva, N., Anderson, S., Andrén, C., Ariano-Sánchez, D., Arredondo, J.C., Auliya, M., Austin, C.C., Avci, A., Baker, P.J., Barreto-Lima, A.F., Barrio-Amorós, C.L., Basu, D., Bates, M.F., Batistella, A., Bauer, A., Bennett, D., Böhme, W., Broadley, D., Brown, R., Burgess, J., Captain, A., Carreira, S., Castañeda, M.D.R., Castro, F., Catenazzi, A., Cedeño-Vázquez, J.R., Chapple, D.G., Cheylan, M., Cisneros-Heredia, D.F., Cogalniceanu, D., Cogger, H., Corti, C., Costa, G.C., Couper, P.J., Courtney, T., Crnobrnja-Isailovic, J., Crochet, P.-A., Crother, B., Cruz, F., Daltry, J.C., Daniels, R.J.R., Das, I., de Silva, A., Diesmos, A.C., Dirksen, L., Doan, T.M., Dodd Jr., C.K., Doody, J.S., Dorcas, M.E., Duarte de Barros Filho, J., Egan, V.T., El Mouden, E.H., Embert, D., Espinoza, R.E., Fallabrino, A., Feng, X., Feng, Z.-J., Fitzgerald, L., Flores-Villela, O., França, F.G.R., Frost, D., Gadsden, H., Gamble, T., Ganesh, S.R., Garcia, M.A., García-Pérez, J.E., Gatus, J., Gaulke, M., Geniez, P., Georges, A., Gerlach, J., Goldberg, S., Gonzalez, J.-C.T., Gower, D.J., Grant, T., Greenbaum, E., Grieco, C., Guo, P., Hamilton, A.M., Hare, K., Hedges, S.B., Heideman, N., Hilton-Taylor, C., Hitchmough, R., Hollingsworth, B., Hutchinson, M., Ineich, I., Iverson, J., Jaksic, F.M., Jenkins, R., Joger, U., Jose, R., Kaska, Y., Kaya, U., Keogh, J.S., Köhler, G., Kuchling, G., Kumlutas, Y., Kwet, A., La Marca, E., Lamar, W., Lane, A., Lardner, B., Latta, C., Latta, G., Lau, M., Lavin, P., Lawson, D., LeBreton, M., Lehr, E., Limpus, D., Lipczynski, N., Lobo, A.S., López- Luna, M.A., Luiselli, L., Lukoschek, V., Lundberg, M., Lymberakis, P., Macey, R., Magnusson, W.E., Mahler, D.L., Malhotra, A., Mariaux, J., Maritz, B., Marques, O.A.V., Márquez, R., Martins, M., Masterson, G., Mateo, J.A., Mathew, R., Mathews, N., Mayer, G., McCranie, J.R., Measey, G.J., Mendoza-Quijano, F., Menegon, M., Métrailler, S., Milton, D.A., Montgomery, C., Morato, S.A.A., Mott, T., Muñoz-Alonso, A., Murphy, J., Nguyen, T.Q., Nilson, G., Nogueira, C., Núñez, H., Orlov, N., Ota, H., Ottenwalder, J., Papenfuss, T., Pasachnik, S., Passos, P., Pauwels, O.S.G., Pérez-Buitrago, N., Pérez-Mellado, V., Pianka, E.R., Pleguezuelos, J., Pollock, C., Ponce-Campos, P., Powell, R., Pupin, F., Quintero Díaz, G.E., Radder, R., Ramer, J., Rasmussen, A.R., Raxworthy, C., Reynolds, R., Richman, N., Rico, E.L., Riservato, E., Rivas, G., da Rocha, P.L.B., Rödel, M.-O., Rodríguez Schettino, L., Roosenburg, W.M., Ross, J.P., Sadek, R., Sanders, K., Santos-Barrera, G., Schleich, H.H., Schmidt, B.R., Schmitz, A., Sharifi, M., Shea, G., Shi, H.-T., Shine, R., Sindaco, R., Slimani, T., Somaweera, R., Spawls, S., Stafford, P., Stuebing, R., Sweet, S., Sy, E., Temple, H.J., Tognelli, M.F., Tolley, K.,

Tolson, P.J., Tuniyev, B., Tuniyev, S., Üzüm, N., van Buurt, G., Van Sluys, M., Velasco, A., Vences, M., Vesely, M., Vinke, S., Vinke, T., Vogel, G., Vogrin, M., Vogt, R.C., Wearn, O.R., Werner, Y.L., Whiting, M.J., Wiewandt, T., Wilkinson, J., Wilson, B., Wren, S., Zamin, T., Zhou, K., Zug, G., 2013. The conservation status of the world's reptiles. Biol. Conserv. 157, 372–385.
Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320, 1444–1449.
Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F., Rey-Benayas, J.M., 2011. Restoration of ecosystem services and biodiversity: Conflicts and opportunities. Trends Ecol. Evol. 26, 541–549.
Carpenter, S.R., Bennett, E.M., Peterson, G.D., 2006. Scenarios for ecosystem services: an overview. Ecol. Soc. 11.
Carpenter, S.R., Mooney, H.A., Agard, J., Capistrano, D., DeFries, R.S., Diaz, S., Dietz, T., Duraiappah, A.K., Oteng-Yeboah, A., Pereira, H.M., Perrings, C., Reid, W.V., Sarukhan, J., Scholes, R.J., Whyte, A., 2009. Science for managing ecosystem services: beyond the millennium ecosystem assessment. Proc. Natl. Acad. Sci. USA 106, 1305–1312.
Chan, K.M.A., Shaw, M.R., Cameron, D.R., Underwood, E.C., Daily, G.C., 2006. Conservation planning for ecosystem services. Plos Biol. 4, 2138–2152.
Coops, N.C., Waring, R.H., 2011. Estimating the vulnerability of fifteen tree species under changing climate in Northwest North America. Ecol. Model. 222, 2119–2129.
Costanza, R., Fisher, B., Mulder, K., Liu, S., Christopher, T., 2007. Biodiversity and ecosystem services: a multi-scale empirical study of the relationship between species richness and net primary production. Ecol. Econom. 61, 478–491.
Crawley, M.J., 2007. The R Book. John Wiley & Sons, West Sussex.
Daily, G., 1997. Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington DC.
Daniel, T.C., Muhar, A., Arnberger, A., Aznar, O., Boyd, J.W., Chan, K.M.A., Costanza, R., Elmqvist, T., Flint, C.G., Gobster, P.H., Gret-Regamey, A., Lave, R., Muhar, S., Penker, M., Ribe, R.G., Schauppenlehner, T., Sikor, T., Soloviy, I., Spierenburg, M., Taczanowska, K., Tam, J., von der Dunk, A., 2012. Contributions of cultural services to the ecosystem services agenda. Proc. Natl. Acad. Sci. USA 109, 8812–8819.
DellaSala, D.A., 2011. Temperate and Boreal Rainforests of the World: Ecology and Conservation. Island Press, Washington DC.
DellaSala, D.A., Williams, J.E., 2006. Special section: the northwest forest plan: a global model of forest management in contentious times. Conserv. Biol. 20, 274–276.
DellaSala, D.A., Karr, J.R., Olson, D.M., 2011. Roadless areas and clean water. J. Soil Water Conserv. 66, 78A–84A.
Di Falco, S., Chavas, J.P., 2006. Crop genetic diversity, farm productivity and the management of environmental risk in rainfed agriculture. Eur. Rev. Agric. Econom. 33, 289–314.
Diaz, S., Fargione, J., Chapin, F.S., Tilman, D., 2006. Biodiversity loss threatens human well-being. Plos Biol. 4, 1300–1305.
Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol. Model. 196, 483–493.
Duffy, J.E., 2009. Why biodiversity is important to the functioning of real-world ecosystems. Front. Ecol. Environ. 7, 437–444.
Egoh, B., Reyers, B., Rouget, M., Bode, M., Richardson, D.M., 2009. Spatial congruence between biodiversity and ecosystem services in South Africa. Biol. Conserv. 142, 553–562.
Nations, F.a.A.O.o.t.U., 2010. Global Forest Resources Assessment 2010, Main report, Rome.
Fischer, B., Turner, R.K., Morling, P., 2009. Defining and classifying ecosystem services for decision making. Ecol. Econom. 68, 643–653.
Fitzgerald, J., DellaSala, D.A., McNeely, J., Grumbine, E., 2011. A gobal strategy for rainforests in the era of climate change. In: DellaSala, D.A. (Ed.), Temperate and Boreal Rainforests of the World: Ecology and Conservation. Island Press, Washington DC, pp. 260–274.
Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574.
Gamfeldt, L., Hillebrand, H., Jonsson, P.R., 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. Ecology 89, 1223–1231.
Gamfeldt, L., Snall, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Froberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andren, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4.
Geijzendorffer, I.R., Roche, P.K., 2013. Can biodiversity monitoring schemes provide indicators for ecosystem services? Ecol. Indicators 33, 148–157.
Gobster, P.H., Nassauer, J.I., Daniel, T.C., Fry, G., 2007. The shared landscape: what does aesthetics have to do with ecology? Landscape Ecol. 22, 959–972.
Gonzalez, P., Neilson, R.P., Lenihan, J.M., Drapek, R.J., 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Global Ecol. Biogeogr. 19, 755–768.
Griffith, D.A., Peres-Neto, P.R., 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. Ecology 87, 2603–2613.
Haines-Young, R., Potschin, M., Kienast, F., 2012. Indicators of ecosystem service potential at European scales: mapping marginal changes and trade-offs. Ecol. Indicators 21, 39–53.
Hanspach, J., Kuhn, I., Schweiger, O., Pompe, S., Klotz, S., 2011. Geographical patterns in prediction errors of species distribution models. Global Ecol. Biogeogr. 20, 779–788.
Hector, A., Bagchi, R., 2007. Biodiversity and ecosystem multifunctionality. Nature 448, 188-U186.
Hernandez-Morcillo, M., Plieninger, T., Bieling, C., 2013. An empirical review of cultural ecosystem service indicators. Ecol. Indicators 29, 434–444.
Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.
Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., O'Connor, M.I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486, U105–U129.
Ingram, J.C., Redford, K.H., Watson, J.E.M., 2012. Applying Ecosystem Services Approaches for Biodiversity Conservation: Benefits and Challenges. S.A.P.I.EN.S 5, pp. 1–10.
Lal, R., 2004. Soil carbon sequestration impacts on global climate change and food security. Science 304, 1623–1627.
Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.
Legendre, P., Legendre, L., 2012. Numerical Ecology. Elsevier Science BV, Amsterdam.
Little, E.L., Jr, 1978. Atlas of United States trees. Department of Agriculture Miscellaneous Publication 1361.
MA, 2005. Millennium Ecosystem Assessment. Ecosystems and Human Well-being: Synthesis, Washington DC.
Mace, G.M., Norris, K., Fitter, A.H., 2012. Biodiversity and ecosystem services: a multilayered relationship. Trends Ecol. Evol. 27, 19–26.
Marrs, R.H., Galtress, K., Tong, C., Cox, E.S., Blackbird, S.J., Heyes, T.J., Pakeman, R.J., Le Duc, M.G., 2007. Competing conservation goals, biodiversity or ecosystem services: element losses and species recruitment in a managed moorland-bracken model system. J. Environ. Manage. 85, 1034–1047.
Maskell, L.C., Crowe, A., Dunbar, M.J., Emmett, B., Henrys, P., Keith, A.M., Norton, L.R., Scholefield, P., Clark, D.B., Simpson, I.C., Smart, S.M., 2013. Exploring the ecological constraints to multiple ecosystem service delivery and biodiversity. J. Appl. Ecol. 50, 561–571.
Mckenney, D.W., Pedlar, J.H., Lawrence, K., Campbell, K., Hutchinson, M.F., 2007. Potential impacts of climate change on the distribution of North American trees. Bioscience 57, 939–948.
McShane, T.O., Hirsch, P.D., Trung, T.C., Songorwa, A.N., Kinzig, A., Monteferri, B., Mutekanga, D., Thang, H.V., Dammert, J.L., Pulgar-Vidal, M., Welch-Devine, M., Brosius, J.P., Coppolillo, P., O'Connor, S., 2011. Hard choices: making trade-offs between biodiversity conservation and human well-being. Biol. Conserv. 144, 966–972.
Mori, A.S., Furukawa, T., Sasaki, T., 2013. Response diversity determines the resilience of ecosystems to environmental change. Biol. Rev. 88, 349–364.
Naidoo, R., Balmford, A., Costanza, R., Fisher, B., Green, R.E., Lehner, B., Malcolm, T.R., Ricketts, T.H., 2008. Global mapping of ecosystem services and conservation priorities. Proc. Natl. Acad. Sci. USA 105, 9495–9500.
Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D.R., Chan, K.M.A., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H., Shaw, M.R., 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Front. Ecol. Environ. 7, 4–11.
O'Farrell, P.J., Reyers, B., Le Maitre, D.C., Milton, S.J., Egoh, B., Maherry, A., Colvin, C., Atkinson, D., De Lange, W., Blignaut, J.N., Cowling, R.M., 2010. Multi-functional landscapes in semi arid environments: implications for biodiversity and ecosystem services. Landscape Ecol. 25, 1231–1246.
Ontl, T.A., Schulte, L.A., 2012. Soil carbon storage. Nat. Education Knowledge 3, 35.
Pinsky, M.L., Springmeyer, D.B., Goslin, M.N., Augerot, X., 2009. Range-wide selection of catchments for pacific salmon conservation. Conserv. Biol. 23, 680–691.
Raudsepp-Hearne, C., Peterson, G.D., Bennett, E.M., 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. Proc. Natl. Acad. Sci. USA 107, 5242–5247.
Ridder, B., 2008. Questioning the ecosystem services argument for biodiversity conservation. Biodiv. Conserv. 17, 781–790.
Rodriguez, J.P., Beard, T.D., Bennett, E.M., Cumming, G.S., Cork, S.J., Agard, J., Dobson, A.P., Peterson, G.D., 2006. Trade-offs across space, time, and ecosystem services. Ecol. Soc. 11.
Sakamoto, Y., Ishiguro, M., Kitagawa, G., 1986. Akaike Information Criterion Statistics. D. Reidel Publishing Company, Dordrecht/Tokyo.
Schneiders, A., Van Daele, T., Van Landuyt, W., Van Reeth, W., 2012. Biodiversity and ecosystem services: complementary approaches for ecosystem management? Ecol. Indicators 21, 123–133.
Schoonmaker, P.K., von Hagen, B., Wolf, E.C., 1997. The Rain Forests of Home: Profile of a North American Bioregion. Island Press, Washington DC.
Schwenk, W.S., Donovan, T.M., Keeton, W.S., Nunery, J.S., 2012. Carbon storage, timber production, and biodiversity: comparing ecosystem services with multi-criteria decision analysis. Ecol. Appl. 22, 1612–1627.
Shmueli, G., 2010. To Explain or to Predict? Statistical Sci. 25, 289–310.
Simon, S., Bouvier, J.C., Debras, J.F., Sauphanor, B., 2010. Biodiversity and pest management in orchard systems. A review. Agronomy Sustain. Develop. 30, 139–152.
Simpson, I.C., 1949. Measurement of diversity. Nature 163, 688.

Sircely, J., Naeem, S., 2012. Biodiversity and ecosystem multi-functionality: observed relationships in smallholder fallows in Western Kenya. Plos One 7.
Tallis, H., Polasky, S., 2009. Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. Ann. New York Acad. Sci. 1162, 265–283.
Tilman, D., Reich, P.B., Isbell, F., 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proc. Natl. Acad. Sci. USA 109, 10394–10397.
Todd, I.H., Weidner, E., 2010. Valuing drinking water as an ecosystem service. The Pinchot Letter Winter 2010, 1–13.
Turner, W.R., Brandon, K., Brooks, T.M., Costanza, R., da Fonseca, G.A.B., Portela, R., 2007. Global conservation of biodiversity and ecosystem services. Bioscience 57, 868–873.
Vira, B., Adams, W.M., 2009. Ecosystem services and conservation strategy: beware the silver bullet. Conserv. Lett. 2, 158–162.
Wang, T.L., Campbell, E.M., O'Neill, G.A., Aitken, S.N., 2012. Projecting future distributions of ecosystem climate niches: uncertainties and management applications. For. Ecol. Manage. 279, 128–140.
Woodbury, P.B., Smith, J.E., Heath, L.S., 2007. Carbon sequestration in the U.S. forest sector from 1990 to 2010. For. Ecol. Manage. 241, 14–27.

View publication stats

Forest Restoration and Fire: Principles in the Context of Place

RICHARD T. BROWN,* JAMES K. AGEE,† AND JERRY F. FRANKLIN†

*Defenders of Wildlife, 1880 Willamette Falls Drive, Suite 200, West Linn, OR 97068, U.S.A., email rbrown@defenders.org
†Division of Ecosystem Sciences, College of Forest Resources, Box 352100, University of Washington, Seattle, WA 98915, U.S.A.

Abstract: *There is broad consensus that active management through thinning and fire is urgently needed in many forests of the western United States. This consensus stems from physically based models of fire behavior and substantial empirical evidence. But the types of thinning and fire and where they are applied are the subjects of much debate. We propose that low thinning is the most appropriate type of thinning practice. Treating surface fuels, reducing ladder fuels, and opening overstory canopies generally produce fire-safe forest conditions, but large, fire-resistant trees are also important components of fire-safe forests. The context of place is critical in assigning priority for the limited resources that will be available for restoration treatments. Historical low-severity fire regimes, because of their current high hazards and dominance by fire-resistant species, are the highest priority for treatment. Mixed-severity fire regimes are of intermediate priority, and high-severity fire regimes are of lowest priority. Classification systems based on potential vegetation will help identify these fire regimes at a local scale.*

Restauración de Bosques y Fuego—Principios en el Contexto del Sitio

Resumen: *Existe un amplio consenso de que en muchos bosques del oeste de EE.UU. se requiere con urgencia un manejo activo mediante tala y fuego. Este consenso se basa en modelos físicos de comportamiento de fuego, así como en importante evidencia empírica que aumenta cada año. Pero los tipos de tala y fuego y el lugar en que se aplican, son temas de mucho debate. Proponemos que la tala reducida es la más apropiada. El tratamiento de combustibles de superficie, la reducción de combustibles escalera y la apertura de doseles generalmente producen condiciones a salvo de fuego en los bosques, pero árboles grandes resistentes al fuego también son componentes importantes de bosques a salvo de fuego. El contexto del lugar es crítico en la asignación de prioridades a los limitados recursos disponibles para tratamientos de restauración. Los regímenes de fuego de baja intensidad, debido a sus altos riesgos actuales y la dominancia de especies resistentes al fuego, son la mayor prioridad para el tratamiento. Los regímenes de fuego de severidad mixta son de prioridad intermedia y los regímenes de fuego de alta severidad son de menor prioridad. Los sistemas de clasificación basados en la vegetación potencial ayudarán a identificar estos regímenes de fuego a escala local.*

Introduction

Transformation of the forested landscape in the western United States, especially dry, low-elevation forests dominated by ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), began in the second half of the nineteenth century with the introduction of livestock grazing. Beginning in the late nineteenth century and accelerating after World War II, selective logging of old, fire-resistant trees, extensive road building to facilitate logging, fire exclusion, and livestock grazing continued trends of forest and watershed degradation. Approaches to addressing these daunting problems are being developed and implemented, but a strategic approach will be required because restoration resources are limited. Strategically focused, integrated approaches are needed that will provide maximum benefits for a given cost while minimizing unintended adverse effects (Agee 1996; Rieman et al. 2000; Finney 2001). We summarize here the restoration potential of active management and principles related to fire resiliency that

Paper submitted November 14, 2003; revised manuscript accepted January 28, 2004.

should be applied when considering active management, and we emphasize a context of place in the planning process.

Restoration Concepts

There is broad agreement that restoration in some form and to some degree—of fire regimes, habitats, populations of fish and wildlife, productivity of soils, watershed integrity, and disturbance patterns—is appropriate (ICBEMP 2000; U.S. Department of Agriculture Forest Service 2000; Weatherspoon & Skinner 2002). However, there is more disagreement concerning restoration objectives and implementation strategies. Restoring landscapes to some semblance of pre-1850 conditions, or their "historic range of variability," is one common suggestion. Advocates presume that forest stands and landscapes restored to past conditions are more likely to support healthy populations of wildlife and fish. Habitats would be more like those to which species had adapted over thousands of years, and disturbance processes (fire, insects, disease, flooding, landsliding) could operate more sustainably in a more resilient landscape. However, although knowledge of historical conditions will be useful in guiding restoration efforts, attempts to precisely recreate past conditions will not be desirable or feasible (Christensen 1988; Swanson et al. 1994; Gregory 1997; Hessburg et al. 1999; Landres et al. 1999; Millar & Woolfenden 1999; Moore et al. 1999; Tiedemann et al. 2000; Allen et al. 2002).

Knowledge of historic conditions can help clarify the types, extent, and causes of ecosystem changes and can help identify management objectives and restoration priorities (Hessburg et al. 1999). Climates are now different than at any historic time, however, and will be different in the future (Millar & Woolfenden 1999). Species have been irrevocably added and subtracted, and the undesirable portion of the modern human imprint cannot be entirely eliminated. Historical reconstructions can provide good estimates of the large-tree component of past forests, but they are less reliable for small trees or other ecosystem elements such as herbaceous vegetation or wildlife (Fulé et al. 1997; Harrod et al. 1999). Although past fire regimes may be more accurately estimated than forest structure and composition (Stephenson 1999), "the natural fire regimes of the past are not the regimes of the present, nor will they be the regimes of the future" (Agee 1998). Conditions other than historic (or "natural") may need to be maintained to provide essential habitat for at-risk wildlife (ICBEMP 2000; Wisdom et al. 2000). Conditions that are "unnatural" yet sustainable and desirable may be quite appropriate for many state, private, and Native American lands.

Potential conflicts or trade-offs among reasonable objectives need to be recognized in setting restoration goals. Creating stands that are highly resistant to severe fire may unintentionally disturb soil, reduce canopy cover, and affect some fish and wildlife species (Rieman & Clayton 1997; Gresswell 1999). There are also fire-behavior trade-offs. Thinning of codominant trees will contribute to restoration of more open stand conditions in some areas and increase the growth of forbs and shrubs, which retain moisture until later in the season, reducing fire behavior (Agee et al. 2002). Yet opening the canopy can increase fire behavior by lowering the moisture content of dead surface fuels and increasing surface windspeed (van Wagtendonk 1996; Weatherspoon 1996; Agee et al. 2000).

Roads have many adverse ecological effects (Furniss et al. 1991; Noss & Cooperrider 1994; Rieman & Clayton 1997; Jones et al. 2000; Trombulak & Frissell 2000) but are paradoxical in terms of fire management. They open access so that human-caused ignitions increase but also decrease response time to wildfires, act as holding lines, and make prescribed fire easier to apply (Agee 2002). Most restoration effort can be focused on the substantially roaded portion of the landscape. In unroaded areas needing active management, prescribed fire with minimal necessary thinning and no road construction may be appropriate to maintain these important areas as reservoirs of biological diversity and ecological baselines (Noss 1999). The spatial focus of active management to alleviate road impacts and that to improve forest integrity will overlap considerably (Lee et al. 1997; Rieman et al. 2000).

Restoration Treatments

Ecological restoration efforts are often categorized as either active or passive. This can be a useful distinction, but the term *passive restoration* suffers from potential confusion with *passive management*, which some people consider equivalent (at least in some circumstances) to mere neglect or inattention to the needs of the land (Agee 2002). Passive restoration is the "cessation of . . . activities that are causing degradation or preventing recovery" (Kauffman et al. 1997) and can be considered the first step in restoration (National Research Council 1996).

The primary active restoration techniques we considered are thinning and prescribed fire. However, other active treatments focused on roads, weeds, livestock, and streams will also be needed. Thinning appropriate for restoration will focus on the cutting and removal of small trees and is variously known as understory thinning, thinning from below, or low thinning. Possible standards for placing boundaries on appropriate low thinning include diameter limits and percentile approaches. Diameter limits, such as restricting removal to trees <30 cm or <50 cm is one way to approach the problem, but the limit should vary by site. Trees that invaded some forests after fire

Table 1. Factors that increase fire resilience (adapted from Agee [2002] and Hessburg & Agee [2003]).

Principle	*Effect*	*Advantage*	*Concerns*
Reduce surface fuels	reduces potential flame length	control easier; less torching	surface disturbance less with fire than other techniques
Increase height to live crown	requires longer flame length to begin torching	less torching	opens understory; may allow surface wind to increase
Decrease crown density	makes tree-to-tree crown fire less probable	reduces potential for crown fire	surface wind may increase and surface fuels may be drier
Keep big trees of resistant species	less mortality for same fire intensity	generally restores historic structure	less economical; may keep trees at risk for insects

exclusion became effective can exceed 50–60 cm diameter, whereas on other sites trees that are 200 years old can be well below this size. Another approach is a percentile method, in which trees are ranked by size, and some size limit, such as the seventy-fifth percentile, is defined. This assures that the largest 25% of trees is left. Both approaches are likely to work best if applied in the context of place rather than being arbitrarily defined to fit all situations.

The majority of the trees removed in such thinnings are too small to have commercial value by conventional standards, but efforts are underway in the West to develop processing methods and markets for ever-smaller material. Before private investment emerges, assurances will be required that a supply of such material will be provided. Some trees thinned as a by-product of restoration activities will have commercial value (R. F. Noss. 2000. Society for Conservation Biology comment letter on U.S. Forest Service Roadless Areas Protection Initiative.). Restoration thinning may appropriately include the removal of dead trees, but traditional "salvage" logging will not provide restoration benefits. Removal of large, pre-1850 trees solely to pay for treatment will undermine the credibility of restoration efforts (Weatherspoon & Skinner 1995; Agee 1997*b*). Thinning is unlikely to meet all ecological objectives unless it is combined with prescribed fire (Weatherspoon 1996; National Research Council 1999; Lynch et al. 2000; Weatherspoon & Skinner 2002). Despite considerable anecdotal, modeling, and common-sense support for restoration thinning, scant empirical research has been done on the subject (van Wagtendonk 1996; Agee 1997*a*; Stephens 1998; Omi & Martinson 2002; Pollet & Omi 2002). Although additional scientific research is necessary, much can also be learned from routine monitoring, especially if it is structured to reflect a more consistent case-study approach (Shrader-Frechette & McCoy 1993).

Restoration objectives may be accomplished by prescribed fire alone in some forest types and conditions (Agee & Huff 1986; Biswell 1989; Weatherspoon 1996). It has been the primary restoration technique in drier forests of U.S. national parks. Yet prescribed fire applied too broadly could homogenize the landscape, create smoke problems, and damage wildlife habitat (Tiedemann et al. 2000). It can kill large trees that are intended to be saved by treatment (Agee 2003). The proportion of a landscape requiring treatment in order to have a significant effect on the spread and severity of wildfire is unknown. It is probable that areas less manipulated will be less effective per unit area, so that larger expanses of the landscape will have to be treated (Agee et al. 2000). Patterns of fuel treatment can affect fire intensity or rate of spread, and this topology has implications for designing landscape-level fuel-treatment patterns (Finney 2001).

Factors of Fire Resilience

A forest that is fire-resilient has characteristics that limit fire intensity and increase the resistance of the forest to mortality (Table 1). The first principle is to manage surface fuels to limit the flame length of a wildland fire that might enter the stand. This is generally done by removing fuel through prescribed fire, pile burning, or mechanical removal. This reduces the potential energy of a wildland fire and makes it more difficult for a fire to jump into the canopy (Scott & Reinhardt 2001). The second principle is to make it more difficult for canopy torching to occur by increasing the height to flammable crown fuels. This can be accomplished through pruning, prescribed fire that scorches the lower crown, or removal of small trees. The third principle is to decrease crown density by thinning overstory trees, making tree-to-tree crowning less probable. This will not be necessary on all sites and will be effective only if linked to the application of the first two principles (Perry et al. 2004 [this issue]). The fourth principle is to keep large trees of fire-resistant species (Hummel & Agee 2003). If fire behavior is successfully reduced but the fire is burning under fire-sensitive trees, high-severity fire will still occur as the trees may still all be killed. Active management can have positive or negative effects on fire-hazard potential (Table 2).

The influence of species composition and large trees on fire-resilient forests is illustrated by a simulation of fire effects (Fig. 1) based on the First Order Fire Effects Model (Reinhardt et al. 2002). A forest type with a historic low-severity fire regime—low-elevation

Table 2. Immediate effects of fuel treatment on factors that can affect fire behavior (Scott & Reinhardt 2001).*

Fuel treatment	*Surface fuel load*	*Dead fuel moisture*	*Canopy base height*	*Bulk density*	
				wind	*canopy*
Overstory thinning	I	D	I/NE	I	D
Understory removal	I		I		D/NE
Pruning	I		I		
Pile burning	D				
Whole-tree yarding	D				
Broadcast burning	D		I/NE		

A blank indicates no effect; I, increase; D, decrease; NE, no effect.

ponderosa pine/Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco)—is contrasted with a historic high-severity fire regime—high-elevation subalpine fir (*Abies lasiocarpa* [Hook.] Nutt. and of lodgepole pine (*Pinus contorta* Dougl. ex Loud.) at various flame lengths. The ponderosa pine stand with historic structure suffers little mortality until flame lengths exceed 1.8 m. A similar species composition of smaller trees, similar to many second-growth pine-fir stands across the western United States, suffers higher mortality, but loss of basal area remains below 25% until flame lengths are 1.8 m or greater. If fuel treatments can reduce flame lengths under worst-case fire weather to 1.2 m or less, these forests will survive wildfire well. Restoration here will be ecologically effective at reducing wildfire damage.

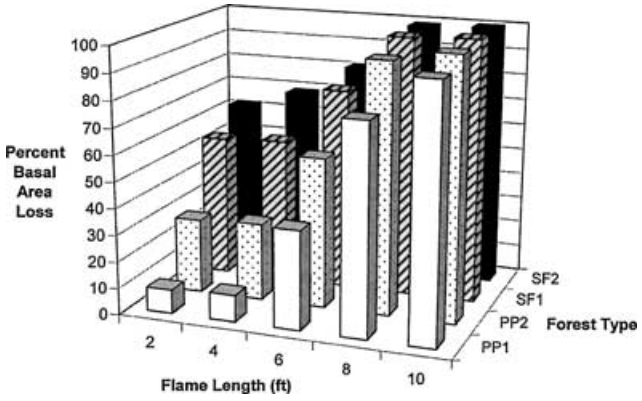


Figure 1. Percent loss of basal area by flame length for four classes of forest type or structure: PP1, historic mixed-conifer stand dominated by ponderosa pine with some Douglas-fir (density 15/ha, basal area 15 m^2/ha, trees 40–50 cm in diameter); PP2, same species composition and basal areas as PP1 but higher density (50/ha) and therefore smaller trees (15–25 cm in diameter); SF1, stand of subalpine fir and lodgepole pine with the exact structure characteristics of PP2, except these two species are substituted for ponderosa pine and Douglas-fir; SF2, stand of denser subalpine fir and lodgepole pine with 30 m^2/ha of basal area.

The high-elevation forest types have fewer fire-resistant species (Peterson & Ryan 1986), so the subalpine fir–lodgepole pine stand with the same structure as the second-growth ponderosa pine stand incurs about twice the loss of basal area, even at low flame lengths. Flame lengths of 1.8 m or higher create high-severity basal area losses of 70% or more. A typical natural stand structure in subalpine fir and lodgepole pine, with higher density and more small subalpine fir, incurs even greater losses. Investments in fire resistance by fuel treatment will be less effective in these higher-elevation stands.

Scale is an important parameter to consider in restoring fire-resistant forests. If fuel treatments are small and scattered, they may not be effective in fragmenting landscape fuel loads, and their efficacy at the stand level can be overwhelmed. On the 1994 Tyee fire in Washington, small treated areas of mixed-conifer forest underburned while adjacent untreated areas burned with crown fires. The heat created by the crown fires passed over the treated areas and scorched the tops of the trees that were later underburned. Many of these trees later died from the sandwiched scorch effect (J. K. Agee, personal observation). Empirical evidence from wildfires also supports the concept that areas treated with the goal of reducing fire hazard will burn with less severity than adjacent untreated areas (Omi & Martinson 2002). In the 2002 Hayman fire in Colorado, many areas where fuels had been treated before the fire experienced lower-severity effects than adjacent untreated areas (Finney et al. 2002*a*). Fuel treatment was not always successful in lowering severity, particularly during periods of incredibly severe fire weather (winds to 135 kph and fuel moistures of below 6% in all size classes). Under less severe conditions, fuel treatments appeared to alter severity, except where the treatments were carried out on a very small local scale or where they had been applied more than 10–15 years previously.

A Context of Place

Place is the most significant and most misunderstood element of the decision about where to carry out active restoration treatments. Some forest types are in critical need of active restoration, and others need no treatment at all. Recent national analyses suggest that the scale of needed restoration is immense, on the order of over 70 million acres (25 million ha), mostly in the West. Almost all of this area, designated condition class 3, occurs in low-severity fire regimes (Schmidt et al. 2002), and because of the coarse scale of the analysis, is generally not accurate or usable at the subregional scale. We suggest that more local classification such as the plant association (Daubenmire 1968) or plant association group, which is

an aggregation of closely allied plant associations within a forest series, has more utility at the fine scale.

Low-Severity Fire Regimes

Dry pine and mixed-conifer forest comprise most of the western low-severity fire regimes. Forests were typically shaped by what is sometimes referred to as a "stand-maintenance" fire regime of low-intensity, frequent fires that generally burned grasses, brush, small trees, and fallen needles and branches but had little effect on older trees with thick insulating bark. The death of lower branches from shading or the effects of fire raised the bottom of the canopy to the point where it was not adversely affected by typical fires. In extremely hot and dry weather, fires would tend to cover a larger area but still were unlikely to kill overstory trees (Agee 1997*b*). Although ponderosa pine is the most wide-spread forest species exhibiting these characteristics, similar dynamics pertained in areas where other fire-resistant species—Douglas-fir, Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), western larch (*Larix occidentalis* Nutt.), and many species of oak (*Quercus* spp.)—grow either in association with ponderosa pine or as dominants.

Although some areas still resemble historic conditions, it is these dry pine and mixed-conifer forests that typically have been changed the most by human activities in the last 150 years. Heavy livestock grazing depleted the fine fuels that carried the light, frequent fires and exposed mineral soil seedbeds for abundant young ponderosa pine that often became established before 1900 (Belsky & Blumenthal 1997; Miller & Rose 1999; Swetnam et al. 1999). Fire suppression beginning after 1910 allowed far more of these trees to persist, and logging concentrated on large, old trees (Biswell et al. 1973). These forests may have been deprived of 10 or more natural fire cycles. The result is forests that, as the result of continuing fire suppression, tend to burn less frequently, but when they do burn the fire is much more likely to reach the forest canopy and spread as a crown fire, killing many or all of the overstory trees. A historically low-severity fire regime has turned into a high-severity or mixed-severity fire regime over millions of hectares in the West (Morgan et al. 1996; Hann et al. 1997). These higher-severity fires are more apt to have detrimental effects on soils, watersheds, and wildlife habitat. And they can have serious consequences for humans who have settled in and around these forests.

Low-elevation pine and mixed-conifer forests offer the highest priorities for thinning—in conjunction with prescribed fire—to contribute to restoration of wildlife habitat while making forests more resistant to uncharacteristically severe fire (Miller & Urban 2000). Within these forests, priorities are to reduce surface and ladder fuels and raise the bottom of the live canopy (van Wagtendonk 1996; Agee et al. 2000). Thinning is most apt to be appropriate where understory trees are sufficiently large or dense that attempts to kill them with fire would run a high risk of also killing overstory trees (Christensen 1988; Arno et al. 1995; Fulé et al. 1997; Moore et al. 1999; Stephenson 1999). Using prescribed fire alone can be desirable in that it provides the full range of ecological effects of fire. Fire is an imprecise tool, however, whereas individual harvest can provide much more control over which trees are actually killed (Thomas & Agee 1986; Swezy & Agee 1991; Fiedler 1996; Sackett et al. 1996; Pollet & Omi 2002). The larger understory trees that are less likely to be safely thinned with fire are more apt to be large enough to have economic value if they are logged. This presents opportunities to defray expenses and provide employment and wood products, but it also creates economic pressure to cut larger trees. Even where understory trees can safely be thinned with fire, consideration needs to be given to potential smoke production and soil heating during subsequent burns that will be necessary to consume the dead understory trees once they fall to the ground (Agee 1997*a*; Sackett & Haase 1998).

Within the dry forest zone, high forest integrity will generally be associated with the presence of old-growth trees, especially ponderosa pine (Moir & Dieterich 1988; Wickman 1992; Covington & Moore 1994; Henjum et al. 1994; Brown et al. 1999; Kaufmann et al. 1999). Treatment of these areas could help secure the remnant intact stands from wildfire risks and extend more natural stand conditions across the landscape. Care should be taken, at the landscape scale, to retain some patches of young pine trees in an approximation of historic patterns (Allen et al. 2002).

Mid-seral ponderosa pine stands (roughly 60–100 years old) represent a secondary priority for restoration treatments. These stands are often developing old-growth characteristics but are usually too dense. Treatments to help maintain this trend can increase the probability that old-growth habitats are restored more quickly than they would be otherwise. Variable-density thinning mimics the clumped distribution and associated processes found in pre-1850 stands (Franklin et al. 1997; Harrod et al. 1999). Processes other than fire, particularly sources of mortality such as bark beetles, which are a key food source for woodpeckers and influence the subsequent decay of snags (Samman & Logan 2000; George & Zack 2001), should be provided for at the landscape level.

Reaching some desired future condition in one treatment, in contrast to a staged approach, is being debated (Covington 2000; Fulé et al. 2001, 2002; Allen et al. 2002). The debate is about the efficacy of treatment, how much of a landscape needs to be treated, and how to optimize fuel treatment in relation to other ecological objectives. One option is to rapidly emulate historic structure by retaining trees older than a particular year (1870 in the restoration of Fulé et al. 2001) and removing all others. Another is to combine that treatment with others using only minimal thinning or prescribed fire (Fulé et al. 2002).

Allen et al. (2002) argue that restoration should be aimed at resetting ecosystem trends toward an envelope of "natural variability." They caution that impatience, overreaction to risks of crown fire, extractive economics, or hubris could further damage ecosystems desperately in need of restoration.

Support for their call for caution is provided by data from the Grand Canyon provided by Fulé et al. (2002). They applied three treatments to ponderosa pine forest plus a control: a "full" restoration that removed all trees germinating after 1870 and applied fuel treatment, including prescribed burns; a "minimal" treatment that thinned small trees only around old-growth trees and applied the same fuel treatment as for the full treatment, and a "burn" treatment that used only prescribed fire. The most intrusive full treatment reduced crown-fire hazard the most. However, both the burn and control stands had crowning indices requiring windspeeds well above the 97th percentile wind recorded at the site over many years, and therefore crown fire was not a particularly severe threat. The scorch provided by the prescribed fire in the burn treatment reduced torching potential close to that achieved by the full treatment, so from a fire perspective alone a "full" restoration was not necessary at this site.

Mixed-Severity Fire Regimes

Mid-elevation moist forests of the western United States are more difficult to describe in general terms. Cooler, moister conditions allow less drought- and fire-tolerant species such as grand fir (*Abies grandis* [Dougl.] Lindl.), white fir (*Abies concolor* [Gord. & Glend.] Lindl.), Douglas-fir, western larch, and ponderosa pine to grow more densely in these areas. In some areas these sites support ponderosa pine–dominated stands that appear similar to the drier forests at lower elevations, although their fire histories may be more complex and variable over long time periods (Shinneman & Baker 1997; Brown et al. 1999; Veblen et al. 2000). Fire-return intervals of 40–80 years included areas burned from low to high severity, a "mixed-severity" fire regime. Fires of differing severity can occur in close proximity, creating a complex mosaic of forest structures in patches of varying size (Taylor & Skinner 1998). Fire suppression has generally been effective for one to four fire cycles and has allowed the development of denser, multistoried forests on more of the landscape. Although the fire regime can still be described as mixed, the relative proportion of fire types has shifted, and severe fires are more likely to occur on more of the landscape than they would have historically (Agee 1998; Agee 2002).

The mixed-severity fire regimes are less clearly candidates for thinning and/or fire restoration. Changes following decades of fire exclusion will often mean that reintroduction of prescribed fire without thinning will be problematic (Agee & Huff 1986). Past management practices may have led to development of old-growth stands with "unnatural" multiple canopy layers or accumulations of snags and logs, but these areas may provide key habitat that compensates for the loss and degradation of these habitat elements elsewhere (ICBEMP 2000; Wisdom et al. 2000). It may often be appropriate to attempt to secure such habitats from wildfire by treating adjacent areas (Agee 1996, 1998). Attention should be given to protecting large and old trees (Henjum et al. 1994; Allen et al. 2002). Large fir trees, especially those with heartwood decay, provide important habitat for many species (Bull et al. 1992, 1997; Bull & Hohman 1993), and efforts to "cleanse" the landscape of true firs should be avoided. Strategic location of fuel treatments may slow the spread of fire across the landscape (Agee 1999; Finney 2001; Finney et al. 2002*b*), but this concept has been explored only in computer models and needs refinement before being extensively applied. All in all, these complexities appear to recommend a cautious approach to restoration efforts in mixed-severity fire regimes.

High-Severity Fire Regimes

Wet and cold forests have historic fire-return intervals that typically exceed several centuries. In coastal areas, forests of Sitka spruce (*Picea sitchensis* [Bong.] Carr.) may show evidence of a single fire per millennium (Fahnestock & Agee 1983), whereas widespread western hemlock (*Tsuga heterophylla* [Raf.] Sarg.)–Douglas-fir forests had typical fire-return intervals exceeding 200 years (Agee 1993). At higher elevations, forests of subalpine fir, Engelmann spruce (*Picea englemannii* Parry ex Engelm.), mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.), and lodgepole or whitebark pine (*Pinus albicaulis* Engelm.) predominate. These forests also have long fire-return intervals and contain a high proportion of fire-sensitive trees (Fig. 1). At periods averaging a few hundred years, extreme drought conditions would prime these forests for large, severe fires that would tend to set the forest back to an early successional stage, with a large carry-over of dead trees as a legacy of snags and logs in the regenerating forest. Young forests growing within a matrix of unsalvaged snags and logs may be the most depleted forest habitat type in regional landscapes, particularly at low elevations (Lindenmayer & Franklin 2002).

The fire regime for these forests can be described as "weather-dominated" in that high fuel loads are typical and the fire events that determine forest patterns occur under uncommon, extreme weather conditions that can result in stand-replacing fires over large areas (Agee 1997*b*). Although logging and road building have had some detrimental effects on these forests, natural ecological dynamics are largely preserved because fire suppression has been effective for less than one natural fire cycle. Thinning for restoration does not appear to be appropriate in these forests (Agee & Huff 1986). Efforts to

manipulate stand structures to reduce fire hazard will not only be of limited effectiveness (Fig. 1; Agee 1996, 1998) but may also move systems away from pre-1850 conditions to the detriment of wildlife and watersheds (Johnson et al. 1995; Weatherspoon 1996). Fuel levels may suggest a high fire "hazard" under conventional assessments, but wildfire risk is typically low in these settings.

Using Place to Set Priorities

Prioritizing restoration efforts is essential because resources are limited. An initial focus on areas most likely to provide benefits and that present a low risk of degradation of ecological values will build experience and credibility. Strategies for conserving both aquatic and terrestrial resources at multiple scales are based on similar principles: secure areas with high ecological integrity ("anchor habitats"), extend these areas, and connect them at the landscape level (Lee et al. 1997; Gresswell 1999). An approach that considers the condition of a watershed and its associated forests and the status of aquatic populations (Rieman et al. 2000) appears to offer the best prospects for balancing potentially competing objectives (Bisson et al. 2003). Restoration treatments should initially focus on uplands (Johnson et al. 1995; Gregory 1997; Lee et al. 1997). Carefully applied prescribed fire may be the most appropriate treatment in riparian areas that historically burned frequently (Kauffman et al. 1997; Agee 1999; Everett et al. 2003).

Although the principles of fire-safe forest can be applied to any forest, they will be most effective when applied to those that are at risk of uncharacteristically severe wildfire and those that are composed of species that develop fire resistance, primarily with thick bark. At least two scales of priority are likely to exist. At a coarse scale, historically low-severity fire regimes will receive highest priority, mixed-severity fire regimes will have moderate priority, and high-severity fire regimes will have low priority. High priority would be assigned, for example, to the ponderosa pine series, the Douglas-fir dry plant association group (PAG), and the grand fir dry PAG. Moderate priority would be assigned to Douglas-fir and grand fir wet PAGs and to the red fir (*Abies magnifica* Murr.) series. Low priority would be assigned to the Sitka spruce series, western hemlock series, Pacific silver fir (*Abies amabilis* [Dougl.] Forbes) series, mountain hemlock series, and subalpine fir series, unless unusual situations exist in which local treatment was needed. A second scale of priority can be defined within the low-severity fire regimes. Some of the more productive forests with a low-severity fire regime in the grand fir, Douglas-fir, and white fir series have experienced more substantial ecological change (Agee 2003) than drier sites in the ponderosa pine and Douglas-fir series. The accumulated biomass in these systems and their abnormally high tree density and wildfire potential argue for a higher priority for restoration within the low-severity fire regimes. Although treatment costs may be high, these sites also have high potential to offset costs through commercial use of thinned trees.

Conclusions

Action must be taken to reverse trends of ecosystem degradation due to past forest management. Thinning and fire will play a role in these restoration efforts, but both techniques will be controversial. Because thinning is a form of logging and prescribed fire can produce excessive smoke and can escape, these tools need to be strategically applied in ways and locations that will give them the highest prospects for success and the lowest likelihood of unintended consequences. Some areas need no treatment at all. Other areas needing treatment will have to be triaged because of limited resources. Based on current knowledge (adapted from Brown 2000; Allen et al. 2002), it appears that the most credible restoration efforts will

- place highest priority on historically low-severity fire regimes, with secondary priority on mixed-severity fire regimes, and lowest priority on high-severity fire regimes;
- be based on the ecology of the species and site, with presettlement conditions as a sustainable reference, recognizing different goals for a wide variety of landowners;
- be site-specific and consider the landscape context, including watershed conditions and fish and wildlife habitat;
- consider a range of restoration steps, rather than attempt complete restoration with a single treatment everywhere;
- maintain the most fire-resistant, large-tree component of the forest in active-management schemes;
- consider mechanical thinning and prescribed fire as acceptable tools, but in all cases apply fire-safe principles (Table 1);
- where thinning is used, apply minimal-impact harvesting techniques, and focus first on areas where road systems are largely complete; and
- make a commitment to long-term monitoring and adaptive management so that we learn by doing.

Literature Cited

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Agee, J. K. 1996. The influence of forest structure on fire behavior. Pages 52–68 in 17th annual forest vegetation management conference. Forest Vegetation Management Committee, Sacramento, California.

Agee, J. K. 1997*a*. Fire management for the 21st century. Pages 191–201 in K. A. Kohm, and J. F. Franklin, editors, Creating a forestry for the 21st century. Island Press, Washington, D.C.

Agee, J. K. 1997*b*. The severe weather wildfire: too hot to handle? Northwest Science **71:**153–156.

Agee, J. K. 1998. The landscape ecology of western forest fire regimes. Northwest Science **72(special issue):**24–34.

Agee, J. K. 1999. A coarse-filter strategy. Forum for Applied Research and Public Policy **14(1):**15–19.

Agee, J. K. 2002. The fallacy of passive management. Conservation Biology in Practice **3(1):**18–25.

Agee, J. K. 2003. Monitoring postfire tree mortality in mixed-conifer forests of Crater Lake, Oregon. Natural Areas Journal **23:**114–120.

Agee, J. K., and M. H. Huff. 1986. Structure and process goals for vegetation in wilderness areas. Pages 17–25 in R. C. Lucas, compiler. Proceedings of the national wilderness research conference: current research 1985. General technical report INT-212. U.S. Department of Agriculture Forest Service Intermountain Research Station, Ogden, Utah.

Agee, J. K., B. Bahro, M. A Finney, P. N. Omi, D. B. Sapsis, C. N. Skinner, J. W. van Wagtendonk, and C. P. Weatherspoon. 2000. The use of shaded fuelbreaks in landscape fire management. Forest Ecology and Management **127:**55–66.

Agee, J. K., C. S. Wright, N. Williamson, and M. H. Huff. 2002. Foliar moisture content of Pacific Northwest vegetation and its relation to wildland fire behavior. Forest Ecology and Management **167:**57–66.

Allen, C. D., M. S. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications **12:**1418–1433.

Arno, S. F., J. H. Scott, and M. G. Hartwell. 1995. Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relationship to fire history. Research paper INT-RP-481. U.S. Department of Agriculture Forest Service Rocky Mountain Research Station, Fort Collins, Colorado.

Belsky, A. J., and D. M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior West. Conservation Biology **11:**315–327.

Bisson, P. A., B. E. Rieman, C. Luce, P. F. Hessburg, D. C. Lee, J. L. Kershner, G. H. Reeves, and R. E. Gresswell. 2003. Fire and aquatic ecosystems of western USA: current knowledge and key questions. Forest Ecology and Management **178:**213–229.

Biswell, H. H. 1989. Prescribed burning in California wildlands vegetation management. University of California Press, Berkeley.

Biswell, H. H., H. R. Kallander, R. Komarek, R. J. Vogl, and H. Weaver. 1973. Ponderosa fire management. Miscellaneous publication 2. Tall Timbers Research Station, Tallahassee, Florida.

Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecology **14:**513–532.

Brown, R. 2000. Thinning, fire and forest restoration: a science-based approach for national forests in the interior Northwest. Defenders of Wildlife, Washington D.C.

Bull, E. L., and J. E. Hohman. 1993. The association between Vaux's swifts and old growth forest in northeastern Oregon. Western Birds **24:**38–42.

Bull, E. L., R. S. Holthausen, and M. G. Henjum. 1992. Roost trees used by Pileated Woodpeckers in northeastern Oregon. Journal of Wildlife Management **56:**786–793.

Bull, E. L., C. G. Parks, and T. R. Torgersen. 1997. Trees and logs important to wildlife in the interior Columbia River Basin. General technical report PNW-391. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Christensen, N. L. 1988. Succession and natural disturbance: paradigms, problems, and preservation of natural ecosystems. Pages 62–86 in J. K. Agee and D. R. Johnson, editors. Ecosystem management for parks and wilderness. University of Washington Press, Seattle.

Covington, W. W. 2000. Helping western forests heal: the prognosis is poor for United States forest ecosystems. Nature **408:**135–136.

Covington, W., and M. Moore. 1994. Southwestern ponderosa pine forest structure: changes since Euro-American settlement. Journal of Forestry **January 1994:**39–47.

Daubenmire, R. 1968. Plants and environment. Harper and Row, New York.

Everett, R., R. Schellhaas, P. Ohlson, D. Spurbeck, and D. Keenum. 2003. Continuity in fire disturbance between riparian and adjacent sideslope Douglas-fir forests. Forest Ecology and Management **175:**31–47.

Fahnestock, G. R., and J. K. Agee. 1983. Biomass consumption and smoke production by prehistoric and modern forest fires in western Washington. Journal of Forestry **81:**653–657.

Fiedler, C. E. 1996. Silvicultural applications: restoring ecological structure and process in ponderosa pine forests. Pages 39–40 in C. C. Hardy and S. F. Arno, editors. The use of fire in forest restoration. General technical report INT-GTR-341. U.S. Department of Agriculture Forest Service Intermountain Research Station, Ogden, Utah.

Finney, M. A. 2001. Design of regular landscape fuel treatment patterns for modifying fire growth and behavior. Forest Science **47:**219–228.

Finney, M. A., R. Bartlette, L. Bradshaw, K. Close, P. Gleason, P. Langowski, C. W. McHugh, E. Martinson, P. N. Omi, W. Shepperd, and K. Zeller. 2002*a*. Interim Hayman fire case study analysis: report on fire behavior, fuel treatments, and fire suppression. U.S. Department of Agriculture Forest Service Rocky Mountain Research Center, Fort Collins, Colorado. Available from http://www.fs.fed.us/rm/hayman_fire (accessed May 2004).

Finney, M. A., D. B. Sapsis, and B. Bahro. 2002*b*. Use of FARSITE for simulating fire suppression and analyzing fuel treatment economics. Pages 121–136 in Proceedings of a conference on fire in California ecosystems: integrating ecology, prevention and management, 1997. Association for Fire Ecology, Davis, California.

Franklin, J. F., D. R. Berg, D. A. Thornburgh, and J. C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. Pages 111–139 in K. A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st Century. Island Press, Washington, D.C.

Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications **7:**895–908.

Fulé, P. Z., A. E. M. Waltz, W. W. Covington, and T. A. Heinlein. 2001. Measuring forest restoration effectiveness in reducing hazardous fuels. Journal of Forestry **November 2001:**24–29.

Fulé, P. Z., W. W. Covington, H. B. Smith, J. D. Springer, T. A. Heinlein, K. D. Huisinga, and M. M. Moore. 2002. Comparing ecological restoration alternatives: Grand Canyon, Arizona. Forest Ecology and Management **170:**19–41.

Furniss, M. J., T. D. Roelofs, and C. S. Yee. 1991. Road construction and maintenance. Pages 297–323 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. Special publication 19. American Fisheries Society, Bethesda, Maryland.

George, T. L., and S. Zack. 2001. Spatial and temporal considerations in restoring habitat for wildlife. Restoration Ecology **9:**272–279.

Gregory, S. V. 1997. Riparian management in the 21st century. Pages 69–85 in K. A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st Century, Island Press, Washington, D.C.

Gresswell, R. E. 1999. Fire and aquatic ecosystems in forested biomes of North America. Transactions of the American Fisheries Society **128:**193–221.

Hann, W. J., J. L. Jones, M. G. Karl, P. F. Hessburg, R. E. Keane, D. G. Long, J. P. Menakis, C. H. McNicoll, S. G. Leonard, R. A. Gravenmier, and B. G. Smith. 1997. Landscape dynamics of the basin. Pages 337–1055 in T. M. Quigley and S. Arbelbide, technical editors. An assessment of ecosystem components in the interior Columbia Basin. Volume II. General technical report PNW-GTR-405. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Harrod, R. J., B. McRae, and W. E. Hartl. 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. Forest Ecology and Management **114:**433–446.

Henjum, M. G., J. R. Karr, D. L. Bottom, D. A. Perry, J. C. Bednarz, S. G.

Wright, S. A. Beckwitt, and E. Beckwitt. 1994. Interim protection for late-successional forests, fisheries, and watersheds: national forests east of the Cascades crest, Oregon and Washington. Technical reviews 94–2. The Wildlife Society, Bethesda, Maryland.

Hessburg, P. F., and J. K. Agee. 2003. An environmental narrative of inland northwest United States forests, 1800–2000. Forest Ecology and Management **178:**23–59.

Hessburg, P. F., G. B. Smith, and R. B. Salter. 1999. Detecting change in forest spatial patterns from reference conditions. Ecological Applications **9:**1232–1252.

Hummel, S., and J. K. Agee. 2003. Western spruce budworm defoliation effects on forest structure and potential fire behavior. Northwest Science **77:**159–169.

Interior Columbia Basin Ecosystem Management Project (ICBEMP). 2000. Supplemental draft environmental impact statement. ICBEMP, Boise, Idaho.

Johnson, K. N., J. K. Agee, R. Beschta, J. Beuter, S. Gregory, L. Kellogg, W. McComb, J. Sedell, T. Schowalter, and S. Tesch. 1995. Forest health and timber harvest on national forests in the Blue Mountains of Oregon. Report to Governor Kitzhaber. Governor's Natural Resources Office, Salem, Oregon.

Jones, J. A., F. J. Swanson, B. C. Wemple, and K. U. Snyder. 2000. Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. Conservation Biology **14:**76–85.

Kauffman, J. B., R. L. Beschta, N. Otting, and D. Lytjen. 1997. An ecological perspective of riparian and stream restoration in the western United States. Fisheries **22(5):**12–24.

Kaufmann, M. R., L. Huckaby, and P. Gleason. 1999. Ponderosa pine in the Colorado Front Range: long historical fire and tree recruitment intervals and a case for landscape heterogeneity. Proceedings of the joint fire science conference and workshop. Joint Fire Science Program, National Interagency Fire Center, Boise, Idaho.

Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications **9:**1179–1188.

Lee, D. C., J. R. Sedell, B. E. Rieman, R. F. Thurow, and J. E. Williams. 1997. Broadscale assessment of aquatic species and habitats. Pages 1059–1496 in T. M. Quigley and S. Arbelbide, technical editors. An assessment of ecosystem components in the interior Columbia Basin. Volume III. General technical report PNW-GTR-405. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Lindenmayer, D. B., and J. F. Franklin. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington, D.C.

Lynch, D. L., W. H. Romme, and M. L. Floyd. 2000. Forest restoration in southwestern ponderosa pine. Journal of Forestry **98(8):**17–24.

Millar, C. I., and W. B. Woolfenden. 1999. The role of climate change in interpreting historical variability. Ecological Applications **9:**1207–1216.

Miller, C., and D. L. Urban. 2000. Modeling the effects of fire management alternatives on Sierra Nevada mixed conifer forests. Ecological Applications **10:**85–94.

Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush-steppe. Journal of Range Management **52:**550–559.

Moir, W. H., and J. H. Dieterich. 1988. Old-growth ponderosa pine from succession in pine-bunchgrass forests in Arizona and New Mexico. Natural Areas Journal **8:**17–24.

Moore, M. M., W. W. Covington, and P. Z. Fulé. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. Ecological Applications **9:**1266–1277.

Morgan, P., S. C. Bunting, A. E. Black, T. Merrill, and S. Barrett. 1996. Fire regimes in the interior Columbia River Basin: past and present. Final report for RJVA-INT-94913: coarse-scale classification and mapping of disturbance regimes in the Columbia River Basin. Interior Columbia Basin Ecosystem Management Project. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon. Available from http://www.icbemp.gov/science/morgan.pdf (accessed May 2004).

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. Committee on Protection and Management of Pacific Northwest Anadromous Salmonids. National Academy Press, Washington, D.C.

National Research Council. 1999. Environmental issues in Pacific Northwest forest management. National Academy Press. Washington, D.C.

Noss, R. F. 1999. A citizen's guide to ecosystem management. Special report, distributed as Wild Earth special paper 3. Biodiversity Legal Foundation, Boulder, Colorado.

Noss, R. F., and A. Y. Cooperrider. 1994. Saving nature's legacy: protecting and restoring biodiversity. Island Press, Washington, D.C.

Omi, P. N., and E. J. Martinson. 2002. Effects of fuels treatment on wildfire severity. Final report. Joint Fire Science Program Governing Board, Western Forest Fire Research Center, Colorado State University, Fort Collins,. Available from http://www.cnr.colostate.edu/frws/research/westfire/finalreport.pdf (accessed May 2004).

Perry, D., H. Jing, A. Youngblood, and D. Oetter. 2004. Forest structure and fire susceptibility in volcanic landscapes of the eastern High Cascades, Oregon. Conservation Biology **18:**913–926.

Peterson, D. L., and K. C. Ryan. 1986. Modeling post-fire conifer mortality for long-range planning. Environmental Management **10:**797–808.

Pollet, J., and P. N Omi. 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. International Journal of Wildland Fire **11:**1–10.

Reinhardt, E. D., R. E. Keane, and J. K. Brown. 2002. First order fire effects model: FOFEM 4.0, user's guide. General technical report INT-GTR-344 (updated to Windows version 5.0). U.S. Department of Agriculture Forest Service Intermountain Research Station, Ogden, Utah.

Rieman, B. E., and J. Clayton. 1997. Wildfire and native fish: issues of forest health of sensitive species. Fisheries **22(11):**6–15.

Rieman, B. E., D. C. Lee, R. F. Thurow, P. F. Hessburg, and J. R. Sedell. 2000. Toward an integrated classification of ecosystems: defining opportunities for managing fish and forest health. Environmental Management **25:**425–444.

Sackett, S., and S. Haase. 1998. Two case histories of using prescribed fire to restore ponderosa pine ecosystems in northern Arizona. Pages 380–389 in T. L. Pruden and L. A. Brennan, editors. Fire in ecosystem management: shifting the paradigm from suppression to prescription. Proceedings of the 20th Tall Timbers Fire ecology conference. Tall Timbers Research Station, Tallahassee, Florida.

Sackett, S. S., S. M. Haase, and M. G. Harrington. 1996. Lessons learned from fire use for restoring southwestern ponderosa pine ecosystems. Pages 54–61 in W. Covington and P. K. Wagner, technical coordinators. Conference on adaptive ecosystem restoration and management: restoration of cordilleran conifer landscapes of North America. General technical report RM-GTR-278. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Samman, S., and J. Logan, technical editors 2000. Assessment and response to bark beetle outbreaks in the Rocky Mountain area. Report to Congress from Forest Health Protection, Washington Office. General technical report RMRS-GTR-62. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Schmidt, K. M., J. P. Menakis, C. C. Hardy, W. J. Hann, and D. L. Bunnell. 2002. Development of coarse-scale spatial data for wildland fire and fuel management. General technical report RMRS-GTR-87. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Scott, J. H., and E. D. Reinhardt. 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. Research paper RMRS-RP-29. U.S. Department of Agriculture Forest Service, Rocky

Mountain Research Station, Fort Collins, Colorado.

Shinneman, D. J., and W. L. Baker. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. Conservation Biology **11:**1276–1288.

Shrader-Frechette, K. S., and E. D. McCoy. 1993. Method in ecology: strategies for conservation. Cambridge University Press, Cambridge, United Kingdom.

Stephens, S. L. 1998. Evaluation of the effects of silvicultural and fuels treatments on potential fire behavior in Sierra Nevada mixed-conifer forests. Forest Ecology and Management **105:**21–38.

Stephenson, N. L. 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecological Applications **9:**1253–1265.

Swanson, F. J., J. A. Jones, D. O. Wallin and J. H. Cissel. 1994. Natural variability: implications for ecosystem management. Pages 80–94 in M. E. Jensen and P. S. Bourgeron, editors. Eastside forest ecosystem health assessment. II. Ecosystem management: principles and applications. General technical report PNW-GTR-318. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage the future. Ecological Applications **9:**1189–1206.

Swezy, D. M., and J. K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research **21:**626–634.

Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management **111:**285–301.

Thomas, T. L., and J. K. Agee. 1986. Prescribed fire effects on mixed conifer forest structure at Crater Lake, Oregon. Canadian Journal of Forest Research **16:**1082–1087.

Tiedemann, A., J. Klemmedson, and E. Bull. 2000. Solution of forest health problems with prescribed fire: are forest productivity and wildlife at risk? Forest Ecology and Management **127:**1–18.

Trombulak, S. C., and C. A Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology **14:**18–30.

U.S. Department of Agriculture Forest Service (USFS). 2000. Sierra Nevada forest plan amendment project draft environmental impact statement (DEIS): appendix G fire and fuels. USFS, Region 5, Vallejo, California.

van Wagtendonk, J. W. 1996. Use of a deterministic fire growth model to test fuel treatments. Pages 1155–1165 in Sierra Nevada ecosystem project final report to Congress. II. Assessments and scientific basis for management options. Centers for Water and Wildland Resources, University of California, Davis.

Veblen, T. T., T. Kitzberger, and J. Donnegan 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecological Applications **10:**1178–1195.

Weatherspoon, C. P. 1996. Fire-silviculture relationships. Pages 1167–1176 in Sierra Nevada ecosystem project final report to Congress. II. Assessments and scientific basis for management options. Centers for Water and Wildland Resources, University of California, Davis.

Weatherspoon, C. P., and C. N. Skinner. 1995. An assessment of factors associated with damage to tree crowns from the 1987 wildfires in northern California. Forest Science **41:**430–451.

Weatherspoon, C. P., and C. N. Skinner. 2002. An ecological comparison of fire and fire surrogates for reducing wildfire hazard and improving forest health: a research proposal. Pages 239–245 in Miscellaneous publication 1. Association for Fire Ecology, Davis, California.

Wickman, B. E. 1992. Forest health in the Blue Mountains: the influence of insects and disease. General technical report PNW-GTR-295. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Wisdom, M., R. Holthausen, B. Wales, D. Lee, C. Hargis, V. Saab, W. Hann, T. Rich, M. Rowland, W. Murphy, and M. Eames. 2000. Source habitats for terrestrial vertebrates of focus in the interior Columbia Basin: broad-scale trends and management implications. General technical report PNW-GTR-485. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon.



Check for updates

Ecological Applications, 30(2), 2020, e02039
© 2019 The Authors. *Ecological Applications* published by Wiley Periodicals, Inc. on behalf of Ecological Society of America
This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States

Polly C. Buotte [1,3] Beverly E. Law [1] William J. Ripple [1] and Logan T. Berner [2]

[1]*Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, Oregon 97331 USA*
[2]*EcoSpatial Services L.L.C., 2498 North Oakmont Drive, Flagstaff, Arizona 86004 USA*

Citation: Buotte, P. C., B. E. Law, W. J. Ripple, and L. T. Berner. 2020. Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States. Ecological Applications 30(2):e02039. 10.1002/eap.2039

Abstract. Forest carbon sequestration via forest preservation can be a viable climate change mitigation strategy. Here, we identify forests in the western conterminous United States with high potential carbon sequestration and low vulnerability to future drought and fire, as simulated using the Community Land Model and two high carbon emission scenario (RCP 8.5) climate models. High-productivity, low-vulnerability forests have the potential to sequester up to 5,450 Tg CO_2 equivalent (1,485 Tg C) by 2099, which is up to 20% of the global mitigation potential previously identified for all temperate and boreal forests, or up to ~6 yr of current regional fossil fuel emissions. Additionally, these forests currently have high above- and belowground carbon density, high tree species richness, and a high proportion of critical habitat for endangered vertebrate species, indicating a strong potential to support biodiversity into the future and promote ecosystem resilience to climate change. We stress that some forest lands have low carbon sequestration potential but high biodiversity, underscoring the need to consider multiple criteria when designing a land preservation portfolio. Our work demonstrates how process models and ecological criteria can be used to prioritize landscape preservation for mitigating greenhouse gas emissions and preserving biodiversity in a rapidly changing climate.

Key words: biodiversity; carbon sequestration; climate change; Community Land Model (CLM); forest; mitigation; process modeling; western United States.

Introduction

Since the signing of the United Nations Framework Convention on Climate Change in Rio de Janeiro in 1992, the United Nations has recognized the need to formulate a global response to increasing greenhouse gas concentrations in our atmosphere. The subsequent adoptions of the Sustainable Development Goals (United Nations General Assembly 2015) and the Paris Agreement (United Nations Framework Convention on Climate Change (UNFCC) 2015) provided global targets for preserving biodiversity and limiting the negative effects of increasing greenhouse gas concentrations. Limiting global temperature to 1.5°C above the preindustrial average would limit negative climate impacts (IPCC 2018), including negative effects on biodiversity (Smith et al. 2018). Unfortunately, substantial enhancement or over-delivery of emissions goals in the Paris Agreement is necessary to limit warming to less than 2°C (Rogelj et al. 2016). Missing this target could destabilize Earth's climate, terrestrial, and aquatic systems (Steffen et al. 2018) with catastrophic consequences for biodiversity (Davis et al. 2018), ecosystem services, and humans (Barnosky et al. 2012). Already, ample observational evidence exists that changes in climate are inducing ecosystem transformations through tree mortality (Allen et al. 2010, Millar and Stephenson 2015) and changes in species composition (Allen and Breshears 1998, Millar and Stephenson 2015). Process-based (Settele et al. 2014, McDowell et al. 2016) and statistical (Rehfeldt et al. 2006, Williams et al. 2007, Pearson et al. 2013) models indicate a strong potential for continued ecological transformation, and paleological analyses indicate that, if we continue on our current emission trajectory, drastic changes in global ecosystem structure and function are likely by the end of this century (Nolan et al. 2018*a*).

Along with emissions, multiple biogeophysical processes, including carbon uptake by the land and oceans and ocean heat exchange (Solomon et al. 2009), influence atmospheric CO_2 (Canadell et al. 2007, Le Quere et al. 2018) and the integrated Earth system trajectory (Barnosky et al. 2012, Steffen et al. 2018). Recent measurements indicate the ocean heat uptake is at the high end of previous estimates (Resplandy et al. 2018), and decreasing land carbon uptake relative to carbon emissions (Canadell et al. 2007) is contributing to increasing atmospheric CO_2 and chances of climate destabilization (Barnosky et al. 2012, Steffen et al. 2018). Land preservation and timber harvest management (natural climate

Manuscript received 4 March 2019; revised 10 October 2019; accepted 21 October 2019. Corresponding Editor: Yude Pan.
[3] E-mail: pcbuotte@gmail.com

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

solutions) are viable options for avoiding greenhouse gas emissions and increasing the magnitude of the land carbon sink (Griscom et al. 2017).

Forest management (e.g., land preservation, reduced harvest) can contribute to climate change mitigation and the preservation of biodiversity (MEA 2005). Globally, improvements to land management could provide an estimated 37% of the mitigation needed to stabilize warming below 2°C by 2039 (Griscom et al. 2017). Land management can also mitigate the negative effects that climate-induced ecosystem transformations have on biodiversity and watersheds, which influence ecosystem services that contribute to human well-being (Canadell and Raupach 2008, Griscom et al. 2017). The effects of land-use change vary globally (Bright et al. 2017), therefore regional analyses (Cameron et al. 2017, Law et al. 2018) are ideal for prioritizing lands for preservation and improving harvest management.

Here, we simulate potential forest carbon sequestration in the western United States, prioritize forest lands for preservation (i.e., no harvest) based on potential carbon sequestration and vulnerability to drought or fire, and compare this carbon priority ranking with measures of biodiversity to illustrate the spatial synergies and incongruities between these two preservation metrics. We use the Community Land Model 4.5 (CLM) to simulate future forest productivity and vulnerability to drought and fire. We prioritize land based on the spatial convergence of low future vulnerability to natural disturbance and three levels of potential productivity and determine the CO_2 mitigation potential that preserving medium- and high-priority forests could provide. We show the co-benefits and trade-offs to biodiversity preservation and ecosystem resilience by comparing current observations of aboveground carbon (Wilson et al. 2013), soil carbon (Weider et al. 2014), and species richness (Jenkins et al. 2015, USGS National Gap Analysis Program 2018) across the three forest carbon preservation priority categories. We use these combined analyses to underscore the need to consider multiple criteria when selecting forest lands for preservation.

Materials and Methods

Simulations of future forest vulnerability and potential carbon sequestration

We used the Community Land Model, version 4.5 (CLM; Oleson et al. 2013) to simulate the forest carbon cycle across the western United States (Appendix S1: Fig. S1) at a 4 × 4 km spatial resolution. The CLM is the land surface model within the Community Earth System Model (Hurrell et al. 2013). The CLM has prognostic carbon and nitrogen cycles and calculates multiple biogeochemical and biophysical process, such as photosynthesis, autotrophic and heterotrophic respiration, carbon allocation to plant tissues, decomposition, and surface energy balance. It also has a fire module that predicts area burned under future climate and biomass fuel conditions. Here, we used climate projections, described below, prescribed vegetation type (Appendix S1: Fig. S1), and prescribed soil type to drive the model. We employed several modifications that improved the CLM's simulation of aboveground carbon, net primary productivity, and ecosystem respiration across the western United States (Buotte et al. 2019b). In particular, these include specification of physiological parameters controlling photosynthesis for the dominant species in the major forest types (Appendix S1: Fig. S1) of the western United States (Berner and Law 2016, Law et al. 2018, Buotte et al. 2019b), enhanced drought sensitivity through species-specific stomatal response to soil moisture and leaf shedding during periods of drought stress (Buotte et al. 2019b), and improved fire simulation by incorporating regional ignition probabilities and fuel load constraints (Buotte et al. 2019b).

The CLM was started from bare ground and run with 1901–1920 climate data and prognostic fire turned off until soil carbon pools reached equilibrium. Improvements to the representation of drought stress and prognostic fire were implemented beginning in 1901. From 1901 to 1978, we forced CLM with CRUNCEP climate data (Mitchell and Jones 2005) statistically downscaled to 4 × 4 km and bias-corrected to our 1979–2014 climate data. Climate data from 1979 to 2014 were disaggregated from daily to 3-h intervals at 4 × 4 km resolution (Abatzoglou 2013). Downscaling and disaggregation details are provided in Buotte et al. (2019b). Furthermore, we used prescribed harvest to insure the model represented present-day stand ages (Pan et al. 2011).

It is crucial to assess model performance and thus we previously evaluated the modeled present-day carbon stocks, carbon fluxes, and burned area through comparisons with a suite of field and satellite observations (Buotte et al. 2019*a*,*b*). In particular, we compared modeled carbon stocks and fluxes with aboveground biomass interpolated from plot inventories (Wilson et al. 2013), carbon fluxes from five AmeriFlux sites, fluxes derived from plot inventories in Washington, Oregon, and California (Hudiburg et al. 2009, 2011), and net primary productivity estimated from the MODIS satellites (Berner et al. 2017*a*). We also compared modeled burned area with a burned area data set derived from the Landsat satellites (Eldenshenk et al. 2007). As detailed in Buotte et al. (2019b), simulated carbon fluxes agreed well with a variety of observations. Simulated net primary productivity was within the range of observed and satellite-derived net primary productivity at the state level. Across all forests in the western United States, simulated aboveground carbon was within one standard deviation of observation-based aboveground carbon (observed mean = 30.5 Mg C/ha, SD = 39.7 Mg C/ha, CLM mean = 59.1 Mg C/ha, SD = 45.5 Mg C/h, $R^2 = 0.80$). When grouped by forest type, simulated aboveground carbon was highly correlated with

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

observations with a tendency toward higher simulated values ($R^2 = 0.84$, mean bias error = 4%). Over the forested domain, simulated area burned was highly correlated with observed area burned ($R^2 = 0.75$), with a 28.6% overestimate when compared with observations from the Monitoring Trends in Burn Severity (MTBS) database over 1984–2012 (Eldenshenk et al. 2007). However, Whittier and Gray (2016) determined that MTBS underestimates burn area by 20% when compared with inventory data, which implies CLM overestimates may be as low as 8%. These assessments illustrate that the model is accurately simulating important aspects of the current regional forest carbon cycle.

Our future CLM simulations were driven with two future climate projections. We used a Representative Concentration Pathway (RCP) 8.5 carbon dioxide emissions scenario for our future simulations because it best represents our current trajectory (Peters et al. 2013). We chose general circulation models (GCMs) based on data availability, representation of historical climate, and coverage of the range of projected future climate (Buotte et al. 2019b). We selected IPSL-CM5A-MR, which projects warm and dry future conditions, and MIROC5, which is close to the multi-model average for future temperature and precipitation across the western United States (Buotte et al. 2019b). Climate projections for 2015–2099 were downscaled, bias-corrected to the 1979–2014 climate observation data (Abatzoglou 2013), and disaggregated to a 3-h timescale. Downscaling and disaggregation details are provided in Buotte et al. (2019b).

The number of years with low annual allocation to stem growth and/or annual net primary productivity of 0 were used to determine forest vulnerability to drought stress (Buotte et al. 2019b). For each decade, we defined low vulnerability in grid cells with 0 yr of NPP = 0 and low allocation to growth, medium vulnerability in grid cells with 1 yr with NPP = 0 and/or 1–3 yr with low allocation to growth, and high vulnerability in grid cells with more than 1 yr with NPP = 0 and/or more than 3 yr with no allocation to growth (Buotte et al. 2019b). Grid cells were ranked with low, medium, or high vulnerability for both IPSL_CM5A-MR and MIROC5 forced simulations. For every grid cell, we calculated vulnerability to fire based on the increase in simulated area burned in the future compared with the past, weighted by the simulated area burned in the past (Buotte et al. 2019b). Final drought and fire vulnerability rankings included uncertainty due to climate projections by incorporating the drought and fire vulnerability ranking from simulations using each of the two climate projections, such that (1) uncertain, one GCM simulation ranked as low and one simulation ranked as high; (2) low, both GCMs low; (3) med-low, one low and one medium; (4) medium, both GCMs medium; (5) med-high, one medium and one high; (6) high, both GCMs high.

Further details on vulnerability calculation and assessment relative to observed mortality are provided in Buotte et al. (2019b).

We determined potential carbon sequestration (Keith et al. 2009*a*) by running CLM with no prescribed harvest beyond 2014 and summing net ecosystem productivity (NEP) from 2020 to 2099, thereby allowing forest type, soil properties, climate, and CO_2 concentrations to determine productivity. We pooled cumulative NEP across all grid cells and defined three categories of potential carbon sequestration based on the highest one-third ($>1.12 \times 10^5$ g /m^2), middle one-third, and lowest one- third ($<3.27 \times 10^4$ g C/m^2) of the distribution. We then ranked forested areas to identify low, medium, and high carbon preservation priority based on the spatial coincidence of low future vulnerability to drought and fire and potential carbon sequestration (Appendix S1: Fig. S2). Forests with low vulnerability to future drought and fire and the highest potential carbon sequestration were ranked as high priority for preservation as carbon preserves; low vulnerability and medium carbon sequestration potential were ranked as medium priority; all other combinations were ranked as low priority. Hereafter we refer to forest priority for preservation as carbon preserves as "carbon priority."

Tree mortality from bark beetles

Tree mortality from bark beetle attack is an important disturbance in western U.S. forests, but not currently incorporated into CLM. We therefore addressed the potential for future beetle mortality by assessing recent historical beetle mortality (Berner et al. 2017b) and existing future projections of climate suitability for beetle outbreaks (Bentz et al. 2010, Buotte et al. 2017) across our three forest carbon priority rankings.

Above- and belowground carbon stocks

We assessed observation-based estimates of carbon stocks (i.e., not our simulated carbon stocks) across forests in each carbon priority ranking. We used the Regridded Harmonized World Soil Database V1.2 (Weider et al. 2014) for belowground carbon stocks, and a gridded data set of aboveground carbon stocks based on field measurements and remote sensing (Wilson et al. 2013).

Species richness and critical habitat

We examined several aspects of biodiversity across forests with low, medium, and high carbon preservation priority. We acquired published tree species richness maps for the United States (Jenkins et al. 2015), species habitat maps for terrestrial vertebrates (amphibians, reptiles, birds, and mammals) from the U.S. Geological Survey Gap Analysis Program (USGS National Gap Analysis Program 2018), and species habitat maps identifying critical habitat by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2018). Each map was resampled to the 4×4 km CLM grid. We

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

computed terrestrial vertebrate species richness by taxa and across taxa for each grid cell. We also identified whether a terrestrial vertebrate species was listed as threatened or endangered (T&E) by the U.S. Fish and Wildlife Service and then reassessed species richness for this subset of species. Last, we summarized these aspects of species richness and critical habitat by forest carbon priority rank.

Results

High-priority forest distribution and contribution to emissions mitigation

The high-carbon-priority forests are primarily along the Pacific coast and the Cascade Mountains, with scattered occurrences in the northern Rocky Mountains of Idaho and Montana (Fig. 1). Forests with medium carbon priority are more widely scattered throughout the western United States (Fig. 1).

High-carbon-priority forests cover 132,016 km^2 or 10.3% of the forested domain and have the potential to sequester 4,815–5,450 Tg CO_2 equivalent (Tg CO_2 e; 1,312–1,485 Tg C) in aboveground carbon between 2020 and 2099 (Fig. 1, Table 1, Appendix S1: Table S1). Medium-carbon-priority forests cover 9.5% of the forested domain and could sequester 1,842–2,136 Tg CO_2 e (502–582 Tg C). Low-carbon-priority forests cover 80.2% of the forested domain and could sequester 12,789–16,533 Tg CO_2 e (3,485–4,505 Tg C) by 2099. However, because the low-carbon-priority forests have higher future vulnerability, their carbon sequestration potential is less certain.

Co-benefits of preserving high-carbon-priority forests

The forests we identified with the greatest potential to sequester carbon during this century provide multiple ecological co-benefits. Recent tree mortality from bark beetle attack was the lowest in these high-carbon-priority forests (Appendix S1: Fig. S3). These forests have the highest average present-day soil carbon stocks (14% higher than medium and 65% higher than low carbon priority) and aboveground carbon stocks (41% higher than medium and 248% higher than low carbon priority; Fig. 2), and also currently support the highest tree species richness (Fig. 3). Furthermore, high-carbon-priority forests contain the highest proportional area of terrestrial vertebrate habitat for species listed as threatened or endangered by the U.S. Fish and Wildlife Service (Fig. 4), as well as the highest proportion of habitat designated as critical for threatened or endangered species survival (Fig. 4). There is less distinction in terrestrial vertebrate species richness by carbon priority rank, though high-carbon-priority forests tend to have higher amphibian and lower reptilian richness than forests with medium or low carbon priority ranks (Appendix S1: Fig. S4). It is important to highlight that the spatial

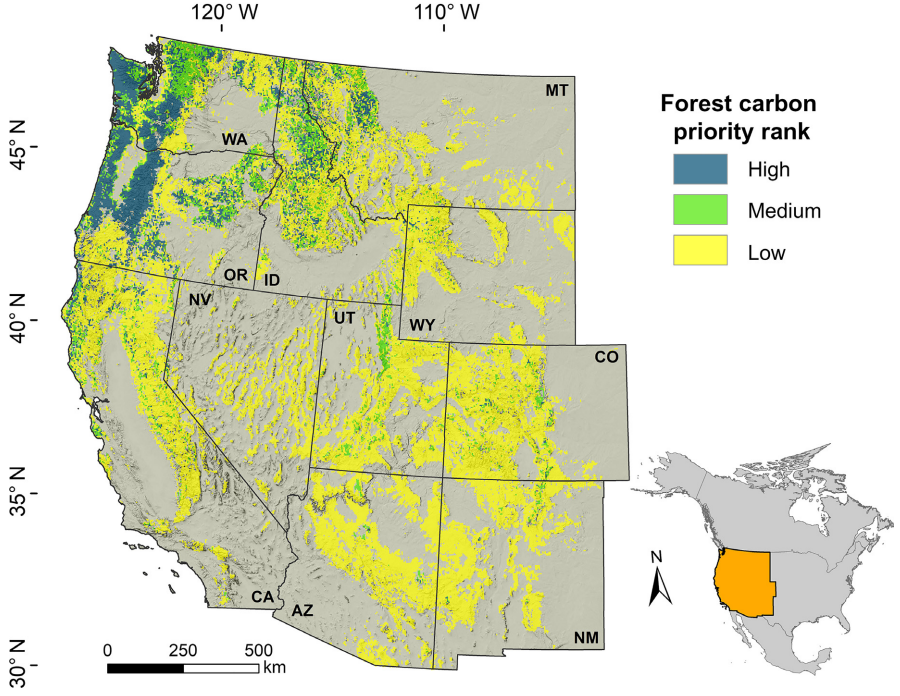


Fig. 1. Forested land in the western conterminous United States classified into priority for preservation to mitigate climate change based on the spatial co-occurrence of low vulnerability to drought and fire and low, medium, and high potential carbon sequestration. WA, Washington; ID, Idaho; MT, Montana; OR, Oregon; CA, California; NV, Nevada; UT, Utah; CO, Colorado; AZ, Arizona; NM, New Mexico.

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1. Area, percentage of forested domain, and carbon sequestration potential during 2020–2099 (calculated as the sum of annual net ecosystem production, with business-as-usual harvest amounts) in each priority category.

Priority ranking	Area (km^2)	Forested domain (%)	Carbon sequestration potential during 2020–2099 (Tg CO_2e)†	Carbon sequestration potential during 2020–2099 (Tg C/km^2)
High	132,016	10.3	4,815–5,450 (1,312–1,485 Tg C)	0.036–0.041
Medium	120,800	9.5	1,842–2,136 (502–582 Tg C)	0.015–0.018
Low	1,023,872	80.2	12,789–16,533 (3,485–4,505 Tg C)	0.012–0.016

† Tg CO_2 equivalent. Values in parentheses are Tg CO_2.

distribution of species richness (Appendix S1: Fig. S5) indicates some areas of exceptionally high species richness (e.g., the Klamath region in southern Oregon and northern California) have a low carbon priority ranking due to medium to high future vulnerability, particularly to fire, or low forest productivity. Summaries of species richness and habitat area by state are provided in Appendix S1: Figs. S6 and S7.

Discussion

Hotter and drier conditions are expected to increase future tree mortality from drought (Allen et al. 2010, McDowell et al. 2016) and fire (Spracklen et al. 2009, Pechony and Shindell 2010) in parts of the western United States, thus preserving forests with the lowest vulnerability to future disturbance is one intuitive component of a land preservation strategy. Forest preservation offers a cost-effective strategy to avoid and mitigate CO_2 emissions by increasing the magnitude of the terrestrial carbon sink in trees and soil, preserve biodiversity, and sustain additional ecosystem services (Griscom et al. 2017). We show considerable potential for forests in the western United States to sequester additional carbon over the coming century and demonstrate that protecting high-carbon-priority areas could help preserve components of biodiversity. However, we also find high biodiversity in some areas with low future carbon sequestration potential due to slow growth or high vulnerability to fire. We therefore suggest that developing area-based retention targets (Maron et al. 2018) for both carbon and biodiversity metrics, along with the consideration of land ownership (Krankina et al. 2014), would allow the development of a portfolio of preserves to meet these criteria.

Preserving high-carbon-priority forests avoids future CO_2 emissions from harvesting and mitigates existing emissions through carbon sequestration. Regional fossil fuel emissions averaged ~260 Tg C/yr from 2003 to 2012 according to the U.S. Energy Information Administration (2015). Preserving the high-carbon-priority forests in the western United States would account for approximately 6 yr of regional fossil fuel emissions, or 18–20% of the global mitigation potential of natural forest management solutions Griscom et al. (2017) identified for the combination of temperate and boreal forests by 2099. This would increase to almost 8 yr of regional emissions, or 27–32% of temperate and boreal forest mitigation potential, if preservation was expanded to include medium-carbon-priority forests. Carbon dioxide emissions from soils in degraded forests account for roughly 11% of global net emissions (Houghton and Nassikas 2017). As the high-carbon-priority forests have the highest soil carbon, preserving these forests avoids

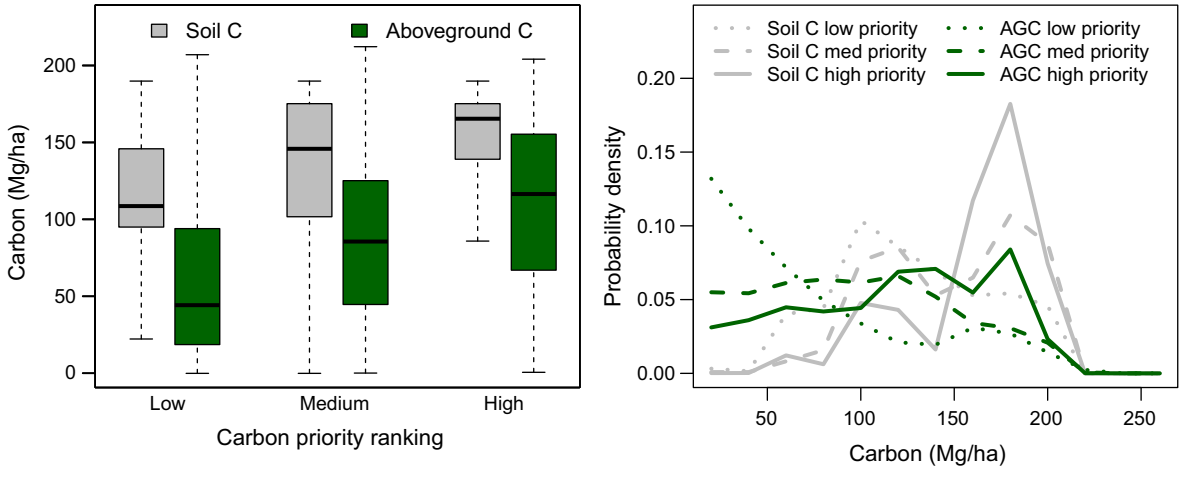


FIG. 2. Conterminous western U.S. forests ranked with the highest priority for preservation for carbon sequestration also have the highest current soil and aboveground carbon stocks. Carbon stocks from gridded measurements interpolated from observations (see *Materials and Methods*). Box plot components are mid line, median; box edges, first and third quartiles; and whiskers, max and min.

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

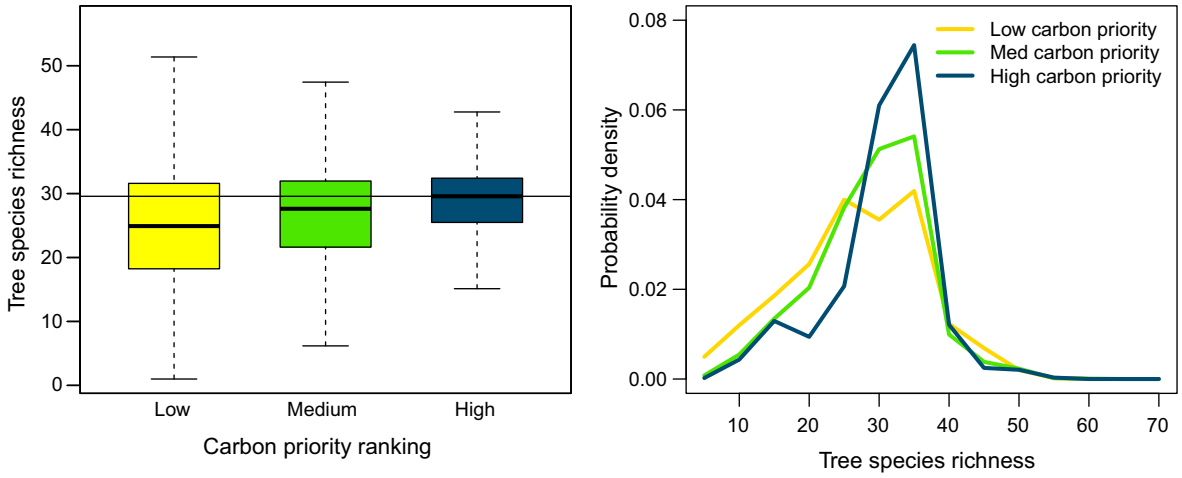


FIG. 3. Conterminous western U.S. forests ranked with the highest priority for preservation for carbon sequestration also have the highest present-day tree species richness (BioDiversityMapping.org richness data).

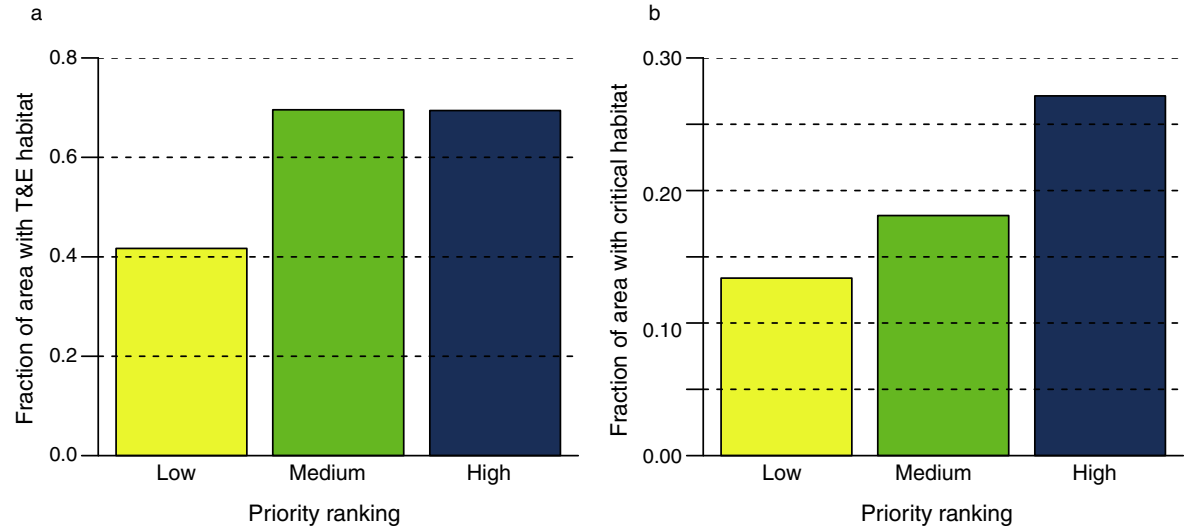


FIG. 4. Fraction of forest in each carbon priority ranking with (a) habitat of all threatened and endangered (T&E) species designated as critical for that species survival and (b) habitat of terrestrial vertebrate species listed as threatened or endangered by the U.S. Fish and Wildlife Service.

additional CO_2 emissions from the soil as surface litter and root material decay after harvest.

We found that high-carbon-priority forests in the western United States exhibit features of older, intact forests with high structural diversity (Keith et al. 2009b, Krankina et al. 2014), including carbon density and tree species richness. Forest resilience and adaptive capacity increase with increasing plant species richness (Morin et al. 2018, Watson et al. 2018), suggesting that preserving the high-carbon-priority forests would provide an added buffer against potential ecosystem transformation to future climate change.

Intact forests are particularly important for watershed protection by regulating soil permeability, overland flow, and erosion (DellaSala et al. 2011, Creed et al. 2016, Moomaw et al. 2019). Across the United States, National Forests are the largest source of drinking water (Furniss et al. 2010). In the Pacific Northwest, conversion of old-growth forests to plantations reduced summer stream flow by an average of 50% (Perry and Jones 2017). Preserving intact forests would provide the greatest benefit to watershed protection and clean water supply (DellaSala et al. 2011). Unfortunately, the area of forest interior (defined as forest area per land area) is declining faster than the total area of forest in the United States (Riitters and Wickham 2012). Remaining primary and intact forests need to be identified and incorporated in land management policies.

Recent studies have found positive relationships between carbon density and biodiversity across multiple biomes (Brandt et al. 2014, Lecina-Diaz et al. 2018), but also weak relationships at the stand scale (Sabatini et al.

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

2019). We show that preserving forests in the western United States with high productivity and low vulnerability to future fire and drought can aid in the maintenance of vertebrate biodiversity, as these forests contain the highest proportion of critical habitat for threatened and endangered species. Because extinction rates are expected to increase with projected climate change (Segan et al. 2016), preserving critical habitat is an important consideration for maintaining biodiversity. Our analysis also shows that benefits to biodiversity depend in part on the biodiversity metric. For example, we found amphibian richness was the highest in forests we identified with high carbon priority, likely because these forests occur most often in the moist maritime climate suitable to amphibians. On the other hand, these wet, high-carbon-priority forests tend to have lower reptile diversity than low-carbon-priority forests, such as those in the Southwest where reptile diversity was highest. We show that spatial overlap in measures of biodiversity and potential carbon sequestration occurs such that land management policies can optimize both priorities. However, we also demonstrate that areas of high biodiversity are found in medium to low-carbon-priority forests. Therefore, sound land preservation strategies need to include multiple priority metrics (Brandt et al. 2014).

Indeed, preservation of carbon-dense primary (Mackey et al. 2015) and intact forests (Watson et al. 2018) is a critical but insufficient criterion for maintaining biodiversity. Secondary forests can support high biodiversity (Donato et al. 2009, Gilroy et al. 2014), as well as different species assemblages compared with primary forests (Ferreira et al. 2018). There are regions identified as globally significant centers of biodiversity (Olson et al. 2012; e.g., the Klamath-Siskiyou region in southwest Oregon) that we identified with medium to high future vulnerability due to fire. Therefore, when protecting biodiversity is a high conservation priority, disturbance-prone forests will need to be included in area-based targets (Maron et al. 2018). Regional assessments (Dass et al. 2018) that simulate vegetation transformation on multi-decadal timescales are needed to elucidate the effect of future disturbance regimes on plant community composition in order to assess potential future biodiversity and determine preservation priority rankings of disturbance-prone forests.

Because secondary forests also arise from a legacy of human intervention, conservation of managed landscapes will be an important component of policies to maintain biodiversity and enhance climate mitigation (Kremen and Merenlender 2018). Regional analyses have shown that lengthening harvest cycles can substantially improve carbon sequestration (Law et al. 2018) and biodiversity (Gilroy et al. 2014) and therefore provide pathways for additional climate mitigation (Griscom et al. 2017). Historical stand structure analysis indicates young trees may have played an important role in buffering against particular types of disturbance (Baker and Williams 2015). However, because young trees can be more vulnerable to drought stress than mature trees (Irvine et al. 2002), assessments of future climate vulnerability of young forests will be a critical factor when evaluating harvest strategies (Nolan et al. 2018b). Regional dynamic vegetation simulations with explicit treatment of forest regeneration are necessary to assess the effects of land management scenarios and develop strategies for managed lands.

Assessing the potential for future forest carbon sequestration has inherent uncertainties concerning realized future climate, forest growth, and sources of forest mortality. We address uncertainties in future climate by using two climate scenarios that span a wide range of variability in temperature and precipitation (Buotte et al. 2019b), though we acknowledge that future climate remains uncertain due to the trajectory of carbon emissions, climate sensitivity to these emissions, and climate feedbacks (Collins et al. 2014, Schuur et al. 2015). Furthermore, simulated forest growth depends on how the model was parameterized (White et al. 2000). Here, we used parameterizations developed specifically for forest types in the western United States (Hudiburg et al. 2013, Law et al. 2018, Buotte et al. 2019b), which improved model agreement with historical observations as compared with more general forest type parameterizations (Buotte et al. 2019b). In response to increasing CO_2 concentration, trees may increase their water use efficiency (Keenan et al. 2013, Schimel et al. 2015), however, this response may depend on nutrient availability (Oren et al. 2001, Norby et al. 2010). The CLM incorporates nitrogen limitation (Oleson et al. 2013), which allows the CLM to accurately simulate recent changes in NPP observed under increasing CO_2 concentrations (Smith et al. 2016).

Mountain pine beetles (*Dendroctonus ponderosae*) were responsible for the majority of tree mortality from beetles in the recent past (Meddens et al. 2012). Previous analysis (Buotte et al. 2019b) indicates our drought metric identifies forests vulnerable to beetle attack due to the presence of drought-stressed trees (Boone et al. 2011), increasing our confidence in our vulnerability metric's ability to capture this important disturbance agent. Importantly, future projections of beetle population dynamics (Bentz et al. 2010) do not indicate increasing beetle populations in areas we define with high carbon priority. Climate suitability for tree mortality from mountain pine beetles is projected to increase in some high-elevation whitebark pine forests (Buotte et al. 2017), which we ranked with low carbon priority due to lower carbon sequestration potential, or medium to high vulnerability to future drought or fire. Predictive models of beetle population dynamics for multiple beetle species, that include host tree status when appropriate, would increase our ability to incorporate specific spatial representation of future forest vulnerability to beetle attack. We simulated future fire, but the model does not capture the potential for anomalous mega-fires.

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Therefore, our estimates of future carbon sequestration potential in the absence of large-scale mortality events are likely to be robust.

Preservation of high carbon density Pacific Northwest forests that are also economically valuable for timber production will have costs and benefits to consider, including socioenvironmental benefits, the feasibility of preservation, and opportunity costs harvest. There is tremendous potential for proforestation, growing existing forests intact to their ecological potential, which is an effective, immediate, and low-cost approach to removing carbon dioxide from the atmosphere (Moomaw et al. 2019). Proforestation serves the greatest public good by maximizing co-benefits such as biological carbon sequestration and unparalleled ecosystem services including biodiversity enhancement, water and air quality, flood and erosion control, and low impact recreation. The development of governance programs to promote forest preservation will be critical. Our study is a first step at identifying areas with the highest potential for natural co-benefits and proforestation.

Conclusions

If we are to avert our current trajectory toward massive global change, we need to make land stewardship a higher societal priority (Chan et al. 2016). Preserving temperate forests in the western United States that have medium to high potential carbon sequestration and low future climate vulnerability could account for approximately 8 yr of regional fossil fuel emissions, or 27–32% of the global mitigation potential previously identified for temperate and boreal forests, while also promoting ecosystem resilience and the maintenance of biodiversity. Biodiversity metrics also need to be included when selecting preserves to ensure species-rich habitats that result from frequent disturbance regimes are not overlooked. The future impacts of climate change, and related pressures as human population exponentially expands, make it essential to evaluate conservation and management options on multi-decadal timescales, with the shared goals of mitigating committed CO_2 emissions, reducing future emissions, and preserving plant and animal diversity to limit ecosystem transformation and permanent losses of species.

Acknowledgments

This research was supported by the Agriculture and Food Research Initiative of the U.S. Department of Agriculture National Institute of Food and Agriculture (Grants 2013-67003-20652, 2014-67003-22065, and 2014-35100-22066) for our North American Carbon Program studies, "Carbon cycle dynamics within Oregon's urban-suburban-forested-agricultural landscapes" and "Forest die-off, climate change, and human intervention in western North America," (and the U.S. Department of Energy (Grant DE-SC0012194). High-performance computing resources to run CLM on Cheyenne (https://doi.org/10.5065/d6rx99hx) were provided by NCAR's Computational and Information Systems Laboratory, sponsored by the National Science Foundation.

Literature Cited

Abatzoglou, J. T. 2013. Development of gridded surface meteorological data for ecological applications and modelling. International Journal of Climatology 33:121–131.

Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest/woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences USA 95:14839–14842.

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Baker, W. L., and M. A. Williams. 2015. Bet-hedging dry-forest resilience to climate-change threats in the western USA based on historical forest structure. Frontiers in Ecology and Evolution 2:1–7.

Barnosky, A. D., et al. 2012. Approaching a state shift in Earth's biosphere. Nature 486:52–58.

Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60:602–613.

Berner, L. T., and B. E. Law. 2016. Plant traits, productivity, biomass and soil properties from forest sites in the Pacific Northwest, 1999-2014. Nature Scientific Data 3:1–14.

Berner, L. T., B. E. Law, and T. W. Hudiburg. 2017*a*. Water availability limits tree productivity, carbon stocks, and carbon residence time in mature forests across the western US. Biogeosciences 14:365–378.

Berner, L. T., B. E. Law, A. J. H. Meddens, and J. A. Hicke. 2017*b*. Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States (2003-2012). Environmental Research Letters 12:065005.

Boone, C. K., B. H. Aukema, J. Bohlmann, A. L. Carroll, and K. F. Raffa. 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. Canadian Journal of Forest Research 41:1174–1188.

Brandt, P., D. J. Abson, D. A. DellaSala, R. Feller, and H. von Wehrden. 2014. Multifunctionality and biodiversity: ecosystem services in temperate rainforests of the Pacific Northwest, USA. Biological Conservation 169:362–371.

Bright, R. M., E. Davin, T. O'Halloran, J. Pongratz, K. G. Zhao, and A. Cescatti. 2017. Local temperature response to land cover and management change driven by non-radiative processes. Nature Climate Change 7:296.

Buotte, P. C., J. A. Hicke, H. K. Preisler, J. T. Abatzoglou, K. F. Raffa, and J. A. Logan. 2017. Recent and future climate suitability for whitebark pine mortality from mountain pine beetles varies across the western US. Forest Ecology and Management 399:132–142.

Buotte, P. C., S. Levis, and B. E. Law. 2019*a*. NACP: forest carbon stocks, fluxes and productivity estimates, western USA, 1979-2099. ORNL DAAC, Oak Ridge, Tennessee, USA. https://doi.org/10.3334/ornldaac/1662

Buotte, P. C., S. Levis, B. E. Law, T. W. Hudiburg, D. E. Rupp, and J. J. Kent. 2019*b*. Near-future forest vulnerability to drought and fire varies across the western United States. Global Change Biology 25:290–303.

Cameron, D. R., D. C. Marvin, J. M. Remucal, and M. C. Passero. 2017. Ecosystem management and land conservation can substantially contribute to California's climate mitigation goals. Proceedings of the National Academy of Sciences USA 114:12833–12838.

Canadell, J. G., and M. R. Raupach. 2008. Managing forests for climate change mitigation. Science 320:1456–1457.

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Canadell, J. G., C. Le Quere, M. R. Raupach, C. B. Field, E. T. Buitenhuis, P. Ciais, T. J. Conway, N. P. Gillett, R. A. Houghton, and G. Marland. 2007. Contributions to accelerating atmospheric CO2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proceedings of the National Academy of Sciences USA 104:18866–18870.

Chan, K. M. A., et al. 2016. Why protect nature? Rethinking values and the environment. Proceedings of the National Academy of Sciences USA 113:1462–1465.

Collins, M., et al. 2014. Long-term climate change: projections, commitments and irreversibility. Pages 1029–1136 *in* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. Climate change 2013: the physical science basis. IPCC, Cambridge, UK, New York, New York, USA.

Creed, I. F., M. Weber, F. Accatino, and D. P. Kreutzweiser. 2016. Managing forests for water in the Anthropocene—the best kept secret services of forest ecosystems. Forests 7:60.

Dass, P., B. Z. Houlton, Y. P. Wang, and D. Warlind. 2018. Grasslands may be more reliable carbon sinks than forests in California. Environmental Research Letters 13:074027.

Davis, M., S. Faurby, and J.-C. Svenning. 2018. Mammal diversity will take millions of years to recover from the current biodiversity crisis. Proceedings of the National Academy of Sciences USA 115:11262–11267.

DellaSala, D. A., J. R. Karr, and D. M. Olson. 2011. Roadless areas and clean water. Journal of Soil and Water Conservation 66:78A–84A.

Donato, D. C., J. B. Fontaine, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. Journal of Ecology 97:142–154.

Eldenshenk, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology Special Issue 3:3–21.

Ferreira, J., et al. 2018. Carbon-focused conservation may fail to protect the most biodiverse tropical forests. Nature. Climate Change 8:744.

Furniss, M. J., et al. 2010. Water, climate change, and forests: watershed stewardship for a changing climate. PNW_GTR_812. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Gilroy, J. J., P. Woodcock, F. A. Edwards, C. Wheeler, B. L. G. Baptiste, C. A. M. Uribe, T. Haugaasen, and D. P. Edwards. 2014. Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism. Nature Climate Change 4:503–507.

Griscom, B. W., et al. 2017. Natural climate solutions. Proceedings of the National Academy of Sciences USA 114:11645–11650.

Houghton, R. A., and A. A. Nassikas. 2017. Global and regional fluxes of carbon from land use and land cover change 1850-2015. Global Biogeochemical Cycles 31:456–472.

Hudiburg, T., B. Law, D. P. Turner, J. Campbell, D. C. Donato, and M. Duane. 2009. Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. Ecological Applications 19:163–180.

Hudiburg, T. W., B. E. Law, C. Wirth, and S. Luyssaert. 2011. Regional carbon dioxide implications of forest bioenergy production. Nature Climate Change 1:419–423.

Hudiburg, T. W., B. E. Law, and P. E. Thornton. 2013. Evaluation and improvement of the Community Land Model (CLM4) in Oregon forests. Biogeosciences 10:453–470.

Hurrell, J. W., et al. 2013. The Community Earth System Model A Framework for Collaborative Research. Bulletin of the American Meteorological Society 94:1339–1360.

IPCC. 2018. Summary for policymakers. *in* V. Masson-Delmotte, P. Zhai, H.-O. P-rtner, D. Roberts, J. Skea, P. R. Shukla, A. Pirani, W. Moufouma-Okia, C. PÕan, R. Pidcock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield, editors. Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. World Meteorological Organization, Geneva, Switzerland, 32 pp.

Irvine, J., B. E. Law, P. M. Anthoni, and F. C. Meinzer. 2002. Water limitations to carbon exchange in old-growth and young ponderosa pine stands. Tree Physiology 22:189–196.

Jenkins, C. N., K. S. Van Houtan, S. L. Pimm, and J. O. Sexton. 2015. US protected lands mismatch biodiversity priorities. Proceedings of the National Academy of Sciences USA 112:5081–5086.

Keenan, T. F., D. Y. Hollinger, G. Bohrer, D. Dragoni, J. W. Munger, H. P. Schmid, and A. D. Richardson. 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. Nature 499:324.

Keith, H., R. Leuning, K. L. Jacobsen, H. A. Cleugh, E. van Gorsel, R. J. Raison, B. E. Medlyn, A. Winters, and C. Keitel. 2009*a*. Multiple measurements constrain estimates of net carbon exchange by a Eucalyptus forest. Agricultural and Forest Meteorology 149:535–558.

Keith, H., B. G. Mackey, and D. B. Lindenmayer. 2009*b*. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. Proceedings of the National Academy of Sciences USA 106:11635–11640.

Krankina, O. N., D. A. DellaSala, J. Leonard, and M. Yatskov. 2014. High-biomass forests of the Pacific Northwest: who manages them and how much is protected? Environmental Management 54:112–121.

Kremen, C., and A. M. Merenlender. 2018. Landscapes that work for biodiversity and people. Science 362:eaau6020.

Law, B. E., T. W. Hudiburg, L. T. Berner, J. Kent, P. C. Buotte, and M. E. Harmon. 2018. Land use strategies to mitigate climate change in carbon dense temperate forests. Proceedings of the National Academy of Sciences USA 115:3663–3668.

Le Quere, C., et al. 2018. Global carbon budget 2018. Earth System Science Data 10:2141–2194.

Lecina-Diaz, J., A. Alvarez, A. Regos, P. Drapeau, A. Paquette, C. Messier, and J. Retana. 2018. The positive carbon stocks-biodiversity relationship in forests: co-occurrence and drivers across five subclimates. Ecological Applications 28:1481–1493.

Mackey, B., et al. 2015. Policy Options for the World's Primary Forests in Multilateral Environmental Agreements. Conservation Letters 8:139–147.

Maron, M., J. S. Simmonds, and J. E. M. Watson. 2018. Bold nature retention targets are essential for the global environment agenda. Nature Ecology & Evolution 2:1194–1195.

McDowell, N. G., et al. 2016. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. Nature Climate Change 6:295–300.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, D.C., USA.

Meddens, A. J. H., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecological Applications 22:1876–1891.

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science 349:823–826.

Mitchell, T. D., and P. D. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. International Journal of Climatology 25:693–712.

Moomaw, W. R., S. Masino, and E. K. Falson. 2019. Intact forests in the United States: proforestation mitigates climate change and serves the greatest good. Frontiers in Forests and Global Change 2:1–10.

Morin, X., L. Fahse, H. Jactel, M. Scherer-Lorenzen, R. Garcia-Valdes, and H. Bugmann. 2018. Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. Scientific Reports 8: 1–12.

Nolan, C., et al. 2018*a*. Past and future global transformation of terrestrial ecosystems under climate change. Science 361:920–923.

Nolan, R. H., D. M. Drew, A. P. O'Grady, E. A. Pinkard, K. Paul, S. H. Roxburgh, P. J. Mitchell, J. Bruce, M. Battaglia, and D. Ramp. 2018*b*. Safeguarding reforestation efforts against changes in climate and disturbance regimes. Forest Ecology and Management 424:458–467.

Norby, R. J., J. M. Warren, C. M. Iversen, B. E. Medlyn, and R. E. McMurtrie. 2010. CO2 enhancement of forest productivity constrained by limited nitrogen availability. Proceedings of the National Academy of Sciences USA 107:19368–19373.

Oleson, K. W., et al. 2013. Technical description of version 4.5 of the Community Land Model (CLM). National Center for Atmospheric Research, Boulder, Colorado, USA.

Olson, D., D. A. DellaSala, R. F. Noss, J. R. Strittholt, J. Kass, M. E. Koopman, and T. F. Allnutt. 2012. Climate change refugia for biodiversity in the Klamath-Siskiyou Ecoregion. Natural Areas Journal 32:65–74.

Oren, R., et al. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO2-enriched atmosphere. Nature 411:469–472.

Pan, Y., J. M. Chen, R. Birdsey, K. McCullough, L. He, and F. Deng. 2011. Age structure and disturbance legacy of North American forests. Biogeosciences 8:715–732.

Pearson, R. G., S. J. Phillips, M. M. Loranty, P. S. A. Beck, T. Damoulas, S. J. Knight, and S. J. Goetz. 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. Nature Climate Change 3:673–677.

Pechony, O., and D. T. Shindell. 2010. Driving forces of global wildfires over the past millennium and the forthcoming century. Proceedings of the National Academy of Sciences USA 107:19167–19170.

Perry, T. D., and J. A. Jones. 2017. Summer streamflow deficits from regenerating Douglas-fir forest in the Pacific Northwest, USA. Ecohydrology 10:e1790.

Peters, G. P., R. M. Andrew, T. Boden, J. G. Canadell, P. Ciais, C. Le Quere, G. Marland, M. R. Raupach, and C. Wilson. 2013. COMMENTARY: the challenge to keep global warming below 2 degrees C. Nature Climate Change 3:4–6.

Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Sciences 167:1123–1150.

Resplandy, L., R. F. Keeling, Y. Eddebbar, M. K. Brooks, R. Wang, L. Bopp, M. C. Long, J. P. Dunne, W. Koeve, and A. Oschlies. 2018. Quantification of ocean heat uptake from changes in atmospheric O2 and CO2 composition. Nature 563:105–108.

Riitters, K. H., and J. D. Wickham. 2012. Decline of forest interior conditions in the conterminous United States. Scientific Reports 2:1–4.

Rogelj, J., M. den Elzen, N. Hohne, T. Fransen, H. Fekete, H. Winkler, R. S. Chaeffer, F. Ha, K. Riahi, and M. Meinshausen. 2016. Paris Agreement climate proposals need a boost to keep warming well below 2 degrees C. Nature 534:631–639.

Sabatini, F. M., et al. 2019. Trade-offs between carbon stocks and biodiversity in European temperate forests. Global Change Biology 25:536–548.

Schimel, D., B. B. Stephens, and J. B. Fisher. 2015. Effect of increasing CO2 on the terrestrial carbon cycle. Proceedings of the National Academy of Sciences USA 112:436–441.

Schuur, E. A. G., et al. 2015. Climate change and the permafrost carbon feedback. Nature 520:171–179.

Segan, D. B., K. A. Murray, and J. E. M. Watson. 2016. A global assessment of current and future biodiversity vulnerability to habitat loss-climate change interactions. Global Ecology and Conservation 5:12–21.

Settele, J., R. Scholes, R. Betts, S. E. Bunn, P. Leadley, D. Nepstad, J. T. Overpeck, and M. A. Taboada. 2014. Terrestrial and inland water systems. Pages 271–359 *in* C. B. Field, et al., editors. Climate change 2014: impacts, adaptation, and vulnerability. Part a: global and sectoral aspects. Contribution of working group ii to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK.

Smith, W. K., S. C. Reed, C. C. Cleveland, A. P. Ballantyne, W. R. L. Anderegg, W. R. Wieder, Y. Y. Liu, and S. W. Running. 2016. Large divergence of satellite and Earth system model estimates of global terrestrial CO2 fertilization. Nature Climate Change 6:306–310.

Smith, P., J. Price, A. Molotoks, R. Warren, and Y. Malhi. 2018. Impacts on terrestrial biodiversity of moving from a 2 degrees C to a 1.5 degrees C target. Philosophical Transactions of the Royal Society a-Mathematical Physical and Engineering Sciences 376.

Solomon, S., G. K. Plattner, R. Knutti, and P. Friedlingstein. 2009. Irreversible climate change due to carbon dioxide emissions. Proceedings of the National Academy of Sciences USA 106:1704–1709.

Spracklen, D. V., L. J. Mickley, J. A. Logan, R. C. Hudman, R. Yevich, M. D. Flannigan, and A. L. Westerling. 2009. Impacts of climate change from 2000 to 2050 on wildfire activity and carbonaceous aerosol concentrations in the western United States. Journal of Geophysical Research: Atmospheres 114:1–17.

Steffen, W., et al. 2018. Trajectories of the Earth System in the Anthropocene. Proceedings of the National Academy of Sciences USA 115:8252–8259.

United Nations Framework Convention on Climate Change (UNFCC). 2015. The Paris Agreement. UNFCC, Paris, France.

United Nations General Assembly. 2015. Transforming our world: the 2030 agenda for sustainable development. United Nations General Assembly, New York, New York, USA.

U.S. Energy Information Administration. 2015. Energy-related carbon dioxide emissions at the state level, 2000–2013. U.S. Department of Energy, Washington, D.C., USA.

U.S. Fish and Wildlife Service. 2018. U.S. FWS threatened & endangered species active critical habitat report. U.S. Fish and Wildlife Service, Washington, D.C., USA.

USGS National Gap Analysis Program. 2018. Gap analysis project species habitat maps CONUS. U.S. Geological Survey, Reston, Virginia, USA.

Watson, J. E. M., et al. 2018. The exceptional value of intact forest ecosystems. Nature Ecology & Evolution 2:599–610.

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Weider, W. R., J. Boehnert, G. B. Bonan, and M. Langseth. 2014. Regridded harmonized world soil database. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.

White, M. A., P. E. Thornton, S. W. Running, and R. R. Nemani. 2000. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. Earth Interactions 4:1–85.

Whittier, T. R., and A. N. Gray. 2016. Tree mortality based fire severity classification for forest inventories: a Pacific Northwest national forests example. Forest Ecology and Management 359:199–209.

Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences USA 104:5738–5742.

Wilson, B. T., C. W. Woodall, and D. M. Griffith. 2013. Imputing forest carbon stock estimates from inventory plots to a nationally continuous coverage. Carbon Balance and Management 8:15.

Supporting Information

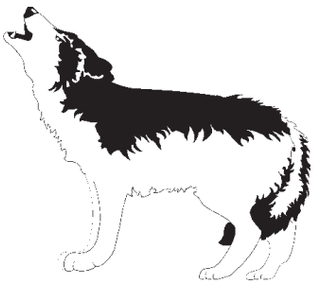
Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2039/full

Data Availability

Simulated carbon fluxes are available from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) at: https://doi.org/10.3334/ornldaac/1662

19395582, 2020, 2, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2039, Wiley Online Library on [01/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

In My Opinion: Managing habitat for dispersing northern spotted owls—are the current management strategies adequate?



Joseph B. Buchanan

When the northern spotted owl (*Strix occidentalis caurina*) was listed under the Endangered Species Act (ESA) as threatened in 1990, a number of challenges immediately became apparent. One of the first to surface was the need to develop definitions of suitable habitat that could be used in the regulatory environment. Consequently, in the early years following ESA listing, much attention was directed at defining habitats that spotted owls used for nesting, roosting, or foraging. The emphasis of research on various aspects of the structure, quality, quantity, or landscape configuration of nesting habitats throughout the owl's distribution was considerable (e.g., Carey et al. 1990, Lehmkuhl and Raphael 1993, Buchanan et al. 1995, Meyer et al. 1998, LaHaye and Gutiérrez 1999) and overshadowed efforts to investigate the habitat conditions used by owls during dispersal (Miller et al. 1997).

After the Northwest Forest Plan was adopted to manage spotted owl populations on federal lands (Forest Ecosystem Management Assessment Team [FEMAT] 1993), regulations were implemented for the management of nonfederal lands in the region. In Washington, for example, the Northwest Forest Plan and state forest practices rules (in 1996) identified key landscape areas where the emphasis of spotted owl conservation would be the management of nesting, roosting, foraging, and dispersal habitats. On federal lands, spotted owl nesting habitat would be managed in late-successional reserves (LSRs). Federal lands between the LSRs would be managed largely for timber production (within the "matrix") or a combination of wildlife and human needs in "adaptive management areas" (FEMAT 1993). Areas between the LSRs would need to facilitate movement by juvenile and adult spotted owls among the LSRs. Nonfederal landscapes designated as Spotted Owl Special Emphasis Areas (SOSEAs) would provide demographic support, dispersal support, or a combination of these 2 functions under the state's forest practices rules (Washington Administrative Code 222-16-086). The SOSEAs are all adjacent to federal lands, and several are expressly designated as, or contain sub-units designated as, landscapes where spotted owl dispersal is of primary management importance.

In 1992 the United States Fish and Wildlife Service (USFWS) approved the first Habitat Conservation Plan (HCP) for spotted owls in the region (Simpson Timber Company 1992). This was followed by implementation of additional HCPs, many of which provided dispersal habitat as mitigation for incidental take permits that allowed harvest of forest used by territorial spotted owls for nesting, roosting, or foraging. These dispersal-based plans have been implemented on hundreds of thousands of hectares in the Pacific Northwest.

Despite this shift from retention of mature and older forests to management of younger forests as dispersal habitat, an interest in investigating the effectiveness of dispersal management plans has not emerged. This is surprising because dispersal long has been recognized as an essential component of spotted owl management (e.g., see Appendix P in Thomas et al. 1990). Moreover, dispersal has been an important ecological and management consideration for other listed species. Researchers and managers in the southeastern United States learned, for example, that poor landscape connectivity required the translocation of red-cockaded woodpeckers (*Picoides borealis*) to establish or maintain population clusters (DeFazio

et al. 1987). Consequently, the importance of developing credible landscape-level dispersal management plans is not a trivial concern. For this reason, I reviewed the available proposed and implemented dispersal management plans for northern spotted owls. The objectives of this paper are to 1) describe and explain the origins of the various definitions of dispersal habitat used in management, and 2) provide a preliminary evaluation of the suite of dispersal management strategies developed for spotted owls in the Pacific Northwest.

Dispersal and dispersal habitat

Dispersal is an important life-history stage for all wildlife species. It is a primary mechanism of gene flow among populations and by which individuals search out and acquire mates and colonize new territories. For this reason a considerable amount of effort has gone into studies of spotted owl dispersal behavior (Forsman et al. 1984, Miller et al. 1997, Ganey et al. 1998, LaHaye et al. 2001, Forsman et al. 2002). Much of this research has been used in ongoing spotted owl conservation efforts. Estimates of λ (lambda; the rate of population growth or decline), an analytical tool used to evaluate population performance, are sensitive to rates of emigration by juveniles (Forsman et al. 1996, Raphael et al. 1996). Dispersal was a key consideration in conservation strategies developed by the Interagency Spotted Owl Scientific Committee (Thomas et al. 1990; see Murphy and Noon 1992), the Spotted Owl Recovery Team (United States Department of the Interior [USDI] 1992), and for implementation of the Northwest Forest Plan (FEMAT 1993). The recovery strategy involved establishing a network of reserves across the landscape that would each support a cluster of breeding pairs. The amount of suitable habitat, size and spacing of reserves, and likelihood of successful dispersal were all important considerations in this reserve network design (Lamberson et al. 1992, 1994).

Dispersal can be defined in several ways. A variety of movements, such as might occur following a failed breeding attempt or efforts to prospect for new mates or territories, might be described as dispersal behavior because they involve an animal moving across a landscape, perhaps in unfamiliar terrain, searching for prey, habitat, or a mate (e.g., this would include "breeding dispersal" by spotted owls; see Forsman et al. 2002). For the purposes of this discussion, however, dispersal is defined as the collective movements of a juvenile during the period starting at departure from the natal area and ending at territory acquisition (Greenwood 1980, Miller et al. 1997). Miller et al. (1997) considered the dispersal process to consist of 2 distinct phases that they referred to as transience and colonization. The transient phase of dispersal included extensive or rapid movement through an area, whereas colonization indicated nonterritorial, short-term residence in an area. Juvenile spotted owls in the Pacific Northwest annually begin dispersing in September and October (Forsman et al. 1984, 2002) and typically move rapidly away from the natal area (transience), followed by varying periods of colonization and transience (Forsman et al. 2002).

Only one study has been conducted to examine the relationship between dispersing spotted owls and forest conditions across a landscape. This study, conducted in western Oregon, found a strong association between locations of dispersing spotted owls and old-growth forests (Miller et al. 1997). During the transience phase of dispersal, old-growth forest was used in proportion to its availability in the landscape (mean use = 35%; mean availability = 31%), whereas during colonization old-growth forest was used more than expected (mean use = 61%, mean availability = 33%; Miller et al. 1997). Closed sapling-pole-sawtimber stands (CSPS; stands of 2.5–53.3 cm dbh [diameter at breast height] trees with canopy closure of >60%) and "other" (reservoirs, rock outcrops, pastures, towns) landscape attributes were used in proportion to their availability during transience. Open sapling-pole stands (OSP; stands of 2.5–22.9 cm dbh trees and <60% canopy closure) and clearcuts (stands of <2.5 cm dbh trees and <40% canopy closure) were used proportionally less than would be expected based on availability during transience. During the colonization phase, the CSPS cover type was used slightly more than expected, and the OSP and "other" cover types were used proportionally less than expected (Miller et al. 1997).

The mortality rate of dispersing owls in western Oregon was associated with differing use of forest cover types (Miller et al. 1997). The mean mortality rate was lower for owls that used more OSP stands, compared to owls that did not use this cover type, and this may have been due to an abundance of an important food source, the dusky-footed woodrat (*Neotoma fuscipes*), in those stands (Miller et al. 1997). The primary sources of mortality among dis-

persing spotted owls were predation (68%) and starvation (26%) (Forsman et al. 2002). The degree to which starvation predisposed dispersing spotted owls to predation was unknown (Forsman et al. 2002). The study by Miller et al. (1997) did not evaluate the influences of landscape composition, in terms of stand age or successional stage, on mortality or the dispersal behavior of spotted owls. Their study landscapes contained stands of older forest and therefore likely differed from most of the landscapes where dispersal plans have been developed on nonfederal lands.

Management strategies for dispersal habitat

A number of different strategies have been developed for spotted owl dispersal management since 1990. These strategies included definitions of stand and landscape level features, some of which have become key elements of ongoing management efforts on federal and nonfederal lands. Many of the 18 proposed or implemented definitions (Table 1) were derived from a definition negotiated for the Murray Pacific Habitat Conservation Plan (Beak Consultants 1993). Some definitions were similar to or adopted the definition proposed by the Interagency Spotted Owl Scientific Committee (the "50-11-40" rule;Thomas et al. 1990).

Although the definitions differed in a number of ways, there were substantial similarities (Table 1). All of the definitions had a component for tree abundance, basal area, or canopy closure. Most definitions (72%) stated a proportion of the landscape that would be managed to a specific stand-level value. Two definitions included a description of the maximum allowable distance between patches of suitable dispersal habitat, and 4 definitions defined minimum patch size. Although several definitions called for snag retention, none of them *required* retention and many allowed snags to be removed and accounted for by "green recruitment trees." In most cases these trees could be small (e.g. 25–30 cm dbh). Nearly all stand-level definitions characterized dispersal habitat as very young forest lacking elements of structural diversity. Several elements of the Beak Consultants (1993) definition were based solely on aspects of forest growth patterns (Table 2). Most importantly, none of the definitions was explicitly linked to empirical data on spotted owls needed to support either the stand- or landscape-level components.

Are the management strategies adequate?

To date, there has been no attempt to empirically evaluate the adequacy of the proposed or implemented strategies for management of spotted owl dispersal habitat. Because of the lack of research to investigate or evaluate the dispersal strategies, a full evaluation of the strategies must await research on the topic. A preliminary evaluation, however, can be based in part on the hypotheses posited to explain the spotted owls' general preference for structurally complex older forests (Carey 1985). An evaluation of the factors identified by the original hypotheses may be useful in that the degree of consistency between the factors and the dispersal management strategies might provide an indication of the appropriateness of the strategies. The hypotheses summarized by Carey (1985) addressed habitat use relating to: nesting requirements, amelioration of heat stress, prey abundance, prey availability, predation risk, and ecological adaptation. The first hypothesis, that structurally complex forest is required for nesting, will not be discussed because nesting opportunities are not required by spotted owls during the dispersal phase. It is noteworthy, however, that successfully dispersing California spotted owls (*S. o. occidentalis*) often settled in previously used territories (LaHaye et al. 2001), indicating that juvenile spotted owls were able to use cues that revealed information about aspects of habitat quality when selecting an area in which to settle.

Amelioration of heat stress

Spotted owls are believed to have little tolerance of high temperatures (Weathers et al. 2001). Forests with multiple canopy layers generally provide greater thermoregulation opportunities for owls compared to conditions found in younger forest stands with simple canopy structure (Forsman 1976, Barrows and Barrows 1978, Barrows 1981, Forsman et al. 1984). Juvenile spotted owls in the Pacific Northwest begin dispersal in September and October (Forsman et al. 2002). Temperatures in the autumn are usually rather moderate compared to the summer months, so heat stress may not be an important factor at the beginning of the natal dispersal period. Conversely, because most first- and second-year owls do not breed, and may not hold territories, they, or other nonterritorial owls (i.e., those engaged in breeding dispersal), may disperse

Table 1. Elements of the 18 strategies developed (or proposed) to provide spotted owl dispersal habitat in Washington or Oregon between 1990 and 1999. The strategies are listed in approximately the sequence of their development; strategies described in Washington Forest Practices Board (2002) were developed in 1996.

Definition	Application area	Stand-level attributes	Landscape-level attributes
Interagency Spotted Owl Scientific Committee "50-11-40 rule" (Thomas et al. 1990)	Federal land in Washington, Oregon and California	Mean tree size of ≥28 cm dbh (diameter at breast height); canopy closure ≥40%.	At least 50% of the landscape outside Habitat Conservation Area (HCA) boundaries would meet stand-level conditions. Also, would have retained patches of ≥32 ha of suitable owl habitat at or near former spotted owl site centers, at an average of seven per township, in areas between HCAs.
Beak Consultants (1993)	Murray Pacific HCP; Western Cascade Mountains, Washington	Conifer forest with ≥70% canopy closure; ≥130 and ≤ 300 trees/0.4 ha that were ≥25 cm dbh (or larger trees of an equivalent basal area); where possible, retained ≥2 dominant or co-dominant trees and 3 snags ≥46 cm dbh per 0.4 ha of harvest; retained ≥2 30-cm diameter, 6.1 m logs per 0.4 ha at harvest.	Arranged forest patches such that stands of dispersal habitat were spaced no more than 0.4 km apart. About 43% of the ownership would meet the defined conditions by year 50, and would remain at this approximate amount between years 50 and 100.
Spotted Owl Science Advisory Group (Buchanan et al. 1994)	Unspecified nonfederal lands; Eastern Cascade Mountains, Washington	Supported "50-11-40" rule of the ISC (see above; Thomas et al. 1990) on an interim basis.	Supported "50-11-40" rule of the ISC (see above; Thomas et al. 1990) on an interim basis.
Spotted Owl Science Advisory Group (Buchanan et al. 1994)	Unspecified nonfederal lands; Western Washington	Supported Beak Consultants (1993) definition (see above) on an interim basis.	Supported Beak Consultants (1993) definition (see above) on an interim basis.
Northwest Forest Plan (USDA and USDI 1994)	Federal lands in Washington, Oregon and California	Not addressed.	In matrix areas (landscapes, between reserved areas, where timber harvest was emphasized) retained a) ≥15% of the green trees on each harvest unit, b) 40 ha of habitat around former owl site centers, and c) forest buffers along streams, ponds and wetlands. The remainder of the forest in matrix areas would be managed on a rotation age of ≥100 years.
Washington Forest Practices Rules (Washington Forest Practices Board 2002)	Nonfederal lands; Western Washington	Forest stands with ≥70% canopy closure; At least 70% composition of conifer trees ≥15 cm dbh; ≥130 and ≤300 trees/0.40 ha with a dbh of ≥25 cm or a basal area of 30 m of 25 cm or larger trees; ≥6.1 m of open space (relatively free of dead limbs) between the top of the understory vegetation and the bottom of the live canopy.	Forest stands ≥2 ha in size.
Washington Forest Practices Rules (Washington Forest Practices Board 2002)	Nonfederal lands; Eastern Cascade Mountains, Washington	Forest stands with ≥50% canopy closure; ≥50 and ≤200 conifer trees/0.4 ha with a dbh of ≥15 cm in even-aged stands, or ≥10 cm in uneven-aged stands (or a quadratic mean diameter of ≥23 cm and a relative density of ≥33); an average tree height of ≥20 m; ≥6.1 m of open space (relatively free of dead limbs) between the top of the understory vegetation and the bottom of the live canopy.	Forest stands ≥2 ha in size.

(*Continued*)

[a] HCP not implemented.

[b] Relative density is the basal area divided by $QMD^{0.5}$ (Curtis 1982).

[c] The quadratic mean is the square root of the arithmetic mean of squared values (Curtis and Marshall 2000).

Table 1 (*continued*). Elements of the 18 strategies developed (or proposed) to provide spotted owl dispersal habitat in Washington or Oregon between 1990 and 1999. The strategies are listed in approximately the sequence of their development; strategies described in Washington Forest Practices Board (2002) were developed in 1996.

Definition	Application area	Stand-level attributes	Landscape-level attributes
Longview Fibre Company (1995)[a]	Columbia Gorge, Washington	Conifer-dominated stands of an average height of ≥15 m with 321 – 741 trees/ha of >10 cm dbh.	Not addressed.
Rayonier Wildlife Plan (WFPB 1996)	Rayonier Wildlife Plan Area; Western Olympic Peninsula, Washington	Forest stands ≥30 years old; ≥70% conifer, <400 trees/0.4 ha, a quadratic mean diameter of 23 cm, and a basal area of 28 m^2/0.4 ha.	An estimated 40% of the plan area would meet or exceed the definition of dispersal habitat by 2020; the average amount of dispersal habitat at 5-year increments between 2025 and 2045 was predicted to be 43.8%. Also, a limit on clearcut size of 49 ha, a commitment that no less than 30% of the plan area would be commercially thinned during a rotation, that 3% of the area would remain in fixed reserves and 5% in floating reserves, and that 5% of the stands would be pruned during a rotation.
Weyerhaeuser Company (1995)	Millicoma Tree Farm; Western Oregon	Forest stands with ≥70% dominant or co-dominant conifers; ≥120 and ≤300 trees/0.4 ha with ≥25 cm dbh (or equivalent basal area constituted by fewer but larger trees); co-dominant tree height of ≥21 m; ≥6 m of clear sub-canopy space; ≥2 live trees or snags/0.4 ha, on average, of ≥9 m height and 28 cm dbh; ≥2 hard logs/0.4 ha ≥5 m long and ≥30 cm) in diameter. Possible future modification up to 400 trees/0.4 ha.	Forest stands ≥2 ha in size.
Plum Creek HCP (Hicks and Stabins 1995, Plum Creek Timber Company, Inc. 2000)	"I-90 Corridor", Western Cascade Mountains, Washington	Foraging and dispersal habitat based on Beak Consultants (1993), but including relative density[b] of 30–48 (equivalent to 175–280 trees/0.4 ha) in uplands,relative density of 48 in riparian areas; quadratic mean diameter (QMD)[c] of 25 cm in stands dominated by conifers.	Between 2006 and 2045, 6–10% of the plan area would meet definition of nesting roosting and foraging habitat; 7–34% would meet definition of foraging and dispersal habitat (combined totals would range between 17 and 42%). These goals will have been considered met if actual values are within 10–20% of the incremental or final targets.
Plum Creek HCP (Hicks and Stabins 1995, Plum Creek Timber Company, Inc. 2000)	"I-90 Corridor", Eastern Cascade Mountains, Washington	Foraging and dispersal habitat based on Beak Consultants (1993), but including forest stands dominated by Douglas-fir, ponderosa pine, and true fir, with a relative density of 33 and a QMD of 23 cm.	See above.
Weyerhaeuser Willamette (Weyerhaeuser Company 1996)[a]	Willamette Tree Farm; Central-western Oregon	At least 4 snags or green trees/0.4 ha of ≥30 cm dbh and ≥9 m height (snags and leave trees could be retained within riparian areas); would retain one live conifer ≥81 cm dbh (9 m tall), if possible, per 8 ha of harvested timber. Foraging habitat (used in landscape definition) defined as stands with ≥30% conifers, ≥70% canopy cover, 115 – 280 stems ≥10 cm dbh/0.4 ha, and dominant and co-dominant trees of ≥26 m (except in thinned stands, where trees could be shorter).	Would maintain ≥40% of the landscape, beyond 2025, in stands of ≥pole timber, including ≥20% foraging habitat (see stand-level attributes) in "zone 1" and ≥10% foraging habitat in "zone 2"; ≤20% of the landscape would be > 0.4 km from reserved areas or stands of ≥pole timber; would maintain approximately 243 ha of suitable habitat in connectivity patches, and temporarily maintain about 486 ha of habitat until equivalent new habitats developed on adjacent federal lands. A 28-ha core around known spotted owl site centers would be protected until the site became inactive, at which point the core could be harvested.

(*Continued*)

[a] HCP not implemented.

[b] Relative density is the basal area divided by $QMD^{0.5}$ (Curtis 1982).

[c] The quadratic mean is the square root of the arithmetic mean of squared values (Curtis and Marshall 2000).

Table 1 (*continued*). Elements of the 18 strategies developed (or proposed) to provide spotted owl dispersal habitat in Washington or Oregon between 1990 and 1999. The strategies are listed in approximately the sequence of their development; strategies described in Washington Forest Practices Board (2002) were developed in 1996.

Definition	Application area	Stand-level attributes	Landscape-level attributes
Crown Pacific (Biota Pacific Environmental Services 1999) [a]	Crown Pacific lands; Northwestern Cascade Mountains, Washington	Basic definition from Beak Consultants (1993) was adopted. In addition, ≥30% coniferous species, codominant trees ≥26 m tall, minimum tree diameter (counting trees ≥10 cm dbh) of 25 cm, tree density (of trees ≥10 cm dbh) of 115–280/0.4 ha, and ≥70 canopy closure. Would retain all safe snags >38 cm dbh along with ≥6 retention trees/0.4 ha (≥25 cm dbh and of which 3 are ≥38 cm dbh) of the harvest area.	Basic definition from Beak Consultants (1993) was adopted. In addition, stand-level definitions would apply to 50% of dispersal habitat on Class I-IV lands; minimum stand size of ≥8 ha and minimum stand width of ≥61 m. All snags or retention trees could be situated in riparian management zones and unstable slope areas.
Oregon Department of Forestry (1995)	Elliot State Forest; Oregon Coast Range	Essentially adopted the "50-11-40 rule" at the scale of quarter-township management areas. For other state lands defined dispersal habitat as forests with a QDBH of 28 to 45 cm.	Essentially adopted the "50-11-40 rule" at the scale of quarter-township management areas. For the North Coast Region, retained 70% of the landscape as dispersal habitat in areas outside breeding clusters; these landscapes would also contain 70% forests older than 50 years (including ≥10% with older forest structure) by year 50 of the plan.
Washington Department of Natural Resources (WDNR 1997)	DNR lands; Western Cascade Mountains, Washington	Forest stands with ≥70% canopy cover; ≥28 cm QDBH for the largest 100 trees/0.4 ha; the 40 tallest trees/0.4 ha ≥26 m tall; retention of ≥4 trees of the largest diameter class at harvest.	Dispersal landscapes would be managed such that 50% of the stands met the stand-level criteria.
Washington Department of Natural Resources (WDNR 1997)	DNR lands; Eastern Cascade Mountains, Washington	Forest stands with ≥50% canopy closure; ≥40 overstory trees/0.4 ha of ≥28 cm dbh; tree height of ≥18 m; retention of ≥4 trees of the largest diameter class at harvest.	Dispersal landscapes would be managed such that 50% of the stands met the stand-level criteria.
Weyerhaeuser-U.S. Forest Service land trade (Foster Wheeler Environmental Corporation 1996, U.S. Fish and Wildlife Service 1997)	Weyerhaeuser lands; Western central Cascade Mountains, Washington	From Washington Forest Practices Rules (Washington Forest Practices Board 2002). Foraging habitat defined as stands with ≥30% conifer stems, ≥70% canopy closure, 115 – 280 stems/0.4 ha of ≥10 cm dbh, and dominant/codominant trees of ≥26 m height, except for commercially-thinned stands where minimum tree height was 21 m. Snags would be retained where feasible and safe.	At least 40% of the plan area would meet the definition of dispersal habitat used in the land trade agreement. At least 37.5% of the dispersal habitat would be foraging habitat. Also, ≤20% of the area (roughly 5,261 ha) would be more than 0.4 km from patches ≥2 ha of dispersal habitat, with wildlife reserve trees (≥3/0.4 ha), if available, that were ≥3 m tall and ≥30 cm dbh, and green retention trees (2/0.4 ha; ≥25 cm dbh, ≥9 m tall, and at least 1/3 of height in live crown) would be retained in harvest units. The reserve and recruitment trees could be clumped in riparian or wetland management zones or across the landscape. In each 0.4 ha of forest harvested 2 downed logs (30 cm dia. at small end and ≥ 6.1 m in length, or an equivalent volume of larger logs) would be retained. A 28-ha core centered on any current spotted owl site center would be retained until site abandonment, at which time the core could be harvested.

[a] HCP not implemented.

[b] Relative density is the basal area divided by $QMD^{0.5}$ (Curtis 1982).

[c] The quadratic mean is the square root of the arithmetic mean of squared values (Curtis and Marshall 2000).

Table 2. Rationale for inclusion of specific required elements in the definition of spotted owl dispersal habitat developed for the Murray Pacific Habitat Conservation Plan (from Beak Consultants 1993). This plan, the first HCP in the Pacific Northwest, was developed for a 21,000+ ha tree farm in the western Cascade Mountains foothills in Washington. The rationale for snags and leave-trees was not provided because snags were not a required element of the plan. See Table 1 for the specific values of the elements included in the definition.

Element	Rationale
Tree species composition	Coniferous forests provide thermal cover and protection from precipitation, particularly during autumn and winter periods.
Tree size and density	25-cm trees provide perch opportunities in and below the canopy because such trees have branches of suitable size (3.8 cm at the base) for an owl to use. Stands grown at a density of ≥130 trees/0.4 ha would self-prune and provide open space for spotted owls flying through the understory. An upper limit of 300 trees/0.4 ha was identified as a compromise density at which tree mortality occurs due to competition.
Canopy "lift"	Spotted owls must be able to fly in the forest understory. An open area of 6.1 m between the ground and the canopy would occur on the plan area when trees were about 25 cm dbh and were able to self-prune if grown at a density of more than 130 trees/0.4 ha.
Canopy closure	This amount of canopy closure would occur at a density of 130 trees/0.4 ha.
Downed wood	The level of retention at harvest reflected current Forest Practices Rules.
Size of and spacing between patches	On average, a stand of 16 ha had an edge-to-interior ratio of 1:1; therefore, the average harvest size in the HCP would be 16 ha, and ranged from 2–49 ha. No rationale was given for using a 0.4-km spacing between patches, but it was inferred to reduce the number of crossings an owl would make over openings or areas of unsuitable habitat.
Percentage of landscape	It was inferred that a landscape with a high proportion of dispersal habitat would reduce the likelihood of predation by creating more cover and reducing the number of times owls would cross open areas where predation risk would be higher.

during subsequent summers (in either transience or colonization mode). These owls would benefit by the presence of structurally complex forest during those periods.

Prey abundance

The spotted owl's primary prey in much of the Pacific Northwest is the northern flying squirrel (*Glaucomys sabrinus*) (e.g., Forsman et al. 1984, 2001). Carey et al. (1999) found that capture rates of squirrels were higher in "niche diversification" (4.0±0.3 /100 trap nights) and old-growth (3.2± 0.1) stands compared to forests in the younger, competitive-exclusion phase of development (2.6± 0.2). They also found that capture rates of squirrels were positively associated with the amount of coarse woody debris in the stand. In fact, presence and amount of coarse woody debris explained 40% of variance in the carrying capacity of flying squirrels. Feen (1997) found that squirrel winter den sites were in areas with a greater basal area of dead conifer trees as compared to random sites. Carey et al. (1997) reported a strong positive association between abundance of large snags and population size of flying squirrels throughout the Pacific Northwest. Among the likely reasons for this relationship were 1) flying squirrels tended to den communally and therefore required larger-diameter snags (Carey et al. 1999), and 2) flying squirrels change dens often and therefore require a good number of snags or cavity trees within the home range (Carey et al. 1997). Also, Amaranthus et al. (1994) found that the abundance of truffles, an important food source for flying squirrels, was 20–30 times higher in 180-year-old forest than in 4–27-year-old forests with 11–14% cover of downed wood. It is unknown at what stage of forest development the abundance of truffles begins to approach levels noted in older forests.

Spotted owls also prey on a wide range of other small-mammal species (Forsman et al. 2001), and the collective abundance of these species may vary as a function of forest structure. Research conducted in the southern Cascade Mountains of Washington found that the combined total number of captures (per 100 trap-nights) of all small mammals was higher in old-growth stands than in fire-regenerated younger stands in both years of study. Capture rates (per 100 trap nights) in young stands were 5.07 and 5.88 in 1984 and 1985, respectively (West 1991). In contrast, capture rates of all small mammals in an intensively managed younger forest in southwestern Washington averaged 2.08/100 trap-nights (Stinson et al. 1997). Similarly, the total abundance of small

mammals was nearly 1.7 times higher in old growth than in managed second-growth forest on the Olympic Peninsula, Washington (Carey and Johnson 1995). In that study the variance in abundance of numerous small-mammal species in managed stands was positively related to the amount of coarse wood debris on the forest floor (Carey and Johnson 1995).

The relationship between prey availability in and owl use of particular cover types is obviously important. Owls that fail to consume an adequate amount of prey will starve to death (Miller et al. 1997), and those that struggle to secure adequate prey will experience nutritional stress, may become more susceptible to predation (Hirons et al. 1979), and may have lowered reproductive success (Newton 1779). The relationship between prey abundance and complex forest structure was consistent with the spotted owl's use of old-growth forest during transience and colonization phases of dispersal (Miller et al. 1997).

Prey availability

The spotted owl is a sit-and-wait predator, in that it scans its surroundings from a perch before locating and attacking prey. The relevance of this predatory behavior to the prey-availability hypothesis involves the availability of hunting perches (Forsman 1976, Forsman et al. 1984) and the susceptibility of prey present in the forest. Forests with complex structure provide perch locations at various locations in the canopy and subcanopy that likely provide more opportunities for owls to locate prey, and this likely equates to a greater availability of prey. In addition, the varied structure in the canopy, subcanopy, and forest floor in these forests likely provides a more diverse array of niches that serve as prey refugia interspersed with areas where the prey are vulnerable to predators (Carey 1985). Second-growth forests are in comparatively early stages of successional development and typically have less complex structure and provide less of this dispersion of within-stand patches, and fewer perch sites low in the sub-canopy (Oliver 1981). The ecological significance of these supposed differences in forest structure relative to prey availability to the spotted owl has not been evaluated, but the apparent relationship between structural complexity and a greater availability of prey is consistent with the preference for old-growth forests during dispersal (Miller et al. 1997).

Predation risk

The chief predators of the spotted owl are the northern goshawk (*Accipiter gentilis*), red-tailed hawk (*Buteo jamaicensis*), and great horned owl (*Bubo virginianus*) (Forsman et al. 1984, Miller and Meslow 1985, Carey et al. 1990). Northern goshawks are rather uncommon in substantial parts of the northern spotted owl's range (Watson et al. 1999), and appear to be rare in some designated spotted owl dispersal areas, probably due to the lack of suitable habitat in managed-forest landscapes (DeStephano and McCloskey 1997). In other areas they are more common, nest in the same cover types used by spotted owls, and build nests that may eventually be used by spotted owls (Forsman et al. 1984, Buchanan et al. 1993). Red-tailed hawks nest in forest and forage in clear-cuts and other open cover types. Anecdotal information suggests that goshawks and red-tailed hawks occasionally kill spotted owls, but their significance as predators of the owl is unknown (Gutiérrez et al. 1995, Forsman et al. 2002).

The great horned owl is a common and widespread species of forested landscapes within the range of the northern spotted owl (e.g., Irwin et al. 1991). In some areas, such as southwestern Washington and the Oregon Coast Range, it is much more numerous than the spotted owl (USDI 1992), and in some areas it may be the primary predator of spotted owls (Forsman et al. 1984, 2002; Gutiérrez et al. 1995). In the central Cascade Mountains in Oregon, 500-ha areas around great horned owl locations contained forests with a greater edge-to-old-forest area ratio, greater areas of shrub and forb vegetation, and lesser amounts of old and interior forest, compared to comparable areas around spotted owl locations (Johnson 1993). Compared to spotted owls, great horned owls were more often detected in landscape areas with only 10–20% old forest and were less commonly detected than spotted owls as the amount of old forest in the landscape increased beyond about 60% (Johnson 1993). Consequently, landscapes with high amounts of old forest will support fewer great horned owls, and landscapes with little old forest will support high densities of great horned owls. The landscapes being maintained or created for spotted owl dispersal were characterized by conditions that will support comparatively high densities of great horned owls (see Table 1), and this could result in higher mortality rates than in landscapes with fewer great horned owls.

Ecological adaptation

Prior to European settlement, the coniferous

forests of the Pacific Northwest were dominated by older forests and fire-regenerated younger-aged stands (Wimberly et al. 2000). At any given time, perhaps 30–45 percent of landscapes in western Washington and Oregon were generally unsuitable for spotted owls because of an incompatible vegetation association or the presence of forests lacking complex structure due to regeneration following wildfires (Eby and Snyder 1990, Wimberly et al. 2000). The remaining 55–70 percent of the region consisted of fire-regenerated young-, mature-, and old-forest cover types that would have been suitable for spotted owls. The owls likely dispersed through these forests and through a mosaic of remnant patches of old forest scattered throughout landscapes otherwise converted to the stand-regeneration phase (Oliver 1981) by stand-replacing fires. A preference for old-forest cover types (Gutiérrez et al. 1995) suggests that spotted owls adapted to disperse through landscapes dominated by structurally complex forest, although it is unclear whether juveniles seek old-forest cover types innately or as a learned response, perhaps to conditions at the natal site or foraging areas that support an abundance of prey (Carey 1985, E. Forsman personal communication). Given the reduction in both amount of old forest and abundance of snags on the landscape over the past century (e.g., Spies and Cline 1988, Thomas et al. 1990), the condition of forest landscapes currently available for spotted owls certainly is unprecedented.

Overview of the dispersal management strategies

Examination of the hypotheses associating spotted owls with various forest attributes and ecological conditions indicate inconsistencies between the function of forest attributes associated with dispersal management plans and the habitat attributes identified as important to spotted owls. Given the lack of understanding about dispersal habitat needs at the landscape level, this should be cause for concern. The greatest potential shortcoming in management strategies for dispersal habitat is the general lack of structurally complex forest conditions. For example, definitions of dispersal habitat generally have not required substantive retention of snags or downed wood following timber harvest. Although several of the management strategies recommended protection of snags at the time of harvest, these provisions essentially were voluntary and did not *require* retention of snags (i.e., snags generally could be removed for safety and operational reasons). Intensively managed forests are characterized by a dearth of snags (Spies and Cline 1988), and the requirement of snag retention is therefore unlikely to be achieved in most cases without dedicated management. Furthermore, with only one exception (and in a plan that was not implemented), strategies that retain green trees have not *required* that these trees become snags at any time during the life of the plan, typically a period of 50–100 years. Therefore, most of the implemented dispersal management strategies will result in landscapes dominated by younger, second-growth forests. These forests are managed on short rotations (e.g., 50 years) and typically lack the structural components (e.g., snags; Spies and Cline 1988, Wilhere 2003) of forests used by spotted owls.

Although Thomas et al. (1990) were unable to identify a threshold value of foraging habitat that would facilitate dispersal, they clearly recognized the importance of foraging requirements during dispersal. In addition, as a guiding principle Thomas et al. (1990) cited Wiens (1989:227), in stating "To establish reserves according to ecological insights requires both a consideration of broad-scale landscape configurations and knowledge of the ecological requirements of the species that are important in particular situations." Although many dispersal management plans required that 40–50% of the landscape meet a stand-level definition of dispersal habitat, it is unknown whether these targets are sufficient to support dispersing spotted owls, particularly given the lack of structural complexity in the vast majority of stands in dispersal landscapes. In Washington there are several regulatory definitions of suitable spotted owl habitat (WAC 222-16-085), including foraging habitat, and these or similar definitions do not appear in most of the 18 dispersal habitat plans. It is not evident that the majority of dispersal management plans have adhered to this guiding principle. Unfortunately, almost none of the plans contain an adaptive management element that would initiate different management practices to achieve a different target condition based on new knowledge. Therefore, in both the near term and the long term, the proposed and implemented strategies for management of spotted owl dispersal habitat may not produce conditions preferred by spotted owls and may result in dispersal-related mortality (due to starvation or predation) or other consequences that negatively influence juvenile recruitment.

Potential competition with barred owls

Although direct evidence demonstrating competition between the barred owl (*Strix varia*) and spotted owl is lacking, there is a growing concern that the barred owl, now sympatric with the northern spotted owl (Dark et al. 1998), is a superior competitor for resources (Kelly and Forsman 2003, Pearson and Livezey 2003). This potential competitive advantage is likely to occur in all seasons, including during dispersal.

Barred owls differ ecologically from spotted owls in a number of ways. Barred owls are habitat and prey generalists (in the Pacific Northwest), they appear to have greater reproductive output, and they disperse substantially longer distances (Mazur and James 2000) than is typical for spotted owls (Forsman et al. 2002). Consequently, if spotted owls compete with barred owls for resources during the nesting season, they may face an even greater challenge as they move across large dispersal landscapes dominated by younger forests of arguably lower-quality habitat. These dispersal forests provide nesting (e.g., in riparian hardwoods; J. Buchanan, personal observation) and foraging opportunities not exploited by spotted owls. Consequently, barred owls (local adults and their young as well as dispersing birds from adjacent areas) likely are present in dispersal landscapes when spotted owls begin dispersing. Given the generalist nature of prey selection by barred owls (Mazur and James 2000), these owls can persist in such landscapes and may well reduce populations of prey species that in many cases were probably marginal but otherwise available for spotted owls. Research will be required to understand the relationship between these 2 species during dispersal.

Recommendations

An empirical evaluation of the effectiveness of the current dispersal management strategies will be a complex task. A complete assessment of dispersal efficacy in intensively managed forest landscapes will require evaluation of both the suite of ecological conditions and relationships experienced by spotted owls and the influence of dispersal on the demographic health of the population (McPeek and Holt 1992). This is a daunting challenge because an investigation to identify stand- or landscape-level habitat conditions experienced by dispersing spotted owls that eventually influence population performance will be substantial and expensive. Addressing the relationship between dispersal and population demography likely would require that the demography and dispersal landscapes be contiguous, or approximately so.

Cost and logistical constraints are not the only barriers to a better understanding of the habitats used by spotted owls during dispersal. With the exception of a dispersal management strategy implemented by the Washington Department of Natural Resources (WDNR 1997), all other management strategies within HCPs are static and not subject to modification based on new information on spotted owl habitat requirements or the effectiveness of the original strategy. For this reason, the absence of adaptive management provisions seriously limits motivation to evaluate or modify the strategies. Evaluating and subsequently modifying dispersal management strategies, if necessary, may require using adaptive management principles in future Habitat Conservation Plans or other forest management planning efforts. In addition, it may be possible to employ tools such as conservation easements to offset costs that would otherwise be imposed on the United States Fish and Wildlife Service to modify existing HCPs on nonfederal lands.

Significant ecological factors that influence, or have the potential to influence, behavior and survival of spotted owls include the amount, quality, and distribution of suitable habitat, the availability and abundance of prey, and the presence of predators or competitors. It would be insightful to associate the ecological factors with assessments of survival, physiological condition (e.g., mass loss or rate of mass change; see Williams et al. 1999), and behavior (e.g., rate of movement, amount of colonization activity; Forsman et al. 2002). Radiotelemetry would be required to accurately link spotted owl area use with specific stand- and landscape-level attributes. In addition, measures of prey and predator abundance and the habitats they use could be obtained to evaluate the potential importance of these factors. A variety of modeling efforts could be applied (Mooij and DeAngelis 2003), and models could be generated that improve the management strategies currently in use (see Peterson et al. 2003).

There are certainly limitations in conducting the type of research described above. Every landscape or landscape segment is unique in some way, and this will influence predator and prey densities and

habitat functionality. These conditions will place certain limitations on the types of study designs and analytical procedures that can be applied. On the other hand, it should be possible to determine the ecological or environmental factors that influence the success of dispersing spotted owls. Research design should allow for credible investigation, and the information derived from research should be used to develop better dispersal management plans for spotted owls. We should learn from the example of the red-cockaded woodpecker and avoid relying on strategies that may not deliver.

Acknowledgments. I thank W. B. Ballard, M. A. Cronin, and E. D. Forsman for providing comments that improved the manuscript.

Literature cited

AMARANTHUS, M. P., J. M. TRAPPE, L. BEDNAR, AND D. ARTHUR. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. Canadian Journal of Forest Research 24: 2157–2165.

BARROWS, C. W. 1981. Roost selection by spotted owls: an adaptation to heat stress. Condor 83: 302–309.

BARROWS, C., AND K. BARROWS. 1978. Roost characteristics and behavioral thermoregulation in the spotted owl. Western Birds 9: 1–8.

BEAK CONSULTANTS, INC. 1993. Habitat conservation plan for the northern spotted owl (*Strix occidentalis caurina*) on timberlands owned by the Murray Pacific Corporation Lewis County, Washington. Murray Pacific Corporation, Tacoma, Washington, USA.

BIOTA PACIFIC ENVIRONMENTAL SERVICES. 1999. Multi-species Habitat Conservation Plan. Hamilton Tree Farm. Crown Pacific, Ltd., Hamilton, Washington, USA.

BUCHANAN, J., E. HANSON, D. HAYS, AND L. YOUNG. 1994. An evaluation of the Washington Forest Practices Board Wildlife Committee preferred alternative for a spotted owl protection rule. Unpublished report to the Washington Forest Practices Board. Washington Department of Natural Resources, Olympia, USA.

BUCHANAN, J. B., L. L. IRWIN, AND E. L. MCCUTCHEN. 1993. Characteristics of spotted owl nest trees in the Wenatchee National Forest. Journal of Raptor Research 27: 1–7.

BUCHANAN, J. B., L. L. IRWIN, AND E. L. MCCUTCHEN. 1995. Within-stand nest site selection by spotted owls in the eastern Washington Cascades. Journal of Wildlife Management 59: 301–310.

CAREY, A. B. 1985. A summary of the scientific basis for spotted owl management. Pages 100–114 *in* R. J. Gutiérrez and A. B. Carey, editors. Ecology and management of the spotted owl in the Pacific Northwest. United States Department of Agriculture Forest Service General Technical Report PNW – 185.

CAREY, A. B., AND M. L. JOHNSON. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological Applications 5: 336–352.

CAREY, A. B., J. KERSHNER, B. BISWELL, AND L. DOMINGUEZ DE TOLEDO. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs 142.

CAREY, A. B., J. A. REID, AND S. P. HORTON. 1990. Spotted owl home range and habitat use in southern Oregon Coast Ranges. Journal of Wildlife Management 54: 11–17.

CAREY, A. B., T. M. WILSON, C. C. MAGUIRE, AND B. L. BISWELL. 1997. Dens of northern flying squirrels in the Pacific Northwest. Journal of Wildlife Management 61: 684–699.

CURTIS, R. O. 1982. A simple index of stand density for Douglas-fir. Forest Science 28: 92–94.

CURTIS, R. O., AND D. D. MARSHALL. 2000. Why quadratic mean diameter? Western Journal of Applied Forestry 15: 137–139.

DARK, S. J., R. J. GUTIÉRREZ, AND G. I. GOULD. 1998. The barred owl (*Strix varia*) invasion in California. Auk 115: 50–56.

DEFAZIO, J. T., JR., M. A. HUNNICUTT, M. R. LENNARTZ, G. L. CHAPMAN, AND J. A. JACKSON. 1987. Red-cockaded woodpecker translocation experiments in South Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 41: 311–317.

DESTEPHANO, S., AND J. MCCLOSKEY. 1997. Does vegetation structure limit the distribution of northern goshawks in the Oregon Coast Ranges? Journal of Raptor Research 31: 34–39.

EBY, J. R., AND M. C. SNYDER. 1990. The status of old growth in western Washington: a Landsat perspective. Washington Department of Wildlife, Olympia, USA.

FEEN, J. S. 1997. Winter den site habitat of northern flying squirrels in Douglas-fir forests of the south-central Oregon Cascades. Thesis, Oregon State University, Corvallis, USA.

FOREST ECOSYSTEM MANAGEMENT ASSESSMENT TEAM. 1993. Forest ecosystem management: an ecological, economic, and social assessment. United States Government Printing Office 1993–793–071. Washington, D.C., USA.

FORSMAN, E. D. 1976. A preliminary investigation of the spotted owl in Oregon. Thesis, Oregon State University, Corvallis, USA.

FORSMAN, E. D., R. G. ANTHONY, J. A. REID, P. J. LOSCHL, S. G. SOVERN, M. TAYLOR, B. L. BISWELL, A. ELLINGSON, E. C. MESLOW, G. S. MILLER, K. A. SWINDLE, J. A. THRAILKILL, F. F. WAGNER, AND D. E. SEAMAN. 2002. Natal and breeding dispersal of northern spotted owls. Wildlife Monographs 149.

FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs 87.

FORSMAN, E. D., I. A. OTTO, S. G. SOVERN, M. TAYLOR, D. W. HAYS, H. ALLEN, S. L. ROBERTS, AND D. E. SEAMAN. 2001. Spatial and temporal variation in diets of spotted owls in Washington. Journal of Raptor Research 35: 141–150.

FORSMAN, E. D., S. G. SOVERN, D. E. SEAMAN, K. J. MAURICE, M. TAYLOR, AND J. J. ZISA. 1996. Demography of the northern spotted owl on the Olympic Peninsula and east slope of the Cascade Range, Washington. Studies in Avian Biology 17: 21–30.

FOSTER WHEELER ENVIRONMENTAL CORPORATION. 1996. Final environmental impact statement for the Huckleberry land exchange. Mt. Baker-Snoqualmie National Forest. Skagit, Snohomish, King, Pierce, Lewis, Kittitas, and Cowlitz counties, Washington. Foster Wheeler Environmental Corporation, Bellevue, Washington, USA.

GANEY, J. L., W. M. BLOCK, J. K. DWYER, B. E. STROHMEYER, AND J. S. JENNESS. 1998. Dispersal movements and survival rates of juvenile Mexican spotted owls in northern Arizona. Wilson Bulletin 110: 206–217.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28: 1140–1162.

GUTIÉRREZ, R. J., A. B. FRANKLIN, AND W. S. LAHAYE. 1995. Spotted owl (*Strix occidentalis*). Account 179 *in* A. Poole and F. Gill, editors. The Birds of North America, The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D. C., USA.

HICKS, L. L., AND H. STABINS. 1995. Spotted owl habitat descriptions for Plum Creek's Cascades Habitat Conservation Plan. Technical Report No. 4. Plum Creek Timber Company, Seattle, Washington, USA.

HIRONS, G. J., A. R. HARDY, AND P. I. STANLEY. 1979. Starvation of young tawny owls. Bird Study 26: 59–63.

IRWIN, L. L., T. L. FLEMING, S. M. SPEICH, AND J. B. BUCHANAN. 1991. Spotted owl presence in managed forests of southwestern Washington. National Council of the Paper Industry for Air and Stream Improvement Technical Bulletin No. 601. Corvallis, Oregon, USA.

JOHNSON, D. H. 1993. Spotted owls, great horned owls, and forest fragmentation in the central Oregon Cascades. Thesis, Oregon State University, Corvallis, USA.

KELLY, E.G., AND E. D. FORSMAN. 2003. Are barred owls displacing spotted owls? Condor 105: 45–53.

LAHAYE, W. S., AND R. J. GUTIÉRREZ. 1999. Nest sites and nesting habitat of the northern spotted owl in northwestern California. Condor 101: 324–330.

LAHAYE, W. S., R. J. GUTIÉRREZ, AND J. R. DUNK. 2001. Natal dispersal of the spotted owl in southern California: dispersal profile of an insular population. Condor 103: 691–700.

LAMBERSON, R. H., R. MCKELVEY, B. R. NOON, AND C. VOSS. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. Conservation Biology 6: 505–512.

LAMBERSON, R. H., B. R. NOON, C. VOSS, AND R. MCKELVEY. 1994. Reserve design for terrestrial species: the effects of patch size and spacing on the viability of the northern spotted owl. Conservation Biology 8: 185–195.

LEHMKUHL, J. F., AND M. G. RAPHAEL. 1993. Habitat pattern around northern spotted owl locations on the Olympic Peninsula, Washington. Journal of Wildlife Management 57: 302–315.

LONGVIEW FIBRE COMPANY. 1995. Multi-species Habitat Conservation Plan. Mid-Columbia Tree Farm, Skamania County, Washington. Longview Fibre Company, Longview, Washington, USA.

MAZUR, K.M. AND P.C. JAMES. 2000. Barred owl (*Strix varia*). Account 508 *in* A. Poole and F. Gill, editors. The Birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C., USA.

MCPEEK, M.A., AND R. D. HOLT. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 140: 1010–1027.

MEYER, J. S., L. L. IRWIN, AND M. S. BOYCE. 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. Wildlife Monographs 139.

MILLER, G. S., AND E. C. MESLOW. 1985. Dispersal data for juvenile spotted owls: the problem of small sample size. Pages 69–73 *in* R. J. Gutiérrez and A.B. Carey, editors. Ecology and management of the spotted owl in the Pacific Northwest. United States Department of Agriculture Forest Service General Technical Report GTR - PNW - 185.

MILLER, G. S., R. J. SMALL, AND E. C. MESLOW. 1997. Habitat selection by spotted owls during natal dispersal in western Oregon. Journal of Wildlife Management 61: 140–150.

MOOIJ, W. M., AND D. L. DEANGELIS. 2003. Uncertainty in spatially explicit animal dispersal models. Ecological Applications 13: 794–805.

MURPHY, D. D., AND B. R. NOON. 1992. Integrating scientific methods with habitat conservation planning: reserve design for the northern spotted owl. Ecological Applications 2: 3–17.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota, USA.

OLIVER, C. D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management 3: 153–168.

OREGON DEPARTMENT OF FORESTRY. 1995. Elliott State Forest Habitat Conservation Plan. Oregon Department of Forestry, Coos District, Coos Bay, USA.

PEARSON, R. R., AND K. B. LIVEZEY. 2003. Distribution, numbers, and site characteristics of spotted owls and barred owls in the Cascade Mountains of Washington. Journal of Raptor Research 37: 265–276.

PETERSON, G. D., G. S. CUMMING, AND S. R. CARPENTER. 2003. Scenario planning: a tool for conservation in an uncertain world. Conservation Biology 17: 358–366.

PLUM CREEK TIMBER COMPANY, INC. 2000. Central Cascades Habitat Conservation Plan [originally printed June, 1996; revised December, 2000]. Plum Creek Timber Company, Inc., Seattle, Washington, USA.

RAPHAEL, M. G., R. G. ANTHONY, S. DESTEPHANO, E. D. FORSMAN, A. B. FRANKLIN, R. HOLTHAUSEN, E. C. MESLOW, AND B. R. NOON. 1996. Use, interpretation, and implications of demographic analyses of northern spotted owl populations. Studies in Avian Biology 17: 102–112.

SIMPSON TIMBER COMPANY. 1992. Habitat Conservation Plan for the northern spotted owl on the California timberlands of Simpson Timber Company. Simpson Timber Company, Arcata, California, USA.

SPIES, T. A., AND S. P. CLINE. 1988. Coarse woody debris in forests and plantations of coastal Oregon. Pages 4–24 *in* C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, editors. From the forest to the sea: a story of fallen trees. United States Department of Agriculture Forest Service General Technical Report PNW - GTR - 229.

STINSON, D. W., D. E. RUNDE, AND K. A. AUSTIN. 1997. A small mammal community in managed forest of southwestern Washington. Weyerhaeuser Company, Tacoma, Washington, USA.

THOMAS, J. W., E. D. FORSMAN, J. B. LINT, E. C. MESLOW, B. R. NOON, AND J. VERNER. 1990. A conservation strategy for the northern spotted owl. United States Department of Agriculture, Forest Service; and United States Department of Interior, Bureau of Land Management, Fish and Wildlife Service, and National Park Service. Portland, Oregon, USA.

UNITED STATES DEPARTMENT OF AGRICULTURE AND UNITED STATES DEPARTMENT OF INTERIOR. 1994. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl. Standards and guidelines for management of habitats for late-successional and old-growth forest related species within the range of the northern spotted owl. United States Government Printing Office, Washington, D.C., USA.

UNITED STATES DEPARTMENT OF INTERIOR. 1992. Recovery plan for the northern spotted owl-final draft (two volumes). United States Government Printing Office, Washington, D.C., USA.

UNITED STATES FISH AND WILDLIFE SERVICE. 1997. Environmental

Assessment. Habitat management agreement for northern spotted owl (*Strix occidentalis caurina*) dispersal support habitat in the I-90 West Spotted Owl Special Emphasis Area. United States Fish and Wildlife Service, Olympia, Washington, USA.

WASHINGTON DEPARTMENT OF NATURAL RESOURCES. 1997. Final Habitat Conservation Plan. Washington Department of Natural Resources, Olympia, USA.

WASHINGTON FOREST PRACTICES BOARD. 1996. Final Environmental Impact Statement on forest practices rule proposals for northern spotted owl, marbled murrelet, and western gray squirrel. Washington Forest Practices Board, Olympia, USA.

WASHINGTON FOREST PRACTICES BOARD. 2002. Forest practices rule book. Washington Forest Practices Board, Olympia, USA.

WATSON, J. W., D. W. HAYS, AND D. J. PIERCE. 1999. Efficacy of northern goshawk broadcast surveys in Washington state. Journal of Wildlife Management 63: 98–106.

WEATHERS, W. W., P. J. HODUM, AND J. A. BLAKESLEY. 2001. Thermal ecology and ecological energetics of California spotted owls. Condor 103: 678–690.

WEST, S. D. 1991. Small mammal communities in the southern Washington Cascade range. Pages 268–283 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. United States Department of Agriculture Forest Service General Technical Report PNW - GTR - 285.

WEYERHAEUSER COMPANY. 1995. Habitat Conservation Plan for the northern spotted owl. Millicoma Tree Farm, Coos and Douglas counties, Oregon. Weyerhaeuser Company, North Bend, Oregon, USA.

WEYERHAEUSER COMPANY. 1996. Multispecies Habitat Conservation Plan for the Willamette Timberlands. Benton, Douglas, Lane, and Linn counties, Oregon. Weyerhaeuser Company, Springfield, Oregon, USA.

WIENS, J. A. 1989. The ecology of bird communities. Volume 2: processes and variations. Cambridge University Press, New York, New York, USA.

WILHERE, G. F. 2003. Simulations of snag dynamics in an industrial Douglas-fir forest. Forest Ecology and Management 174: 521–539.

WILLIAMS, T. D., C. G. GUGLIELMO, O. E. EGELER, AND C. J. MARTYNIUK. 1999. Plasma lipid metabolites provide information on mass change over several days in captive western sandpipers (*Calidris mauri*). Auk 116: 994–1000.

WIMBERLY, M. C., T. A. SPIES, C. J. LONG, AND C. WHITLOCK. 2000. Simulating historical variability in the amount of old forests in the Oregon Coast Range. Conservation Biology 14: 167–180.

Author's address: Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501, USA; e-mail: buchajbb@dfw.wa.gov.

Joseph B. Buchanan, a wildlife biologist with the Washington Department of Fish and Wildlife since 1991, began studying spotted owls in 1988 while employed by the National Council for Air and Stream Improvement. His research on spotted owls has focused primarily on habitat use. For the last decade he has been the lead biologist with WDFW on a wide range of conservation and management issues involving spotted owls on state and private lands. He received a B.S. from Evergreen State College in 1981 and an M.S. in wildlife sciences from the College of Forest Resources, University of Washington, in 1991. He has broad interests in ornithology and avian conservation, and is particularly interested in the status, ecology, and behavior of shorebirds and their falcon predators.

Forest Service Large Fire Area Burned and Suppression Expenditure Trends, 1970–2002

David E. Calkin, Krista M. Gebert, J. Greg Jones, and Ronald P. Neilson

ABSTRACT

Extreme fire seasons in recent years and associated high suppression expenditures have brought about a chorus of calls for reform of federal firefighting structure and policy. Given the political nature of the topic, a critical review of past trends in area burned, size of fires, and suppression expenditures is warranted. We examined data relating to emergency wildland fire suppression expenditures, number of fires, and acres burned and developed statistical models to estimate area burned using drought indices for the USDA Forest Service from 1970–2002.

Keywords: wildland fire, Forest Service suppression expenditure trends, Palmer Drought Severity Index (PDSI)

Unprecedented expenditures on wildland firefighting over the past several years have brought federal wildland fire management to the forefront of political debate. Extreme fire seasons have occurred in 3 of the last 4 years (2000, 2002, and 2003), with federal expenditures on emergency fire suppression exceeding $1 billion in each of those 3 years. The fire season of 2002 was the most expensive on record. Federal firefighting expenditures totaled $1.6 billion, with the USDA Forest Service alone spending over $1.1 billion (National Interagency Fire Center 2003). In 2002, three western states experienced their largest single wildfire seasons on record: the Hayman fire in Colorado, the Rodeo-Chediski in Arizona, and the Biscuit in Oregon; an estimated 6.9 million acres burned nationwide. Our focus is on USDA Forest Service fire suppression expenditures, which account for nearly three-fourths of all federal suppression expenditures.

A variety of explanations have been offered for the high levels of emergency fire suppression expenditures, including excessive fuel loading caused by decades of successful fire suppression, increased development in the wildland-urban interface (WUI), lack of financial accountability of fire managers, and severe and prolonged drought (National Academy of Public Administration 2002). In fire-adapted ecosystems common throughout much of the West, there is strong evidence that past fire suppression has resulted in fuel loads well outside historic regimes and is largely responsible for the increased size and severity of some wildland fires (Arno and Brown 1991, Arno et al. 2000). Residential development in the WUI and the emphasis of federal firefighting organizations on protecting residential structures has also been mentioned as a potential factor increasing suppression expenditures (Snyder 1999). Additionally, there is much discussion about the lack of financial accountability of fire managers and an incentive system that makes fire managers more risk averse than socially optimal (USDA, USDI, NASF 2003). Risk aversion can cause both excessive use of firefighting resources and substitution of expensive (but less risky) capital resources for less expensive (but more risky) labor resources.

The influence of weather on fire season severity is well established. A number of recent studies have explored the relationship between drought and fire season severity (Westerling et al. 2003, Swetnam and Betancourt 1998, Balling et al. 1992). In a much-cited study of subalpine pine forest types, Bessie and Johnson (1995) state "forest fire behavior is determined primarily by weather variation among years rather than fuel variation associated with stand age." However, Agee (1997) and Betancourt et al. (2003) argue that, while weather is the dominant factor in determining fire severity and size in forest types that typically burn infrequently and at high intensity, fuel buildup cannot be discounted in the drier forest types that typically burn frequently but at low intensity.

Given the extreme fire seasons and associated suppression expenditures that have recently been experienced, it is important to examine the data to identify real trends and dispel any incorrect assumptions regarding USDA Forest Service emergency fire suppression expenditures. The following analysis is a first step in understanding emergency firefighting expenditures by critically exam-

ining macro-level data for the USDA Forest Service.

Methods

We examined data relating to emergency wildland fire suppression expenditures, number of fires, and acres burned for the USDA Forest Service from 1970 to 2002 for individual USDA Forest Service regions and aggregated for the continental United States. These data have been compiled from the USDA Forest Service's accounting system (Central Accounting Data Inquiry (CADI) for data prior to fiscal year 2000 and Foundation Financial Information System (FFIS) for fiscal year 2000 and beyond) and the National Interagency Fire Management Integrated Database (NIFMID), the USDA Forest Service's fire occurrence database. Financial data for the continental United States are from fiscal year 1971 to 2002, while regional acreage burned data are from calendar year 1970 to 2002. We compiled data on the total number of fires and all fires greater than or equal to 300 ac (class E, F, and G), which we call large fires, the cost per acre of suppressing the large fires, and total area burned by all fires and by large fires. Expenditure data are for emergency wildland fire suppression; initial attack funding is not included in this analysis. This focus was necessary due to changes in accounting structures within the initial attack budget. Historical data at the regional and national level were graphed, and, where appropriate, econometric models were developed to identify relevant trends.

A number of recent studies have used a common measure of drought, the Palmer Drought Severity Index (PDSI, Palmer 1965), to predict fire season severity including Balling et al. (1992), Swetnam and Betancourt (1998), and Westerling et al. (2003). The PDSI is a measure of the scope, severity, and frequency of prolonged periods of abnormally dry or wet weather and is useful as an indicator of general conditions and not local variations (National Oceanic and Atmospheric Administration, National Weather Service 2003). Swetnam and Betancourt (1998) identified a strong correlation between tree-ring-reconstructed regional fire-scar chronology and June-Aug. PDSI time series for the Southwest. Westerling et al. (2003) investigated associations between the PDSI and seasonal acres burned in western wildfires and identified positive correlations with PDSI 12–15 months prior to Aug. The authors conclude that this result appears to reflect a trade-off between fuel accumulation and flammability, with wet conditions in the previous year contributing to fuel accumulation and wet conditions in the current year suppressing fire activity by moistening the fuels, and, conversely, dry conditions in the previous year inhibiting fuel accumulation and dry conditions in the current year enhancing fire activity by drying the fuels.

There are indications of significant shifts in long-term weather regimes, influenced by interdecadal oceanic oscillations, over the period of analysis (Swetnam and Betancourt 1998). Weather in North America is affected by interdecadal oceanic circulation regimes in all three oceans that ring the continent, the Pacific, Arctic, and Atlantic Oceans (Hurrel 1995, Thompson and Wallace 1998, Mantua and Hare 2002). Among the most prominent were ocean-climate regime shifts in the early 1940s, mid-1970s, around 1987–89, and most recently around 1997 (Hare and Mantua 2000). The regime shifts in the 1940s and 1970s are associated with a three-decade cooling trend in the middle of an otherwise continuous warming trend over the 20th century (Folland et al. 2001). With the regime shift in the mid-1970s, the western United States has undergone two extreme wet-dry cycles unlike anything since the onset of the 20th century. The extreme El Niños in 1983 and 1998 punctuate the wet episodes, while the 1987–89 regime shift and the most recent years (ca. 2000–2002) were among the driest in historic times. The 1987–89 regime shift produced prominent signals in all three oceans, but persisted in the Arctic and North Atlantic to the present. These wet and dry periods may have increased the severity of fire seasons, especially since 1987. Vegetation fuels increased during the extended wet periods, while fires were more limited, and then the fuels were dried and easily combusted during the extended dry periods.

Table 1. Fire season months by region (provided by Tom Wordell, Wildland Fire Analyst, National Interagency Coordination Center).

Region	Fire season months
Pacific Northwest	June, July, Aug.
Northern California	July, Aug., Sept., Oct.
Southern California[a]	July, Aug.
Western Great Basin	June, July, Aug., Sept.
Eastern Great Basin	June, July, Aug., Sept.
Northern Rockies	June, July, Aug.
Rocky Mountain	June, July, Aug., Sept.
Southwest	May, June, July
South	Mar., Apr., May, June
East	Mar., Apr., May

[a] Additionally, we evaluated a fire season for Southern California including July, Aug., Sept., Oct., and Nov. to represent the effects of Santa Ana winds in the fall months. Results for both models are presented in Table 2.

We developed statistical models to predict area burned for individual Geographic Area Coordination Center (GACC) regions using Palmer drought indices as explanatory variables. We used the following base model:

$$\text{area burned}_t = \text{fn}\ (\text{PDSI(fire)}_t,\ \text{PDSI}_{t-1},\ \text{annual dummy})$$

Area burned is total area burned by all USDA Forest Service fires in the specified region. PDSI(fire)_t is the average PDSI over the fire season, and PDSI_{t-1} is the previous year's average annual PDSI for that region. Palmer drought indices used in this analysis were provided by Neilson and aggregated at the GACC regions. PDSI(fire) was averaged for the individual regions based on the primary fire season months shown in Table 1. For the Southern California region, we examined two alternative fire season definitions. The first, including only July and Aug., was identified by Tom Wordell of the National Interagency Coordination Center (NICC). The second included the months of July and Aug. as well as Sept., Oct., and Nov. to represent the potential effects of Santa Ana winds on fire season severity. The annual dummy variable was included to test for variation in area burned related to weather regime shifts over the study period.

Results

Emergency firefighting expenditures are spent to suppress escaped fires, wildland fires 300 ac or larger (classes E, F, and G). Most fire starts are contained before the fire meets the definition of escaped wildfire. Over the period of analysis, between 97.2 and 99.7% of all fires were contained in the smaller fire classes A through D. However, a

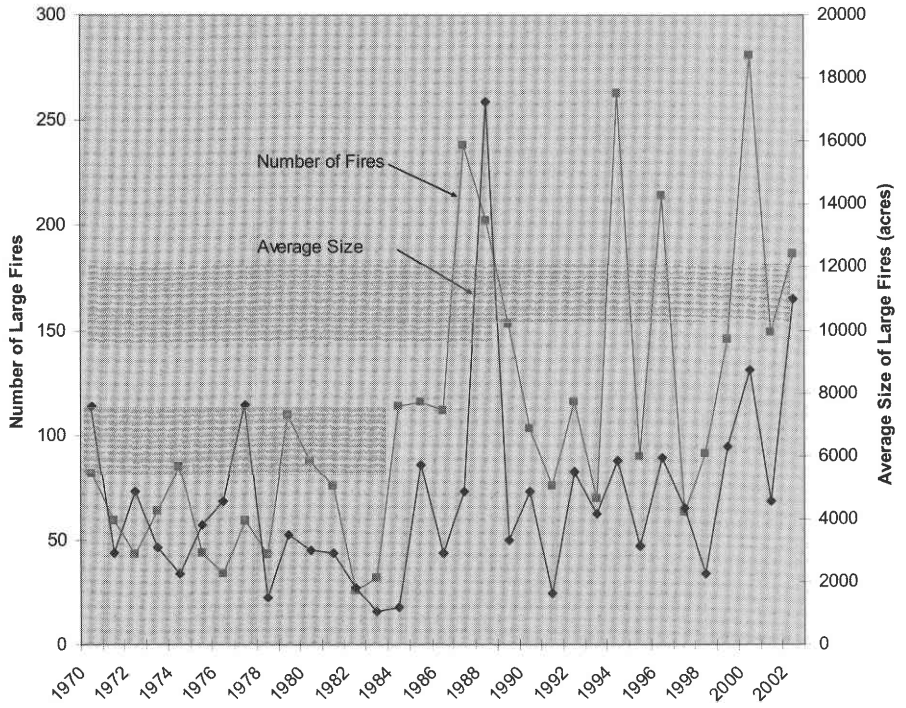


Figure 1. Number and average size of USDA Forest Service large fires (class E, F, and G).

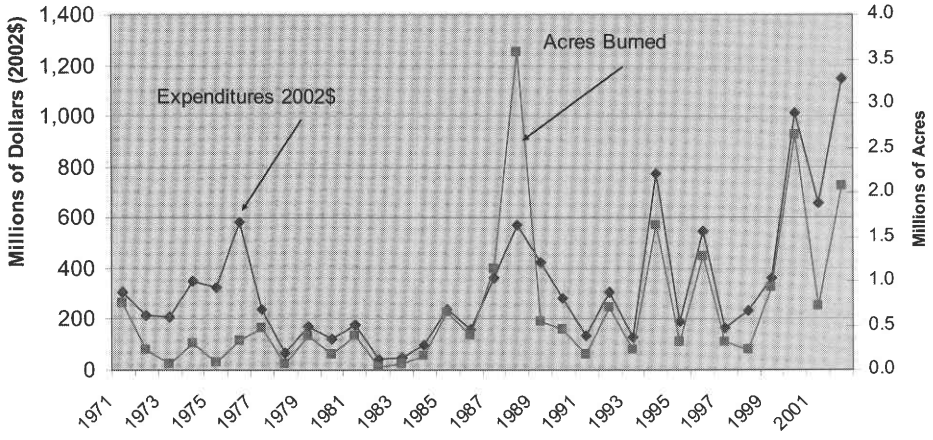


Figure 2. USDA Forest Service suppression expenditures (2002$) and area burned.

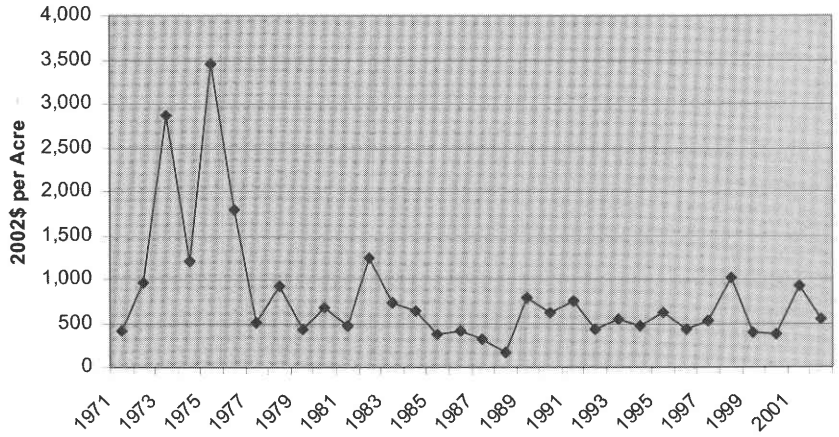


Figure 3. USDA Forest Service suppression expenditures per acre (2002$).

majority of all acres burned occurred in the larger fire classes. Averaged over the length of the study period, large fires accounted for only 1.1% of all fires but accounted for 97.5% of the area burned. Furthermore, there appears to be a trend of an increasing number of large fires and average size of these large fires over time (Figure 1).

Total annual emergency firefighting expenditures are extremely volatile, but an increasing trend is obvious in the data with nine of the 10 most expensive fire seasons (adjusted to 2002 dollars) occurring since 1987 (see Figure 2). Moreover annual suppression expenditures exceeded $1 billion in both 2000 and 2002.

Total expenditures can be broken down into two parts, total acres burned on large fires and the cost per acre of fighting these fires. Figure 3 displays that emergency suppression expenditures per acre burned have, in fact, exhibited a downward trend that starts to flatten out in the late 1980s. However, total area burned shows a different trend, increasing and becoming far more volatile around 1987 (Figure 2). If you simply take the average of area burned from 1970–1986 and 1987–2002, you see that the average has increased from approximately 285,000 to over 1,000,000 ac per year. Simply put, suppression expenditures increased and became erratic when acres burned increased and became erratic. Graphing emergency fire expenditures against total area burned (Figure 2) shows the close correlation between total expenditures and area burned (Pearson's correlation coefficient equaled 0.76 while the correlation between expenditures and cost per acre was an insignificant −0.019).

Results of modeling area burned as a function of PDSI were regional specific, but common patterns were evident. From the generic model described in Equation 1, the following model was developed:

$$\text{Ln (area burned}_t) = B_0 + B_1\text{*PDSI(fire)}_t + B_2\text{*PDSI}_{t-1} + B_3\text{*D1987}_t$$

Coefficient values, levels of significance, and model fit for the individual regional models are presented in Table 2. We transformed area burned using the natural logarithm to improve model fit based on results from Box-Cox tests (Green 1993). Not surprisingly, PDSI fire season was negative and significant in all regions; area burned increases when the fire season is drier. The previous year's PDSI was positive and significant (at

Table 2. Econometric model results for individual GACC regions (all results significant at the 0.05 level unless italicized with significance level in parenthesis).

Region	Constant	$PDSI(fire)_t$	$PDSI_{t-1}$	$D1987_t$	R^2
Pacific Northwest	9.453	–0.578	*0.185 (0.202)*	1.357	0.56
Northern California	9.717	–0.405	*0.204 (0.101)*	0.885	0.38
Southern California (July, Aug.)	10.776	–0.175	0.466	*0.503 (0.124)*	0.43
Southern California (July—Nov.)[a]	10.802	–0.193	0.454	*0.447 (0.176)*	0.43
Western Great Basin	7.652	–0.351	0.505	1.908	0.56
Eastern Great Basin	9.934	–0.600	0.699	1.847	0.67
Northern Rockies	9.211	–1.086	0.509	1.462	0.74
Rocky Mountain	8.894	–0.817	0.690	1.183	0.58
Southwest	10.212	–0.220	*0.268 (0.073)*	0.942	0.37
South	10.135	–0.361	0.271	0.627	0.56
East	9.028	–0.429	0.375	*0.087 (0.691)*	0.29

[a] Two fire season definitions were examined for Southern California. The first includes only July and Aug., while the second includes July and Aug. as well as Sept., Oct., and Nov. to represent the effects of Santa Ana winds on fire season severity.

the 0.05 level) in all regions except the Pacific Northwest and Northern California (significant at the 0.202 and 0.101 levels, respectively). These results are consistent with Westerling et al. (2003); moist growing seasons in the previous year increase fuel loading and thus area burned in the following fire season. Residual analysis of a model using only the two PDSI variables, as well as recursive residuals and Chow tests (Green 1993), confirmed that a structural shift in the model occurred around 1987 consistent with a significant shift in weather regimes. The annual dummy variable (D1987) was defined as 0 for years 1970–1986 and 1 for 1987 forward. The coefficient for D1987 was positive and significant in eight of the 10 models, indicating that after accounting for variations in PDSI, total area burned increased significantly starting in 1987. The coefficient for the dummy was positive but insignificant for the Southern California and Eastern regions (significant at the 0.124 and 0.691 level, respectively). The two alternative fire season definitions for Southern California performed equally well in predicting area burned with only modest changes in model parameters.

We calculated estimated area burned using a "smearing" estimate (Duan 1983) from the individual regional models and aggregated these results to determine estimated total area burned in the continental United States. Figure 4 presents the results of graphing estimated area burned against actual area burned for the United States over the length of the data series. The estimated acres burned tracks the actual acres burned very closely ($R^2 = 0.90$).

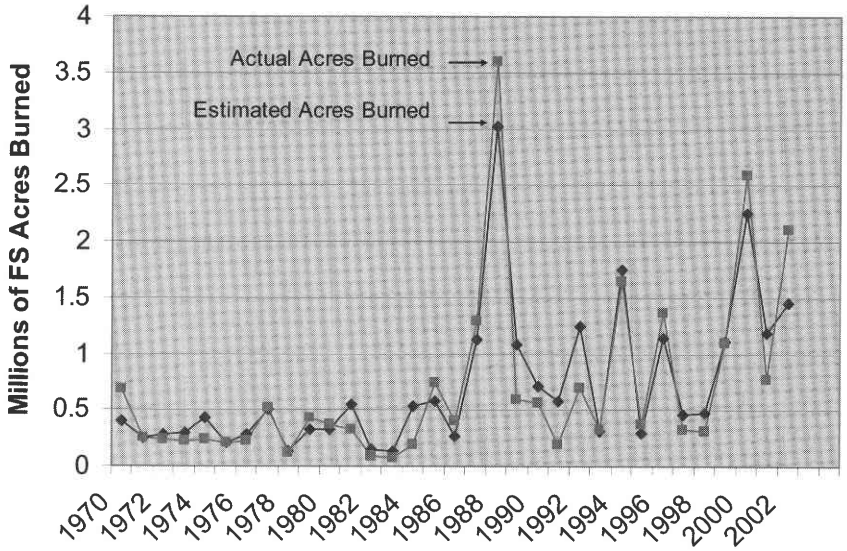


Figure 4. Estimated versus actual USDA Forest Service area burned.

Discussion

Total USDA Forest Service emergency fire suppression expenditures have been increasing over time with expenditures exceeding $1 billion in 3 of the last 4 years (including FY 2003). This increase in suppression expenditures appears to be related to the increase in acres burned (which also increased substantially over the same period) and not a per acre increase in suppression expenditures (trend for average per acre expenditures did not increase). Large fires represent a small number of the total fires, but constitute the bulk of total area burned; 1.1% of all fires burned 97.5% of total area. Both the number of large fires and average size of large fires appear to have increased over time.

Total area burned tracks suppression expenditures very well. Area burned can be modeled successfully using current and past regional drought indices, yet a significant dummy variable improves model fit, implying that total area burned significantly increased after 1987. The common rationales for increasing fire expenditures do not account for this structural shift. Increasing development within the wildland-urban interface has been increasing over the study period, but does not account for any distinct shifts. Firefighting agencies are likely focusing more resources on structural protection, reflecting the development trends in the WUI, but those shifts are also continuous and do not explain a major change occurring in 1987. Excessive fuel loading has certainly been responsible for the increased size and severity of some wildland fires, but fuel loading has been building for decades. The key factor that we believe is driving the system and interacting with the excessive fuel loads is the weather. Over the past 15 years, a long-term weather regime shift, caused by oceanic interdecadal oscillations, has increased the length and intensity of the wet and dry periods. During wet periods, fine fuel growth increases fuel loading where fuel loads are often already well above historic

conditions due to past fire exclusion. During prolonged, intense dry periods, these fuels dry out, and then if a fire starts, it is more likely to be large and of high intensity.

Currently, cost containment strategies are being put forward as the means to control the unprecedented suppression expenditures seen in the last several years. In the fall of 2003, a blue ribbon panel is being convened by the USDI and USDA to address cost containment. The Large Fire Cost Reduction Action Plan (USDA, USDI, NASF 2003) highlighted this issue, stating that "we must elevate cost containment commensurate with other objectives." Along these lines, there have been recommendations to reduce utilization of high cost resources such as aircraft. We do not deny that inefficiencies in fire suppression efforts likely exist and that these actions should be identified and addressed. However, making assumptions that reducing the use of high-cost resources will improve cost containment is premature. The production functions for fire suppression resources are largely unknown, as is the effect in certain instances of not applying suppression resources. Without this additional information, high cost, highly effective resources may be replaced with lower cost, but less effective resources. The results of our analysis suggest that the current level of suppression expenditures is largely a function of acres burned, and acres burned are largely a function of weather-related variables. Current weather patterns are exacerbating a difficult firefighting environment due to fuels accumulation and WUI development. Strategies to contain costs based on anecdotal information without carefully thought out analysis may in fact increase fire damages and overall costs.

Literature Cited

AGEE, J.K. 1997. The severe weather wildfire—Too hot to handle. *Northwest Sci.* 71(1): 153–156.

ARNO, S.F., AND J.K. BROWN. 1991. Overcoming the paradox in managing wildland fire. *Western Wildlands* 17(1):40–46.

ARNO, S.F., D.J. PARSONS, AND R.E. KEANE. 2000. Mixed-severity fire regimes in the Northern Rocky Mountains: Consequences of fire exclusion and options for the future. P. 225–232 in *Wilderness science in a time of change conference, vol. 5: Wilderness ecosystems, threats and management*, Cole, D.N., S.F. McCool, W.T. Borrie, and J. O'Loughlin (comps.). USDA Forest Service Rocky Mountain Research Station, Proceedings RMRS-P-15-VOL-5.

BALLING, R.C., G.A. MEYER, AND S.G. WELLS. 1992. Relation of surface climate and burned area in Yellowstone National Park. *Agric. For. Meteor.* 60:285–293.

BESSIE, W.C., AND E.A. JOHNSON. 1995. The relative importance of fuels and weather on fire behavior in subalpine pine forests. *Ecology* 76: 747–762.

BETANCOURT, J.L., T.W. SWETNAM, C.D. ALLEN, AND M. SAVAGE. 2003. Fire in the West: It's no simple story. *High Country News* July 7, 2003, Paonia, CO.

DUAN, N. 1983. Smearing estimate: A nonparametric retransformation method. *J. Am. Statist. Assoc.* 78:605–610.

FOLLAND, C.K., T.R. KARL, J.R. CHRISTY, R.A. CLARKE, G.V. GRUZA, J. JOUZEL, M.E. MANN, J. OERLEMANS, M.J. SALINGER AND S.-W. WANG. 2001. Observed climate variability and change. P. 99–182 in *Climate change 2001: The scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, Houghton, J.T., Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C.A. Johnson (eds.). Cambridge University Press, Cambridge, United Kingdom. 881 p.

GREEN, W.H. 1993. *Econometric analysis*, 2nd Ed. Prentice Hall Inc., Englewood Cliffs, NJ. 791 p.

HARE, S.R., AND N.J. MANTUA. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* 47(2–4): 103–146.

HURRELL, J.W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science* 269:676–679.

MANTUA, N.J., AND S.R. HARE. 2002. The Pacific Decadal Oscillation. *J. Oceanogr.* 58:35–44.

NATIONAL ACADEMY OF PUBLIC ADMINISTRATION. 2002. *Wildfire suppression: Strategies for containing costs.* National Academy of Public Administration, Washington, DC. 66 p.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, NATIONAL WEATHER SERVICE. 2003. *Explanation.* Available online at www.cpc.ncep.noaa.gov/products/analysis_monitoring/cdus/palmer_drought/wpdanote.shtml; accessed April 15, 2005.

NATIONAL INTERAGENCY FIRE CENTER. 2003. *Fire Statistics.* Available online at www.nifc.gov/stats/index.html; accessed Oct. 3, 2003.

PALMER, W.C. 1965. *Meteorological drought. Research paper no. 45.* US Department of Commerce Weather Bureau, Washington, DC.

SNYDER, G.W. 1999. Strategic holistic integrated planning for the future: Fire protection in the urban/rural/wildland interface (URWIN). P. 159–170 in *Proceeding of the symposium on fire economics planning, and policy: Bottom lines*, Gonzalez-Caban, A. and P.N. Omi (tech. coords.). USDA For. Serv. Gen. Tech. Rep. PSW-GTR-173.

SWETNAM, T.W., AND J.L. BETANCOURT. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J. Climate* 11:3128–3147.

THOMPSON, D.W.J., AND J.M. WALLACE. 1998. The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. *Geophys. Res. Lett.* 25(9):1297–1300.

USDA FOREST SERVICE, USDI BUREAU OF LAND MANAGEMENT, AND NATIONAL ASSOCIATION OF STATE FORESTERS. 2003. *Large fire cost reduction action plan.* Available online at www.fs.fed.us/fire/management/action_plan/cost_reduction.html; accessed Oct. 23, 2003.

WESTERLING, A.L., A. GERSHUNOV, T.J. BROWN, D.R. CAYAN, AND M.D. DETTINGER. 2003. Climate and wildfire in the Western United States. *Bull. Am. Meteorol. Soc.* 84(5):595–604.

David Calkin (decalkin@fs.fed.us) is research forester, Krista Gebert (kgebert@fs.fed.us) is economist, and Greg Jones (jgjones@fs.fed.us) is research forester, USDA Forest Service, Rocky Mountain Research Station, 800 East Beckwith, Missoula, MT 59801. Ronald Neilson (rneilson@fs.fed.us) is bioclimatologist, USDA Forest Service, Pacific Northwest Research Station. 3200 S.W. Jefferson Way, Corvallis, OR 97331.

PNAS OPINION

Wildland-urban fire disasters aren't actually a wildfire problem

David E. Calkin[a,1], Kimiko Barrett[b], Jack D. Cohen[c,2], Mark A. Finney[d], Stephen J. Pyne[e,2], and Stephen L. Quarles[f]



Major fires like this one, a damaging wind-fueled fire near Superior, Colorado, in December 2021, are typically defined as an issue of *wildfires* that involved houses. In reality, they are *urban fires* initiated by wildfires. That's an important distinction. Image credit: iStock/milehightraveler.

Consider several of the most devastating fire disasters of the last century. In August 2023, the wildfire-initiated urban conflagration of Lahaina, Hawaii, damaged or destroyed more than 2,200 structures and killed 98 people. In December 2021, the Marshall Fire sparked conflagrations in Superior and Louisville, Colorado, destroying 1,084 structures and killing two. In September 2020, the Almeda Drive Fire in the communities of Talent and Phoenix, Oregon, destroyed 2,600 homes and killed three. In November 2018, the Camp Fire initiated ignitions in Paradise, California, destroyed 18,804 buildings, and killed 85. In November 2016, fires spread through Gatlinburg and Pigeon Forge, Tennessee, destroying 2,460 structures and killing 14.*

These fire disasters burned in vastly different environments. But all had human causes (power lines contributed to at least three), were near communities, occurred during extreme wind events, then inflicted their damage as urban conflagrations. Almost all destruction occurred within the first 12 hours after ignition. These fires immediately overwhelmed wildland and structural firefighting efforts, which were largely ineffective during the initial and extreme phase of the fire. Further, all these fires occurred since 2016. It's clear that structures and whole communities were vulnerable to ignition and burning—irrespective of what initiated the fires.

Society largely regards the wildfire problem as the destruction of human communities. Collectively, disaster fires, such as those mentioned here, have been

*Although the Chimney Tops 2 Fire on the Great Smoky Mountains National Park ignited on November 23, 2016, may have contributed to the burning of Gatlinburg and Pigeon Forge, multiple power line ignitions during the extreme weather event of November 28 preclude the ability to identify a single or dominant ignition source that resulted in the community destruction.

Author contributions: D.E.C., K.B., J.D.C., M.A.F., S.J.P., and S.L.Q. wrote the paper.

The authors declare no competing interest.

Copyright © 2023 the Author(s). Published by PNAS. This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

Any opinions, findings, conclusions, or recommendations expressed in this work are those of the authors and have not been endorsed by the National Academy of Sciences.

[1]To whom correspondence may be addressed. Email: David.calkin@usda.gov.

[2]Retired.

Published December 13, 2023.

Downloaded from https://www.pnas.org by 199.68.205.95 on January 9, 2024 from IP address 199.68.205.95.

lumped into a category of wildland–urban interface fires. These problem fires were defined as an issue of *wildfires* that involved houses. In reality, they are *urban fires* initiated by wildfires. That's an important distinction—and one that has big repercussions for how we prepare for future fires. To date, these repercussions have not received enough attention.

The Right Framing

Community fire destruction has become a national crisis, a systemic problem that will only worsen without aggressive, appropriate intervention—and this intervention will have to look far different than the current dominant paradigm. Climate change is blurring the boundaries that had defined where, when, and how fires burn (1). The needed changes will challenge ideas, institutions, and policies. The first step: reframing, from a focus on the wildlands to one centered on the structure and its immediate surroundings.

To effectively address this urban conflagration crisis requires that we fundamentally redefine the WU fire problem. Calkin et al. (2) developed a community wildfire risk framework that starts with a focus at the individual home level and identifies realistic objectives, effective mitigations, and responsible parties to reduce WU fire risk. The framework highlights the critical role of individual homeowners and local government, while recognizing that the traditional federal and state land-management agencies with responsibilities for wildland fuels management and suppression response have limited impact on community destruction. However, many of the recent investments to address wildfire risk to communities, such as the Bipartisan Infrastructure Investment and Jobs Act of 2021 and the Inflation Reduction Act of 2022, are primarily directed toward fuel treatments in natural areas governed by public land-management agencies.

The practice of modifying the built environment to growing wildfire risk requires multidisciplinary understanding of wildfire behavior, structural ignition vulnerabilities, urban resilience, and landscaping vegetation.

The wildfire management system's default response is to suppress wildfire wherever and whenever possible, with few exceptions (3). It extends an urban fire service model into the wildlands. With fire exclusion as the primary solution to both community and wildland protection, risk reduction translates to fire suppression and landscape fuel reduction. As wildfire losses increase, the assumption that community protection should be a primary focus of federal wildfire management efforts has become entrenched within both agency culture and federal legislation.

But even as wildfire suppression costs and use of technology have skyrocketed, we are experiencing more damaging urban fires. Clearly, the answer to community adaptation resides in the communities themselves (2, 4), and until the WU fire problem statement is redefined to recognize the key role of structure ignition and focus on creating ignition-resistant communities, risk-reduction strategies will continue to be ineffective and insufficient.

The Right Response

In 2022, the US Forest Service released the *Wildfire Crisis Strategy*, outlining an ambitious goal of treating an additional 20 million acres of US Forest Service land and 30 million acres of other federal, tribal, state, and privately owned land "to address wildfire risks to critical infrastructure, protect communities, and make forests more resilient" (ref. 5; see also ref. 6). While federal land-management agencies—primarily the US Forest Service and Department of Interior—have been tasked with wildfire risk reduction, most wildfire ignitions are caused by humans and occur on private lands (7), including those that destroy a majority of structures in the western United States (8). Furthermore, what has often been considered a western United States issue has now come to the fore in locations with limited wildfire experience, such as Gatlinburg, Tennessee, and Lahaina, Hawaii, thus creating additional challenges. As a result, actions on private land are essential to achieving fire-adapted communities across the country.

The community disaster sequence occurs when more homes are ignited than responders can protect (Fig. 1). Once structures are burning in a community, they become sources of lofted embers, radiant heat, and flame contact. Thus, community fire growth can accelerate quickly, resulting in urban conflagration that's exacerbated in higher-density development due to structure-to-structure fire spread. Reducing the likelihood that a home will ignite interrupts the disaster sequence by enabling effective structure protection. New construction siting, design, construction materials, and landscaping requirements should take wildfire potential into account. This will improve community resilience and ensure that new development does not increase community risk. The best way to make existing wildfire-vulnerable developments ignition resistant is to work within the limited area of the "home ignition zone"—a home and its surroundings within 100 feet (which may include neighboring homes). There are ways to reduce home ignition risk. Homeowners should install nonignitable roofing materials and flame- and ember-resistant vents; clean gutters of flammable debris; ensure that wooden steps, fences, and decks do not directly contact a home's flammable materials; and remove flammable materials immediately surrounding buildings and under attached decks (9–11).

Initiating substantial changes to the built environment requires that all levels of society address deeply rooted cultural expectations and develop a fundamentally new paradigm for community and homeowner responsibility. Such changes will take time. Communities need robust evacuation planning, including resilient early warning systems, identification and enhancement of egress routes, and consideration of support for individuals with mobility difficulties that all recognize the complexity of individual decision-making during emergency events (12). The community disaster sequence typically occurs during extreme wind events; thus, ignition-prevention programs should address infrastructure resilience and human behavior under these conditions.

Unfortunately, many communities and local governments often lack the resources, budget, staff, and experience to implement and maintain parcel- and neighborhood-level risk-reduction measures. The practice of modifying the built

Downloaded from https://www.pnas.org by 199.68.205.95 on January 9, 2024 from IP address 199.68.205.95.

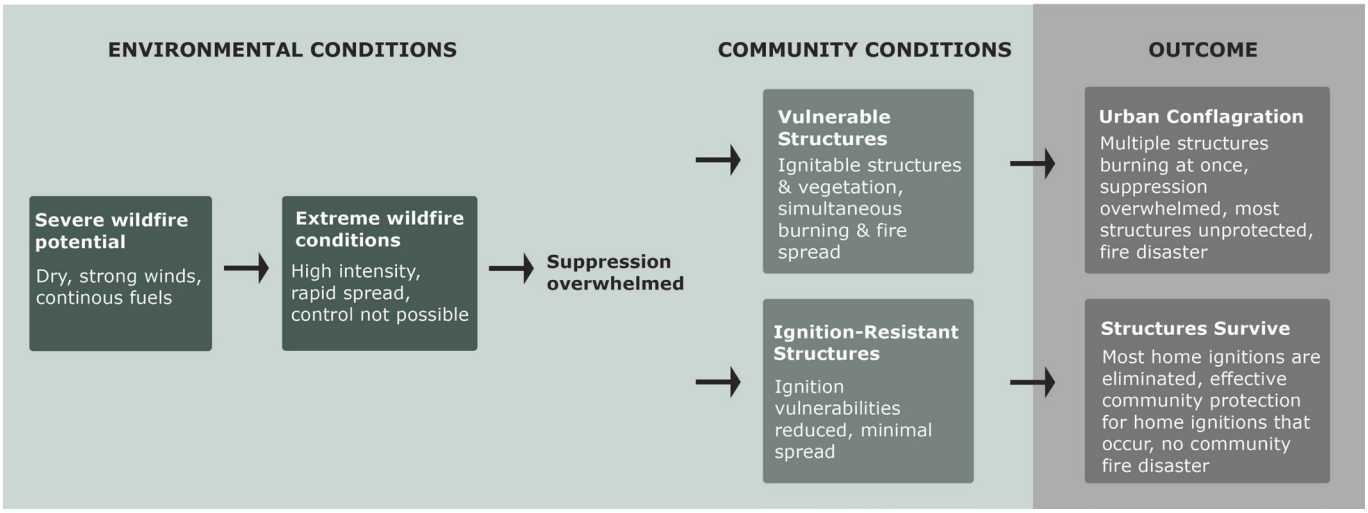


Fig. 1. The community fire disaster sequence. Enabling wildfire conditions set the stage for disaster, but the condition of the community defines the outcome.

environment to growing wildfire risk requires multidisciplinary understanding of wildfire behavior, structural ignition vulnerabilities, urban resilience, and landscaping vegetation. Such know-how is not intrinsic institutional knowledge for public land-management agencies. As such, an appropriate response may resemble public health measures, where protecting the host from infection (home ignition prevention) is emphasized over trying to eliminate the infectious agent (wildfire).

Community leaders and locally elected officials are central to implementing effective wildfire mitigation strategies. And these leaders require significant technical assistance and financial support from federal and state levels. They need administrative mechanisms to direct funding and technical assistance to communities; this will require enhanced interagency coordination among federal and state-level departments, which can administer resources to local jurisdictions. Initial efforts in California, Colorado, and Oregon are structuring home ignition mitigation programs on this model, with the underlying objective of delivering funding, support, and expertise to communities and individual residents (13–15).

A New Perspective

All such projects and reforms must recognize an important truth: The current wildfire management approach has inverted the wildfire problem. wildland fires do not, per se, encroach on communities. Rather, it's communities that have impinged on wildlands, where fires play an important ecological role. Predominant strategies continue to apply limited, risk-averse reactions that emphasize community protection at the expense of both resilient landscapes and safe, effective wildfire responses. Forward-looking ecological and practical thinking would help move communities away from continually degrading fire-adapted ecosystems and underinvesting in community resilience. Instead, this change in thinking will move toward a sustainable approach that consistently promotes ecological and human ecosystem benefits.

Communities and governments need to accept living with wildland fire. They must recognize that fire in the wildlands is ecologically appropriate and inevitable—and it does not significantly influence community fire destruction (16). To do this, we must communicate differently on the nature of the WU fire problem and the ecological necessity of wildland fire. We must empower our public land managers and tribal partners to utilize fire appropriately to sustain resilient ecosystems and adapt our communities to this natural reality.

Inasmuch as people and communities are implicated in the wildfire problem, so, too, are they part of the solution. Federal land-management agencies cannot resolve this crisis alone; we all have a role to play in reducing wildfire risk in the places we live. Stronger collaboration in public and private partnerships, such as those that increase alignment between insurance providers, residents, and local and state governments, could further encourage and incentivize risk-reduction measures at the individual parcel and neighborhood scale.

The Wildfire Partners Program in Boulder County, Colorado, offers a model for an integrated approach to wildfire mitigation. It supports homeowners in reducing risk on their property by local government providing technical and financial support, including individual home assessments, vulnerability reports, and grants to subsidize necessary work, while offering a platform where insurance providers actively engage with homeowners to retain coverage on mitigated homes (17). This interdisciplinary approach builds wildfire resiliency from the bottom up and helps temper the expectation that the federal government is exclusively responsible for community protection.

Wildfire risk is complex, and local context matters. The ability to adapt reflects the realities, resources, and diverse needs of any one community. Effective solutions must account for localized nuance (18). Federal and state administrations can help direct funding, assistance, and technical expertise for wildfire mitigation. Communities with high social vulnerability will likely need additional support.

The recent addendum to the "National Cohesive wildland Fire Management Strategy" (19) specifies an important goal: "Human populations and infrastructure are as prepared as possible to receive, respond to, and recover from wildland fire." Achieving this vision means confronting the failed approach of trying to remove fire from our landscapes. We

Downloaded from https://www.pnas.org by 199.68.205.95 on January 9, 2024 from IP address 199.68.205.95.

must recognize that our communities were developed in a climate and environment that no longer exist. We have the tools and knowledge to reduce community wildfire risks. But we must address the profound and deeply rooted misalignment of political and social expectations regarding what it means to live with wildfire. Now is the time to invest in long-term, economically efficient solutions, rather than short-term, risk-averse tactics.

We have to live with wildland fire. We don't have to live with fire in our communities.

ACKNOWLEDGMENTS. The findings and conclusions in this report are those of the author(s) and should not be construed to represent any official USDA or US Government determination or policy. This research was supported, in part, by the US Department of Agriculture, Forest Service.

Author affiliations: [a]Forestry Science Laboratory, Rocky Mountain Research Station, US Forest Service, Missoula, MT 59807; [b]Headwaters Economics, Bozeman, MT 59715; [c]US Department of Agriculture Forest Service, Missoula, MT 59808; [d]Fire Sciences Laboratory, Rocky Mountain Research Station, US Forest Service, Missoula, MT 59808; [e]Arizona State University, Tempe, AZ 85287; and [f]University of California Cooperative Extension Advisor Emeritus, Mill Valley, CA 94941

1. S. A. Parks, J. T. Abatzoglou, Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985 to 2017. *Geophys. Res. Lett.* **47**, e2020GL089858 (2020).
2. D. E. Calkin, J. D. Cohen, M. A. Finney, M. P. Thompson, How risk management can prevent future wildfire disasters in the wildland-urban interface. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 746–751 (2014).
3. M. P. Thompson, D. G. MacGregor, C. J. Dunn, D. E. Calkin, J. Phipps, Rethinking the wildland fire management system. *J. For.* **116**, 382–390 (2018).
4. A. P. Fischer *et al.*, Wildfire risk as a socioecological pathology. *Front. Ecol. Environ.* **14**, 276–284 (2016).
5. US Department of Agriculture Forest Service, "Confronting the wildfire crisis: A strategy for protecting communities and improving resilience in America's forests" (Tech. Rep., US Government Printing Office, Washington, DC, 2022).
6. US Department of Agriculture Forest Service, Confronting the wildfire crisis: A new strategy for protecting communities and improving resilience in America's forests (2022). https://www.fs.usda.gov/inside-fs/leadership/confronting-wildfire-crisis-new-strategy-protecting-communities-and-improving (accessed 24 August 2023).
7. K. C. Short, Data from "Spatial wildfire occurrence data for the United States (1992–2020)." https://www.fs.usda.gov/rds/archive/catalog/RDS-2013-0009.6 (Accessed 4 December 2023).
8. W. M. Downing, C. J. Dunn, M. P. Thompson, M. D. Caggiano, K. C. Short, Human ignitions on private lands drive USFS cross-boundary wildfire transmission and community impacts in the western US. *Sci. Rep.* **12**, 2624 (2022).
9. J. D. Cohen, Preventing disaster: Home ignitability in the wildland-urban interface. *J. For.* **98**, 15–21 (2000).
10. E. Knapp, Y. Valachovic, S. Quarles, N. Johnson, Housing arrangement and vegetation factors associated with single-family home survival in the 2018 Camp Fire. *Calif. Fire Ecol.* **17**, 25 (2021).
11. A. D. Syphard, T. J. Brennan, J. E. Keeley, The role of defensible space for residential structure protection during wildfires. *Int. J. wildland Fire* **23**, 1165–1175 (2014).
12. S. McCaffrey, R. Wilson, A. Konar, Should I stay or should I go now? Or should I wait and see? *Influences on wildfire evacuations. Risk Anal.* **33**, 1390–1404 (2018).
13. California Governor's Office of Emergency Services, California Wildfire Mitigation Program. https://www.caloes.ca.gov/office-of-the-director/operations/recovery-directorate/hazard-mitigation/california-wildfire-mitigation-program/ (Accessed 4 December 2023).
14. Oregon State Fire Marshal, 2022 community wildfire risk reduction grant application manual. https://www.oregon.gov/osp/programs/sfm/Shared%20Documents/2022%20Community%20Wildfire%20Risk%20Reduction%20Grant%20Application%20Guide%20FINAL.pdf (Accessed 4 December 2023).
15. State of Colorado, Creation of wildfire resilient homes grant program. Colorado HB 23-1273. https://fastdemocracy.com/bill-search/co/2023A/bills/COB00005746/ (Accessed 4 December 2023).
16. D. B. McWethy *et al.*, *Rethinking resilience to wildfire. Nat. Sustain.* **2**, 797–804 (2019).
17. Wildfire Partners Program, Boulder County, CO. https://wildfirepartners.org/ (Accessed 4 December 2023).
18. T. Paveglio *et al.*, Categorizing the social context of the wildland urban interface: Adaptive capacity for wildfire and community "archetypes". *For. Sci.* **61**, 298–310 (2015).
19. Wildland Fire Leadership Council, "National cohesive wildland fire management strategy addendum update" (Tech. Rep., US Department of Agriculture, Washington, DC, 2023). https://forestsandrangelands.gov/documents/strategy/natl-cohesive-wildland-fire-mgmt-strategy-addendum-update-2023.pdf (Accessed 4 December 2023).

Downloaded from https://www.pnas.org by 199.68.205.95 on January 9, 2024 from IP address 199.68.205.95.

Preventing DISASTER

Home Ignitability in the Wildland–Urban Interface

Wildland-urban interface (W-UI) fires are a significant concern for federal, state, and local land management and fire agencies. Research using modeling, experiments, and W-UI case studies indicates that home ignitability during wildland fires depends on the characteristics of the home and its immediate surroundings. These findings have implications for hazard assessment and risk mapping, effective mitigations, and identification of appropriate responsibility for reducing the potential far home lass caused by W-UI fires,

By Jack D. Cohen

Once largely considered a California problem, residential fire losses associated with wildland fires gained national attention in 1985 when 1,400 homes were destroyed nationwide (Laughlin and Page 1987). The wildland fire threat to homes is increasing and is commonly referred to as the wildland—urban interface (W-UI) fire problem. Since 1990, W-UI fires have threatened and destroyed homes in Alaska, Arizona, California, Colorado, Florida, Michigan, New Mexico, New York, and Washington. Extensive or severe fires in Yellowstone in 1988, Oakland in 1991, and Florida in 1998 attracted much media coverage and focused national attention on wildland fire threats to people and property

Federal, state, and local land management and fire agencies must directly and indirectly protect homes from wildfire within and adjacent to wildlands. Davis (1990) indicated that since the mid-1940s, a major population increase has occurred in or adjacent to forests and woodland areas. Increasing residential presence near fire-prone wildlands has prompted agencies to take actions to reduce W-UI fire losses.

When an apparently all-encompassing, seemingly unstoppable W-UI fire occurs, the rapid involvement of many homes over a wide area produces a surreal impression; some homes survive amid the complete destruction of surrounding residences. After the 1993 Laguna Hills fire, some termed this seemingly inexplicable juxtaposition a "miracle.' Miracles aside, the characteristics of the surviving home and its immediate surroundings greatly influenced its survival.

Wildland fire and home ignition research indicates that a home's exterior and site characteristics significantly influence its ignitability and thus its chances for survival. Considering home and site characteristics when designing, building, siting, and maintaining a home can reduce W-UI fire losses.

W-UI Fire Loss Characteristics

W-UI residential fire losses differ from typical residential fire losses. Whereas residential fires usually involve one structure with a partial loss, W-UI fires can result in hundreds of totally destroyed homes. Particularly during severe W-UI fires, numerous

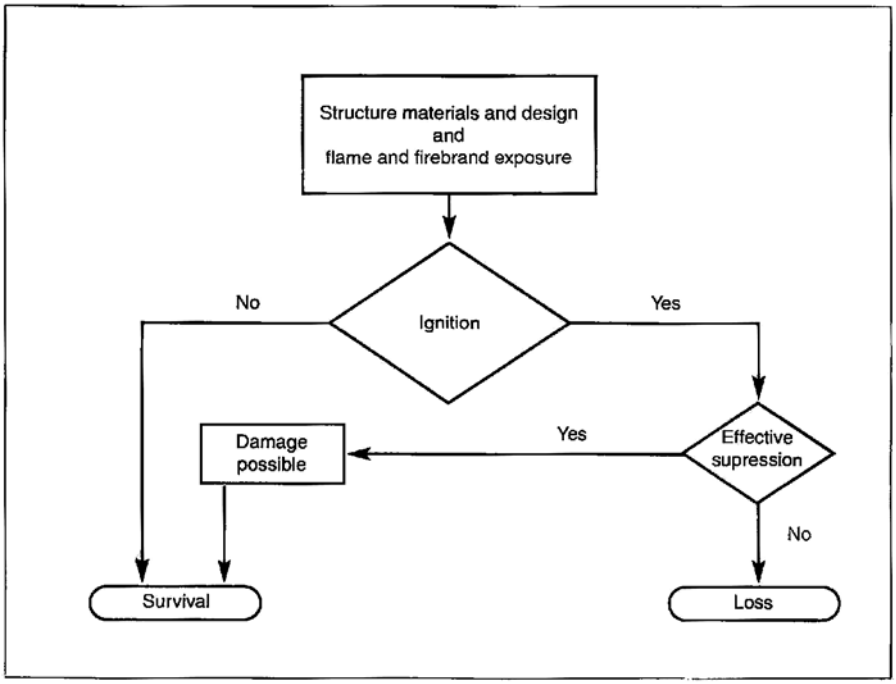


***Figure 1*. The structure survival process**

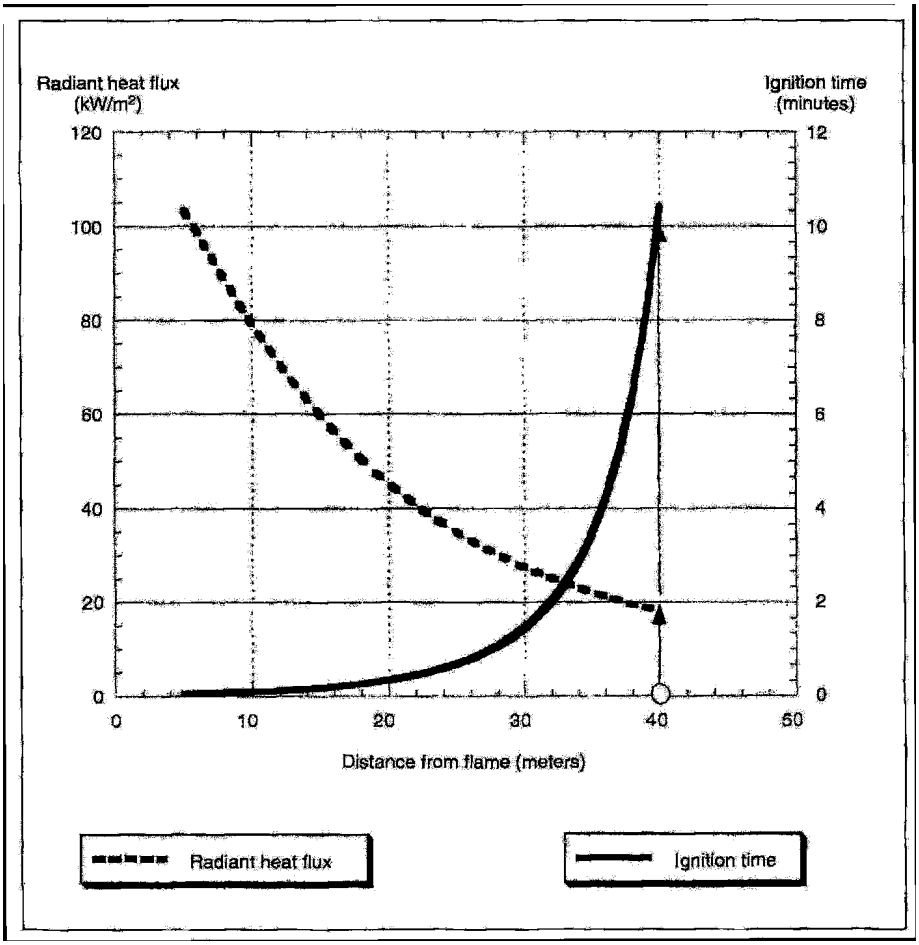


***Figure* 2.The incident radiant heat flux is shown as a function of a wall's distance from a flame 20 meters high by 50 meters wide, uniform, constant, 1,200 K, black-body. The minimum time required for a piloted wood ignition is shown given the corresponding heat flux at that distance.**

homes can ignite in a very short time. The usual result is that a home either survives or is totally destroyed; only a few structures incur partial damage (Foote 1994).

The W-UI Fire commonly originates in wildland fuels. During dry, windy conditions in areas with continuous fine fuels, a wildland fire can spread rapidly, outpacing the initial attack of firefighters. If residences arc nearby, a wildland fire can expose numerous homes to flames and lofted burning embers, or firebrands.

A rapidly spreading wildland fire coupled with highly ignitable homes can cause many homes to burn simultaneously. This multistructure involvement can overwhelm fire protection Capabilities and, in effect, result in unprotected residences. Severe W-UI fires can destroy whole neighborhoods in a few hours—much faster than the response time and suppression capabilities of even the best—equipped and staffed firefighting agencies. For example, 479 homes were destroyed during the 1990 Painted Cave fire in Santa Barbara, most of them within two hours of the initial fire report. The 1993 Laguna Hills fire in southern California ignited and burned nearly all of the 366 homes destroyed in less than five hours.

Whether a home survives depends initially on whether it ignites; if ignitions with continued burning occur, survival then depends on effective fire suppression. *Figure 1* shows that home survival begins with attention to the factors that influence ignition. These factors determine home ignitability and include the structure's exterior materials and design combined with its exposure to flames and firebrands. The lower the home ignitability the lower the chance of incurring an effective ignition.

Ignition: A local Process

Ignition and spread of fire, whether on structures or in wildland vegetation, is a combustion process. Fire spreads as a continuing ignition process whether from the propagation of flames or from the spot ignitions of firebrands. Unlike a flash flood or an avalanche, in which a mass engulfs objects in its path, fire spreads because the requirements for

combustion are satisfied at locations along the path. The basic requirements for combustion—the fire triangle—are fuel, heat, and oxygen. An insufficiency of any one of the three components, which can occur over a relatively short distance, will prevent a specific location from burning. "Green islands" that remain after the passage of a severe, stand-replacement fire demonstrate this phenomenon. Commonly one can find a green, living tree canopy very close to a completely consumed canopy.

The requirements for combustion equally apply to the W-UI fire situation. In the wildland fire context, fire managers commonly refer to vegetation as fuel. However, for the specific context of W-UI residential fire losses, a house becomes the fuel. Heat is supplied by the flames of adjacent burning materials that could include firewood piles, dead and live vegetation, and neighboring structures. Firebrands from upwind fires also supply heat when they collect on a house and adjacent flammable materials. The atmosphere amply supplies the third necessary component, oxygen.

A wildland fire cannot spread to homes unless the homes and their adjacent surroundings meet those combustion requirements. The home ignitability determines whether these requirements are met, regardless of how intensely or fast—spreading distant fires are burning. To use an extreme example, a concrete bunker would not ignite during any wildland fire situation. At the other extreme, some highly ignitable homes have ignited without flames having spread to them. These homes directly ignited from firebrands.

Firebrands are a significant ignition source during W-UI fires, particularly when flammable roofs are involved. Foote (1994) found a significant difference in home survival solely based on roof f1ammability. Homes with nonflammable roofs had a 70 percent survival rate compared with 19 percent for homes with flammable roofs. Davis (1990) reported similar results related to roof flammability.

Reducing W-UI fire losses in the context of home ignitability involves mitigating the fuel and heat components sufficiently to prevent ignitions. However, the question of sufficiency (or efficiency) remains: How much, or perhaps more appropriately, how little fuel and heat reduction must be done to effectively reduce home ignitions? To answer this question, we must first quantify the heat source in terms of the fuel's ignition requirements; specifically, how close can flames be to a home's wood exterior before an ignition occurs?

Research Insights

Diverse research approaches are providing clues for assessing the fuel and heat requirements for residential ignitions. Structure ignition modeling, fire experiments, and W-UI fire case studies indicate that the fuel and heat required for home ignitions only involve the structure and its immediate surroundings—the home ignitability context.

Modeling. The Structure Ignition Assessment Model (SIAM) (Cohen 1995) is currently being developed to asses the potential for structure ignitions from flame exposure and firebrands during W-UI fires. One function of SIAM is to calculate the total heat transferred, both radiation and convection, to a structure for varying flame sizes and from varying distances. From the calculated heat transfer, SIAM calculates the amount of heat over time that common exterior wood products can sustain before the occurrence of a piloted ignition (Tran et al. 1992).

Piloted ignition When wood is sufficiently heated, it decomposes to release combustible volatiles. At a sufficient volatile—air mixture, a small flame or hot spark can ignite it to produce flaming; thus, a piloted ignition.

Based on severe-case assumptions of flame radiation and exposure time, SIAM calculations indicate that wildland flame fronts comparable to crowning and torching trees (flames 20 meters high and 50 meters wide) will not ignite wood surfaces at distances greater than 40 meters (Cohen and Butler, in press). *Figure 2* shows the radiant heat a wall would receive from flames depending on its distance from the fire. The incident radiant heat flux, defined as the rate of radiant energy per unit area received at an exposed surface, decreases as the distance increases.

Figure 2 also shows that the time required for ignition depends on the distance to a flame of a given size. At 40 meters the radiant heat transfer is less than 20 kilowatts per square meter

1 kW/m^2	Maximum for indefinite skin exposure.
10.4 kW/m^2	Pain after three seconds of skin exposure.
16.0 kW/m^2	Second-degree burn after five seconds of skin exposure.

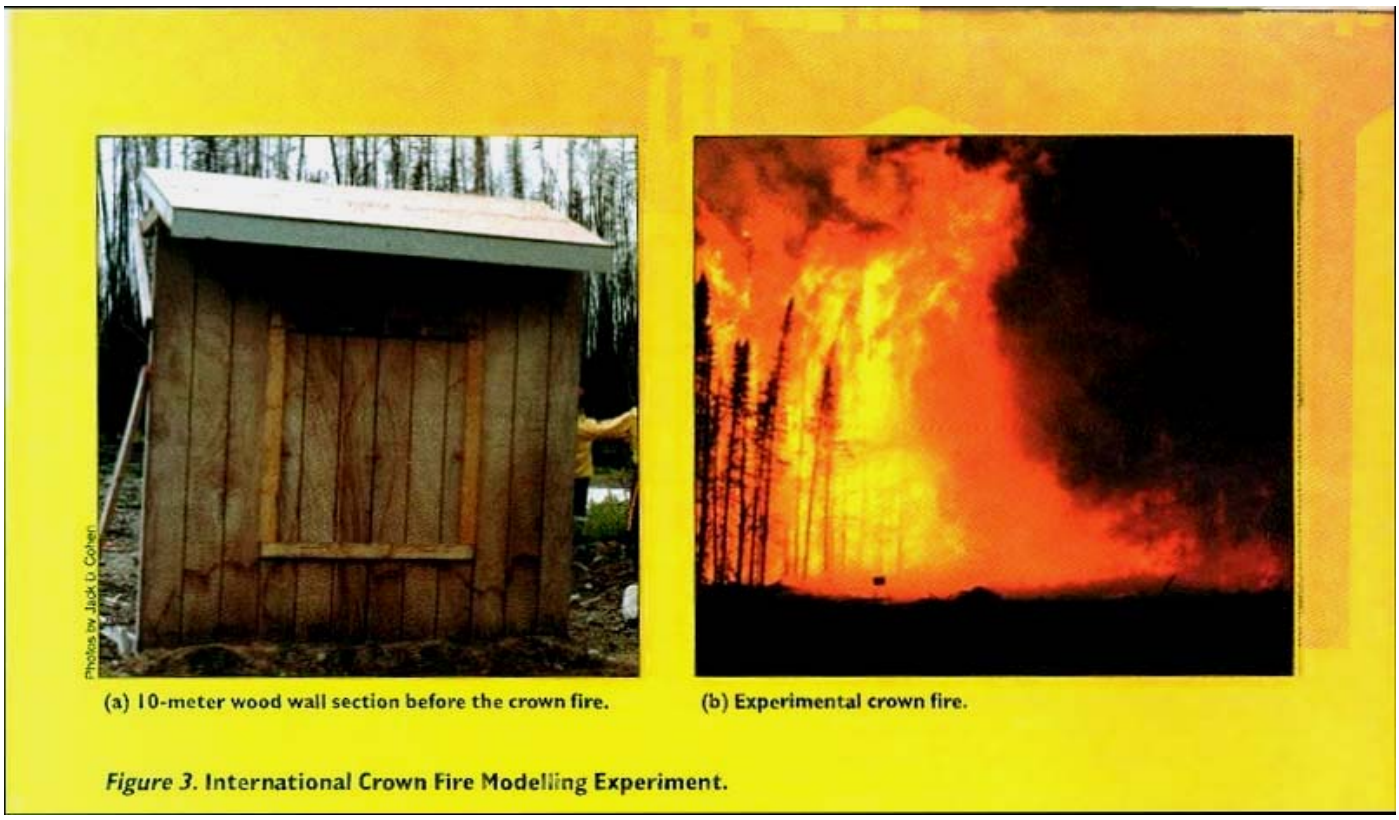
Source: Drysdale 1985.

(kW/m^2), which translates to a minimum piloted ignition time of more than 10 minutes.

Ten minutes, however, is significantly longer than the burning time of wildland flame fronts at a location. Large flames of wildland fires typically depend on fine dead and live vegetation, which limits the intense burning duration at a specific location to less than a few minutes. Recent crown fire experiments have demonstrated a location-specific burning duration of 50 to 70 seconds.

Experiments. Field studies conducted during the International Crown Fire Modelling Experiment (Alexander et al. 1998) provide data for comparisons with SIAM model estimates. Total heat transfer (radiation and convection) and ignition data were obtained from heat flux sensors placed in wooden wall sections.

The instrumented walls were located on flat, cleared terrain at 10, 20, and 30 meters downwind from the edge of the forested plots. The wall section at 10 meters was 2.44 meters wide and 2.44 meters high with a 1.22-meter eave and roof section (*fig. 3a)*. Exterior plywood (T-1-11) covered the wall with oriented-strand board covering the roof section and the eave soffit. Trim boards were solid wood with wood fiber composition board on the cave fascia. None of the materials were treated with fire retardant.



(a) 10-meter wood wall section before the crown fire. (b) Experimental crown fire.

Figure 3. International Crown Fire Modelling Experiment.

The forest was variably composed of an overstory of jack pine *(Pinus banksiana)* about 14 meters high with an understory of black spruce *(Picea mariana).* The spreading crown fire produced flames approximately 20 meters high. *Figures 3b and 3c* show examples of the experimental crown fire.

Five burns were conducted where wall sections were exposed to a spreading crown fire. As the crown fires reached the downwind edge of the plot, turbulent flames extended into the clearing beyond the forest edge. In two of the five burns, flames extended beyond 10 meters to make contact with the 10-meter wall section. When flame contact occurred, the 10-meter walls ignited; however, without flame contact, only scorch occurred, as shown in *figure 3d.* The wooden panels at 20 meters experienced light scorch when flames extended beyond 10 meters from the experimental plot, and no scorch from the other burns. The 30-meter wall section had no scorch from any of the crown fires.

Figure 4 displays the average total incident heat flux (radiation and convection combined) corresponding to the wall at 10 meters *(fig. 3d)* and the crown fire shown in figures *3b and 3c.* The average total incident heat flux is calculated from two sensors placed 1 meter apart in the wall. The amount of heat received by the wall increased as the flame front approached and decreased as the fine vegetation was consumed. The initial heat flux "spike" was caused by a nonuniform crowning flame front.

The flux-time integral shown in *figure 4* indicates whether sufficient heating has occurred to pilot-ignite wood (Tran et al. 992). SIAM uses the flux-time integral for calculating ignition potential, a correlation of the incident heat flux and the time required for piloted wood ignition.

The flux-time correlation identifies two principal ignition criteria: (1) A minimum heat flux of 13 kW/m^2 must occur before a piloted ignition can occur for any exposure time, and (2) piloted ignition depends on attaining a critical heating dosage level (heat transfer and its duration). These criteria are graphed in *figure 4.* The flux-time integral only increases for incident heat fluxes greater than the minimum of 13 kW/m^2, and the flux-time integral threshold value of 11,500 is shown as the ignition threshold. As seen in the figure, the flux-time integral does not reach the ignition threshold, indicating an exposure insufficient for ignition and corresponding to no actual occurrence of a wall ignition. Therefore, a home at some distance from a large flame front, such as a crown fire, may not receive sufficient energy to meet the minimum for ignition over any time period. In addition, a home closer to a large flame front can receive a high heat flux (for example, 46 kW/m^2 as shown in *figure 4*), but without the necessary duration to meet the threshold for ignition.

The flux-time integral plot indicates the duration of the heat transfer relevant to ignition. The heat transfer duration relevant to ignition combines the heat transfer from the approaching crown fire plus the burning time of the fire after it has reached the end of the plot. The observed time required for the flux-time integral to increase from zero to its maximum value corresponds to the heat transfer duration significant for ignition. *Figure 4* indicates a duration of 65 seconds (flux-time plot from 75 seconds to 140 seconds).

Case studies. Case studies of actual W-UI fires provide an independent comparison with SIAM and the crown



(c) Experimental crown fire.

(d) After crown fire exposure the wall scorched but did not ignite. Note the lack of wall scorch under the eave because of the radiation "shading" from the eave.

fire experiments. The actual fires incorporate a wide range of fire exposures. The case studies chosen examine significant factors related to home survival for two fires that destroyed hundreds of structures. The Bel Air fire resulted in 484 homes destroyed (Howard et al. 1973) and the Painted Cave fire destroyed 479 homes (Foote 1994).

Analyses of both fires indicate that home ignitions depend on the characteristics of a structure and its immediate surroundings. Howard et al. (1973) observed 86 percent survival for homes with nonflammable roofs and a clearance of 10 meters or more.

Dicussion

A comparison of the SIAM model calculations in *figure 2* with the observed heat flux from the experimental crown fire in *figure 4* indicated that the model overestimates the heat flux. The model calculation at 10 meters reveals a radiant heat flux of 70 kW/m^2, which exceeds the highest total heat flux of 46 kW/m^2 observed

At the 10-meter wall section in *figure 4*. SIAM calculations

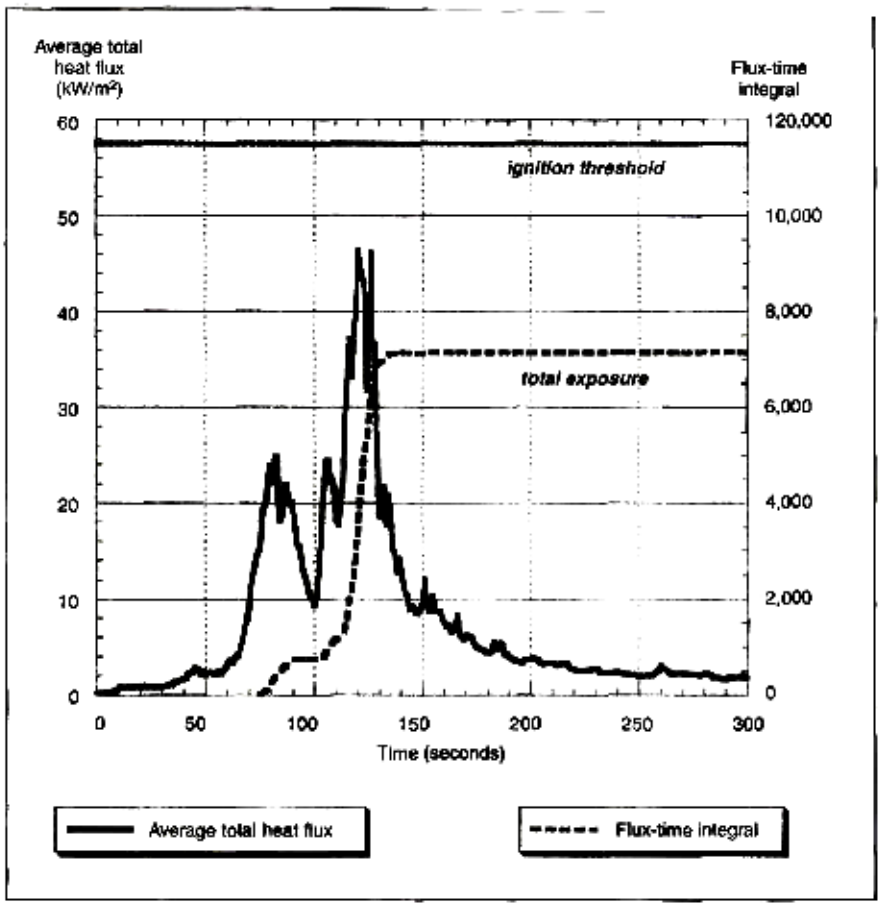


Figure 4. Actual average total incident heat flux and flux-time integral for the crown fire and 10-meter wall section shown in figure 3.

overestimate the heat transfer because the severe-case assumptions designate a homogeneous, black-body radiating flame front. Real flame fronts do not meet these assumptions and produce a significantly smaller radiant heat flux by comparison. For a given flame front, the SIAM calculations represent an extreme-case estimate of radiant heat transfer, and thus an extreme-case estimate of ignition potential.

Given the duration of the experimental heat flux (65 seconds), we can calculate the heat flux and corresponding distance required for ignition. At 65 seconds, the ignition time graph (*fig. 2)* indicates ignition at a flame distance of less than 30 meters. If the heat flux duration is extended by a factor of five to 325 seconds, the flame distance for ignition is less than 40 meters. By comparison, the 10-meter wall sections in the crown fire experiment did not ignite without flame contact and all burns produced little or no scorch to wall sections at 20 and 30 meters. The W-UI fire case studies indicated approximately 90 percent survival with a vegetation clearance on the order of 10 to 20 meters for homes with nonflammable roofs. Thus, the case studies support the general flame-to-structure distance range of 10 to 40 meters as found through modeling and experiments.

However, firebrands can also cause homes to ignite during wildland fires. Although firebrands capable of ignition can originate from a fire several kilometers away, homes can only be threatened if the firebrands ignite the home directly or ignite adjacent flammable materials that then ignite the home.

Analyses of potential home ignitions using modeling, experiments, and case studies did not explicitly address firebrand ignitions. However, firebrand ignitions were implicitly considered because of the firebrand exposures that occurred during the crown fire experiments and the case studies. The experimental crown fires provided a firebrand exposure that resulted in spot ignitions in the dead wood and duff around the wall sections hut not directly on the walls. In the case studies, firebrand ignitions occurred throughout the areas affected by the Bel Air and Painted Cave fires. The high survival rate for homes with nonflammable roofs and 10- to 20-meter vegetation clearances included fire-brands as an ignition factor, thus indicating that firebrand ignitions also depend on the ignition characteristics of the home and the adjacent flammable materials.

Conclusions

The key to reducing W-UI home fire losses is to reduce home ignitability. SIAM modeling, crown fire experiments, and case studies indicate that a home's structural characteristics and its immediate surroundings determine a home's ignition potential in a W-UI fire. Using the model results as guidance with the concurrence of experiments and case studies, we can conclude that home ignitions are nor likely unless flames and firebrand ignitions occur within 40 meters of the structure. This finding indicates that the spatial scale determining home ignitions corresponds more to specific home and community sites than to the landscape scales of wildland fire management. Thus, the W-UI fire loss problem primarily depends on the home and its immediate site.

Consequently if the community or borne site is not considered in reducing W-UI fire losses, extensive wildland fuel reduction will be required. For highly ignitable homes, effective wildland fire actions must riot only prevent fires from burning to home sites, but also eliminate firebrands that would ignite the home and adjacent flammable materials. To eliminate firebrands, wildland fuel reductions would have to prevent firebrand production from wildland fires for a distance of several kilometers away from homes.

Management Implications

Because home ignitability is limited to a home and its immediate surroundings, fire managers can separate the W-UI structure fire loss problem from other landscape-scale fire management issues. The home and its surrounding 40 meters determine home ignitability, home ignitions depend on home ignitability, and fire losses depend on home ignitions. Thus, the W-UI fire loss problem can be defined as a home ignitability issue largely independent of wildland fuel management issues. This conclusion has significant implications for the actions and responsibilities of homeowners and fire agencies, such as defining and locating potential W-UI fire problems (for example, hazard assessment and mapping), identifying appropriate mitigating actions, and determining who must take responsibility for home ignitability

W-UI fire loss potential. Because home ignitions depend on home ignitability, the behavior of wildland fires beyond the home or community site does not necessarily correspond to W-UI home fire loss potential. Homes with low ignitability can survive high-intensity wildland fires, whereas highly ignitable homes can be destroyed during lower-intensity fires.

This conclusion has implications for identifying and mapping W-UI fire problem areas. Applying the term wildland-urban interface to fire losses might suggest that residential fire threat occurs according to a geographic location. In fact, the wildland fire threat to homes is not a function of *where* it happens related to wildlands, but rather to *how* it happens in terms of home ignitability. Therefore, to reliably map the potential for home losses during wildland fires, home ignitability must be the principal mapping characteristic. The home threat information must correspond to the home ignitability spatial scale, that is, those characteristics of a home and its adjacent she within 40 meters.

Home fire loss mitigation. W-UI home losses can be reduced by focusing efforts on homes and their immediate surroundings. At higher densities where neighboring homes may occupy the immediate surroundings, loss reductions may necessarily involve a community. If homes have a sufficiently low home ignitability, a community exposed to a severe wildfire can survive without major fire destruction. Thus, there is a need to examine the reduction of wildland fuel hazard for the specific objective of home protection. There are various land management reasons for conducting wildland vegetation management. However, when considering the use of wildland fuel

hazard reduction specifically for protecting homes, an analysis specific to home ignitability should determine the treatment effectiveness.

Responsibility for home ignitability. If no wildfires or prescribed fires occurred, the wildland fire threat to residential development would not exist. However, our understanding of the fire ecology for most of North America indicates that fire exclusion is neither possible nor desirable. Therefore, homeowners who live in and adjacent to the wildland fire environment most take primary responsibility for ensuring that their homes have sufficiently low home ignitability. Homes should not be considered simply as potential victims of wildland fire, but also as potential participants in the continuation of the fire at their location.

A change needs to take place in the relationship between homeowners and the fire services. Instead of home-related presuppression and fire protection responsibilities residing solely with fire agencies, homeowners must take the principal responsibility for ensuring adequately low home ignitability.

The fire services should become a community partner providing homeowners with technical assistance as well as fire response in a strategy of assisted and managed community self-sufficiency (Cohen and Saveland 1997). For this approach to succeed, it must be shared and implemented equally by homeowners and the fire services.

Literature Cited

ALLXANDER, M.E., B.J. STOCKS, B.M. WOTTON, M.D. FLANNIGAN, J.B. TODD, B.W. BUTLER, and R.A. LANOV1LLE. 1998. The International Crown Fire Modelling Experiment: An overview and progress report. *In Proceedings of the Second Symposium on Fire and Forest Meteorology*, 20-23. Boston: American Meteorological Society.

COHEN, J.D. 1995. Structure ignition assessment model (SIAM). In *Proceedings of Biswell Symposium: Fire Issues and Solutions in Urban Interface and Wildland Ecosystems*, 85-92. General Technical Report PSW-158. Albany, CA: USDA Forest Service, Pacific Southwest Research Station.

COHEN, J.D., and B.W. BUTLER. In press. Modeling potential ignitions from flame radiation exposure with implications for wildland/urban interface fire management. In *Proceedings of the 13th Conference on Fire and Forest Meteorology*. Fairfield, WA: International Association of Wildland Fire.

COHEN, J., and J. SAVELAND. 1997. Structure ignition assessment can help reduce fire damages in the W-UI. *Fire Management Notes* 57(4):19-23.

DAVIS, J.B. 1990. The wildland-urban interface: Paradise or battleground? *Journal of Forestry* 88(1):26-31.

DRYSDALE, D. 1985. *An introduction to fire dynamics*. New York: John Wiley & Sons.

FOOTE, E.I.D. 1994. Structure survival on the 1990 Santa Barbara "Paint" fire: A retrospective study of urban-wildland interface fire hazard mitigation factors. MS thesis, University of California at Berkeley.

HOWARD, R.A., D.W. NORTH, F.L. OFFENSEND, and C.N. SMART. 1973. Decision analysis of fire protection strategy for the Santa Monica mountains: An initial assessment (on file). Menlo Park, CA: Stanford Research Institute.

LAUGHLIN, J., and C. PAGE, eds. 1987. *Wildfire strikes home! Report of the national wildland/urban fire protection conference.* NFPA SPP-86. Quincy, MA: National Fire Protection Association.

TRAN, H.C., J.D. COHEN, and R.A. CHASE. 1992. Modeling ignition of structures in wildland/urban interface fires. In *Proceedings of the First International Fire and Material Conference*, 253-62. London: Inter Science Communications Limited.

Jack D. Cohen (e-mail: jcohen/rmrs_missoula @fs.fed.us) is research physical scientist, USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laborator, PO Box 8089, Missoula, MT 59808.

Wildfire Policy and Public Lands: Integrating Scientific Understanding with Social Concerns across Landscapes

MICHAEL P. DOMBECK,* JACK E. WILLIAMS,† AND CHRISTOPHER A. WOOD‡

*College of Natural Resources, University of Wisconsin–Stevens Point, Stevens Point, WI 54481, U.S.A., email mike.dombeck@uwsp.edu
†The AuCoin Institute, Southern Oregon University, 1250 Siskiyou Boulevard, Ashland, OR 97520, U.S.A.
‡Trout Unlimited, 1300 North 17th Street, Suite 500, Arlington, VA 22209, U.S.A.

Abstract: *Efforts to suppress wildfires have become increasingly problematic in recent years as costs have risen, threats to firefighter safety have escalated, and detrimental impacts to ecosystems have multiplied. Wildfires that escape initial suppression often expand into large, high-intensity summer blazes. Lost is the legacy of smaller fires that likely burned outside extreme weather and fuel conditions and resulted in less severe impacts. Despite the recognized need for modifications to existing policies and practices, resource agencies have been slow to respond. The spread of exotic species, climate change, and increasing human development in wildlands further complicates the issue. New policies are needed that integrate social and ecological needs across administrative boundaries and broad landscapes. These policies should promote a continuum of treatments with active management and reduction of fuel hazard in wildland-urban interface zones and reintroduction of fire in wildlands. Management goals should focus on restoration of the long-term ecological health of the land. Projects that reduce fuel loads but compromise the integrity of soil, water supplies, or watersheds will do more harm than good in the long run. Despite significant ecological concerns, learning to live with fire remains primarily a social issue that will require greater political leadership, agency innovation, public involvement, and community responsibility.*

Key Words: forest management, U.S. Forest Service, policy, public lands, wildfire

Políticas para Fuegos No Controlados y Tierras Públicas: Integrando el Conocimiento Científico con los Intereses Sociales en Paisajes

Resumen: *En años recientes, los esfuerzos para suprimir los fuegos no controlados se han vuelto cada vez más problemáticos por el incremento de costos, el aumento de las amenazas a la seguridad de bomberos y se la multiplicioń de los impactos perjudiciales a los ecosistemas. Los incendios que escapan la supresión inicial a menudo se expanden a grandes conflagraciones estivales de alta intensidad. Se ha perdido el legado de fuegos menores que probablemente se llevaban a cabo en condiciones climáticas y de combustible extremas que tenían impactos menos severos. A pesar del reconocimiento de la necesidad de modificaciones a las políticas y prácticas actuales, las agencias han respondido lentamente. La expansión de especies exóticas, el cambio climático y el incremento del desarrollo humano en áreas silvestres complican el problema aún más. Se requieren políticas nuevas que integren necesidades sociales y ecológicas más allá de límites administrativos y en paisajes amplios. Estas políticas deben promover un continuo de tratamientos con gestión activa y reducción de riesgo de combustión en la interfase área silvestre-urbana y la reintroducción de fuego en áreas silvestres. Las metas de la gestión deben enfocar en la restauración de la salud ecológica a largo plazo. Los proyectos que reducen la carga de combustible pero que comprometen la integridad del suelo, las reservas de agua o cuencas hidrológicas no serán de mucha utilidad en el largo plazo. A pesar de preocupaciones ecológicas*

Paper submitted October 28, 2003; revised manuscript accepted December 16, 2003.

significativas, aprender a vivir con fuego seguirá siendo un aspecto social que requerirá de mayor liderazgo político, innovación de agencias, participación del público y responsabilidad comunitaria.

Palabras Clave: administración de bosques, fuego no controlado, política, Servicio Forestal Estados Unidos, tierras públicas

How Wildfire Defines Policy: Historical Review

The history of wildfire in the United States and our attempts to control it contain many lessons to guide future policies for management of public and private lands. Destructive fires that ravaged the West and Midwest in the late 1800s and early 1900s led to federal policy declaring that all wildfire is bad. Wildfire was viewed as a destructive force that must be contained. Following World War II, this goal of suppressing all wildfires nearly became a reality with the availability of scores of firefighters, heavy construction equipment, smoke jumpers, and aerial tankers. Agencies seemed to be winning the war against wildfire, contributing to the illusion that all wildfire could be excluded from the land. The Yellowstone Fires of 1988, however, served to remind us of the unpredictability and occasional futility of our fire-control policies. Seemingly catastrophic wildfire seasons in recent years have reinforced the contention that a new approach to wildfire is needed.

Much of our western landscape evolved with wildfire and depends on this natural process to recycle nutrients, improve soil productivity, start plant succession processes, and contribute to overall watershed health. Our zealous efforts to suppress wildfire have diminished these ecological functions and altered fire regimes across much of the West (Agee 1993, 1997). Agencies and the scientific community have made progress in recognizing what ails our forests and grasslands, but our legacy of treating fire as a dangerous and destructive force has made agencies slow to translate improved scientific understanding into on-the-ground management changes. As a result, half the year is spent in widespread talk about the need to reintroduce fire into fire-adapted ecosystems, but the other half of the year is spent suppressing all wildfire at substantial economic cost. The federal fire bureaucracy spends hundreds of millions of dollars annually on wildfire suppression, more than a billion dollars in a "bad" fire year, with little oversight or accountability (General Accounting Office [GAO] 1999, 2001).

The years from 1871 to 1910 reshaped public opinion on wildfire. At that time, fire was used to clear land for agriculture or to drive wildlife, or was inadvertently started along railroads. By the late 1800s, the combination of drought and slash left behind by logging began producing large and uncontrollable wildfires. The 1871 Peshtigo Fire in northeastern Wisconsin, in which some 1500 people died and more than 486,000 ha burned, remains the single most tragic wildfire in our history (Pyne 1982). Fires in Michigan, again the legacy of timber cutting, burned another 1.0 million ha that same year (Pyne 1982). Forest cover was destroyed and topsoil turned to ashes or washed away once the forests were burned. The land lost its ability to dampen floods or temper drought. Watershed function—the basic ability to catch, store, and release water over time—was lost across broad landscapes. By 1900, 32 million ha of charred and decimated stump lands lay east of the Mississippi.

The West was not far behind. The year 1910, the year of the Great Fires, created the foundation for how federal agencies would relate to wildfire (Pyne 2001). The U.S. Department of Agriculture Forest Service (USFS), founded only 5 years earlier, was a fledgling agency with few resources. A combination of slash-and-burn forestry, expanding railroads, drought, and wind caused more than 2.0 million ha to burn that year across the West, mostly in Idaho and Montana. Seventy-eight firefighters died, numerous civilians perished, and several towns burned to the ground. Ultimately, the U.S. Army was called in to fight fires throughout the West. The destructive fires of 1910 led the federal government to declare war on wildfires. The USFS responded with military-like zeal and declared fire suppression its primary charge. Leaders in the agency believed that the only solution to fires was "the full-scale development of the forests with roads, trails, telephone lines, lookout towers, and a resident staff sufficient to patrol and attack fires while they were small" (Pyne 2001). By 1935 the "all fires out by 10 AM" policy was formally adopted (Pyne 1982). By the 1940s, the USFS had developed the most effective wildfire-fighting capability in the world. As a result of this early and widespread intervention in wildfire, we lost the legacy of many smaller fires that were likely to have burned at lesser intensities.

Smokey Bear and his slogan—"Remember, only you can prevent forest fires."—was perhaps the most successful public awareness campaign ever. In 1968 a national advertising company noted that Smokey was the most popular symbol in the United States, better known than the president (Pyne 1982). The perception that all wildfire is bad became universal. The National Interagency Fire Center was established in Boise, Idaho, in the 1960s as the wildfire-fighting command center and soon became a model of government interagency cooperation.

In 2000 wildfires were front-page news from May to September, starting with the loss of over 200 homes in the Cerro Grande Fire in Los Alamos, New Mexico, and

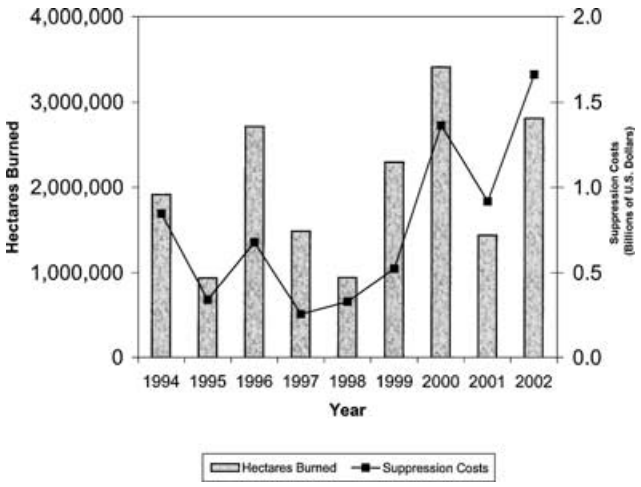


Figure 1. Hectares burned in the United States and wildfire suppression costs for federal agencies, 1994–2002. Data from National Interagency Fire Center (2003).

continuing with multiple large fires in Montana and Idaho. The years 1988, 1994, 2000, and 2002 were clarion calls that society's century-long attempt to control fire in the fire-adapted ecosystems of the West was not working. With advanced technology and an army of firefighters, 98% of wildfires are typically snuffed out in the initial attack. In spite of this extraordinary "success," the total amount of the landscape burned each year has increased in recent decades compared with the mid-1900s (Agee 1997), and more than 2.5 million ha burned each year in 1963, 1969, 1988, 1996, 2000, and 2002 (an average of 1.6 million ha has burned each year between 1960 and 2002) (National Interagency Fire Center 2003). The costs of wildfire suppression have risen in recent years as more land has burned (Fig. 1). More than $1 billion was spent in 2000 and 2002 by federal agencies (National Park Service, Fish and Wildlife Service, Bureau of Indian Affairs, Bureau of Land Management, and Forest Service) fighting fires on public lands. Clearly this is an economic burden that cannot continue indefinitely, especially for federal land-management agencies that are otherwise underfunded for basic resource inventory, monitoring, and management.

For nearly a century, the widespread suppression of fire and other factors, such as livestock grazing, past timber harvest practices, and other human activities, have resulted in altered ecosystems and more broad-scale wildfires during dry years. In many cases, it is our interruption of natural processes that reduces the ability of the land to heal itself, resulting in even more serious problems. Scientific assessments indicate that in the Interior Columbia River Basin, prior to European settlement, about 2.4 million ha burned per year (Hann et al. 1997). With recent intense fire suppression, less than 203,000 ha has burned each year (Hann et al. 1997). In spite of a century of fire suppression, we have learned that the question is not if forests will burn but when, where, and with what intensity.

Challenges of Natural Complexity, Exotic Species, and Suburban Sprawl

For agency policies concerning wildfire to be effective in the long term, they must be specific to local forest conditions and adaptable to new information about the natural environment and to changing social concerns. The spread of exotic species is a good example of the need for policies to adapt to changing situations. The Department of the Interior estimates that noxious weeds spread at a rate of 688,500 ha annually (Bureau of Land Management 1996). Exotic grasses, noxious weeds, and other alien species are among the greatest threats now facing the integrity of public lands (Dombeck et al. 2003).

If their seeds or spores are present, exotic species will thrive and spread, complicating fire-suppression activity. Fire engines, bulldozers, or other vehicles may spread exotic species as well (Backer et al. 2004). Federal agency wildfire policies, management actions, and research on wildfire must respond to such threats from exotic species. For example, burn-area emergency rehabilitation efforts should recognize that grass seeding for erosion control often degrades native species recovery and that long-term damage to ecosystems often overshadows short-term gain in soil stabilization (Beyers 2004 [this issue]). Even the use of "certified weed-free hay" for erosion control may be suspect when the amount free of weeds is only 95% or even 99%. The use of weed-free hay on post-fire recovery efforts in the Klamath National Forest resulted in the introduction and spread of exotic yellow starthistle (*Centaurea solstitialis* L.) on forest lands (J. Perkins, personal communication). During the massive Biscuit Fire in 2002, the USFS required that equipment be power-washed or rinsed with chlorine-treated water to prevent Port-Orford Cedar root disease, which is spread by water or mud contaminated with exotic *Phytophthora* spores. This is a good example of how federal agencies can and should apply ecologically sound management even during emergency wildfire situations.

Wildfire suppression, introduction of exotic species, livestock grazing, timber harvest practices, and replanting cutover lands with dense conifer plantations have changed fuel loads and fire regimes in many western forests and grasslands. A recent broad-scale assessment of national forest lands and land administered by the Bureau of Land Management (BLM) in the Interior Columbia River Basin documented a 25% increase in young trees in dry forest types such as ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and dry grand fir (*Abies grandis* [Dougl.] Lindl.)–white fir (*A. concolor* Gord. & Glend.)

associations in Idaho and western Montana (Hann et al. 1997). The assessment also found that ponderosa pine has been replaced by grand fir and white fir in 19% of its range and by Douglas-fir (*Pseudotsuga menziesii* Mirb.) in another 20%. Open, park-like stands of ponderosa pine were estimated to be at 25% of their historic range, whereas Douglas-fir and true firs had more than tripled their range (Hann et al. 1997). Overall, the assessment concluded that 46% of National Forest and BLM forestlands in Idaho, western Montana, eastern Washington, and eastern Oregon were at a low rating for overall ecological integrity. Most private lands in the region are in even worse condition. Of the lands classified in the report as low in ecological integrity, 61% occur outside of federal management (Quigley & Arbelbide 1997).

By the 1990s, the complexity and patchiness of many fire-adapted forest ecosystems were greatly diminished. Young Douglas-fir, grand fir, and other species formerly controlled by small fires were growing in large numbers. The meadows were disappearing, and the remaining large pines were surrounded by smaller trees that competed for water during droughts and provided "ladder fuels" that allowed fire to reach upper branches to torch and kill trees. The GAO (1999) reviewed the status of western forests and concluded that the over-accumulation of trees presented a severe wildfire risk to approximately 16 million ha in the Intermountain West.

Some forests have naturally high fuel loads and a history of stand-replacing wildfires that burn at high intensity (Agee 1993). Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forests in the West, for example, require high-intensity fires to reseed and restore themselves. Other forests, occurring for example in the Klamath-Siskiyou region of northwest California and southwest Oregon, are characterized by fires that burn at mixed intensities (Odion et al. 2004 [this issue]). Forests characterized by high- or mixed-intensity fires present special concerns that cannot be addressed simply by policies that seek to reduce tree densities or fuel loads.

Wildfires that burned in Oregon's Siskiyou National Forest during 2001 and 2002 illustrate this complex dilemma. In September 2001, lightning started the Craggie fire in the Kalmiopsis Wilderness. The fire was in extremely rugged terrain and posed no threat to structures. The 39,000-ha Silver fire had burned the same area in 1987, and other large fires were known from the same area in 1938 and the summers of 1917 and 1918 (T. Atzet, personal communication). Rather than being allowed to burn, the Craggie fire was immediately attacked by aerial tankers and helicopters. By the time it was controlled, 111 ha had burned with a suppression cost of $2.2 million. Forest Service policy dictated that the fire be attacked and controlled because of dry conditions and high fuel loads despite the shorter days of mid-September and the onset of cooler and moister weather. To some, allowing the Craggie fire to burn might have seemed risky. But the alternative is a fire in some future year that occurs in the middle of summer with even more fuel present.

This is precisely what happened in 2002. In July of that year, during a hot, dry summer, lightning started a series of fires in Oregon, including several in and around the Kalmiopsis Wilderness. Because of the large number of fires burning at that time, no firefighters were available to fight the Kalmiopsis fires for the first 4 days. In the dry, rugged terrain and hot weather, the wildfires grew rapidly. In August, several fires around the Kalmiopsis combined to form the Biscuit fire and spread to 116,000 ha with more than 2000 firefighters on the lines. By the time the Biscuit fire was contained in September, fire had swept across nearly 203,000 ha despite thousands of firefighters, dozens of bulldozers, and many air tankers. Firefighting costs reached $150 million, making this the most expensive fire fought in the nearly 100-year history of the USFS, even more expensive than the previous record, the Yellowstone fires of 1988, which cost $120 million to suppress. The costs of such massive firefighting efforts are not just high in terms of dollars, but also in terms of firefighter safety, damage caused by bulldozers to fragile soils and sensitive botanical areas, and the potential for spread of exotic organisms by firefighting equipment.

In spite of the impression created by media reports that the Biscuit fire destroyed the forest, the fire burned in a classic mosaic pattern across the landscape. This benefits many ecosystem functions and restores habitat diversity. According to burn-area emergency rehabilitation surveys by the USFS, approximately 16% of the area burned at high severity, 23% at moderate severity, and 41% at low severity, and 20% was unburned or burned at very low severity (Siskiyou & Six Rivers National Forests 2002). According to the report, 70% of the area that burned at high severity contained enough surface rock to protect soil against accelerated erosion. In the long run, restoration of fire will occur in one form or another. How fire returns to these fire-adapted ecosystems is the question.

An expanding human population, especially in western states, is the single greatest factor confounding federal fire-management policies. Nearly all western states are growing faster than the national average. According to the U.S. Census Bureau, population increased 13.2% nationally from 1990 to 2000 but increased 28.5% in Idaho, 29.6% in Utah, 30.6% in Colorado, 40.0% in Arizona, and 66.3% in Nevada during this same period. Much of this growth occurred as urban areas sprawled into surrounding wildlands. Only two western states, Montana (12.9% increase) and Wyoming (8.9%), fell below that national average.

With an increase in home construction along wildland boundaries and private inholdings within national forests and BLM public lands, federal agencies are focusing more of their firefighting efforts on protecting human lives and property. But in the debates that followed the intense fire seasons of 2000 and 2002, too little discussion focused

on the central issue of homeowners assuming more responsibility for reducing the vulnerability of their homes to wildfire by building with fire-resistant materials and storing flammable materials away from structures. In the western United States, few communities or local governments have enacted zoning requirements to guide the growth of homes along the wildland-urban interface or building requirements to reduce the flammability of structures. And insurance companies do not require "fire-wise" practices as a condition of insurability.

Toward Policies that Reflect Ecological and Social Needs

The magnitude of the fires in 2000 and a 1999 GAO report on the need for a cohesive strategy for wildfires resulted in development of the National Fire Plan and associated fire-management policies by the USFS, National Park Service, U.S. Fish and Wildlife Service, BLM, Bureau of Indian Affairs, and National Association of State Foresters. The National Fire Plan, developed in 2000, spelled out a $10-billion effort over a 10-year period to protect communities and restore healthy forests in fire-adapted ecosystems (USFS 2000). In 2002 President Bush's Healthy Forests Initiative called for modifications to the National Fire Plan that would expedite fuel-reduction projects by reducing environmental impact analysis, public involvement, and appeals and litigation associated with the National Environmental Policy Act (Office of the President 2002).

Most ecologists and agency administrators agree that reducing the levels of hazardous fuels on forests and rangelands is essential to protect adjacent human communities and to restore healthy watersheds. The agreement ends here, as some in the timber industry call for aggressive logging to restore forests and the environmental community decries such a rationale as simply another way to increase timber cutting. The public land manager walks a fine line. Even the most well-reasoned decisions often result in criticism.

The priority for fuels management should be places where forests and communities intersect, such as wildland-urban interface zones and watersheds that supply municipal drinking water. If such areas contain uncharacteristically high fuel loads, projects that thin small trees and remove brush followed by the careful use of prescribed fire should be welcomed by a broad cross-section of interests. On the other hand, building roads and cutting trees in remote roadless areas far from human communities makes neither ecologic nor economic sense (DellaSala & Frost 2001).

Local communities need to shoulder greater responsibility for regulating sprawl and for encouraging proactive efforts by homeowners to reduce the risk of home ignition during wildfire. In remote or inaccessible wildlands, wildfires should be closely monitored but allowed to burn if outside of extreme summer weather and not threatening to human communities. In roaded and previously logged areas that are not part of the wildland-urban interface, management should focus on utilizing fire processes at a low risk—under acceptable weather conditions and fuel loads—and thinning small-diameter materials as prescribed by the local management context and to restore the health and integrity of the land. Meanwhile, fire programs of federal agencies should focus the overwhelming majority of their hazardous-fuels reduction and suppression efforts on protecting lives and property in the areas where forests and communities meet, including efforts to help landowners reduce fire risk in the immediate vicinity of their homes. Such an approach would help restore natural fire cycles in remote places, save tens of millions of dollars, and, above all, minimize risks to firefighters.

This is not to say that a let-it-burn philosophy should prevail in all areas. The challenge is to put fire back on the land in a way that minimizes the risk to people and communities while mimicking natural fire regimes to the extent possible. We should allow what would have historically been the smaller wildfires to burn, including those that naturally start early or late in the fire season when weather can moderate fire intensity. Many forests evolved with fire and indeed need fire for healthy development. The complicating factor is increasing human population. The sprawl of housing developments in rural areas, foothills, and even on mountainsides is occurring all over the country, especially in fire-prone areas such as California and the Intermountain West. Making matters worse, many homeowners fail to take steps to protect their homes and lives such as avoiding flammable wood roofs and cedar siding, keeping woodpiles away from the home, clearing vegetation adjacent to the house, and other common-sense precautions (Cohen 2000). The most important factors determining whether a building will burn during a wildfire are the degree of flammability of construction materials and fuels within 40 m of buildings (Cohen 1999, 2000). People who build homes in fire-adapted landscapes must assume responsibility for reducing fuels and the ignitability of buildings and the immediate space around their homes. Local government zoning ordinances should take into account fire-prone areas as they already do for flood-prone areas.

Traditional organizational structures and appropriations make increased interagency coordination of wildfire management difficult (GAO 2001). Nonetheless, reducing wildfire risk while restoring healthy watersheds will require a new level of coordination among federal agencies, state governments, and the public. Substantial interagency cooperation has been achieved in fire suppression through the National Interagency Fire Center in Boise, Idaho. It is time that similar levels of cooperation be developed for wildfire reintroduction through careful monitoring of wildfires in roadless and wilderness areas and expanded but judicious use of prescribed fire. Public

Table 1. Recommended principles and rationales for developing wildfire policies that meet ecological and social needs.

Principle	*Rationale*
Integrate policies across both private and public lands.	Wildfires know no boundaries.
Strengthen coordination across agencies and communities for wildfire introduction.	Interagency coordination has improved wildfire suppression, and the same coordination is needed to reintroduce wildfire successfully.
Develop a continuum of priorities and actions between urban and wildland environments.	Meeting social concerns through more active management is appropriate in urban areas, whereas meeting ecological needs is more important in wildland areas
Strengthen homeowner education to reduce ignitability of their homes.	Home characteristics and vegetation within 40 m of structures principally determine potential for home ignition during extreme wildfires.
Value forest diversity and variability in historic fire regimes.	The substantial variation in plant communities, fuel loading, and fire regimes must be recognized to maintain and restore diversity.
Wildland policies should emphasize ecosystem resilience rather than fire control.	Wildfire is critical to maintaining the diversity and productivity of many natural communities.
Encourage reintroduction of ecologically appropriate fire where possible.	Historic fire regimes should be reestablished except where development densities dictate alternate approaches.
Ensure monitoring, evaluation, and public involvement in fire management policy.	Adaptive management is needed to address natural complexity and change; increased public involvement is needed to foster understanding and public trust

participation in the process should be strengthened, not weakened, in order to build trust and integrate the concerns of communities. New relationships must be forged across disciplines and administrative boundaries to successfully implement policies and plans. Some preliminary principles for developing ecologically and socially responsible wildfire policies are presented in Table 1.

It is important that wildfire policies be well founded in ecological principles. It will do little good in the long run if projects that reduce fuel loads compromise the basic integrity of soils, water supplies, or watersheds. Fuel management should be part of a broader strategy of restoring watershed health rather than designed solely on the basis of fuels. As important as ecological principles are, however, living with fire largely remains a social issue that will require greater agency leadership and community responsibility.

Although government agencies and land managers tend to be adverse to risk, leadership must support innovation and adaptive management to achieve success. To avoid risk in wildfire management today is to advocate even larger uncontrolled wildfires with greater threat to human life, property, and ecosystems in the future. Neither thinning nor extensive logging will fire-proof our forests. Planning in fire-adapted ecosystems requires an understanding of local forest type, fire history, potential fire behavior, past management actions, land-use changes, watershed needs, species viability, and relative risk to human communities (USFS 2000). Uncertainty associated with these factors can best be addressed through adaptive management—the process of monitoring, evaluating, and making changes to management based on monitoring results. Acceptance of risk taking or the need to change management direction is a difficult pill to swallow in many agencies. Changing these agency cultures and public attitudes will be among the greatest hurdles to effective wildfire policy.

Acknowledgments

We greatly appreciate the comments of J. Cohen, D. DellaSala, and J. Furnish on earlier drafts of this manuscript. J. McGinley kindly prepared the figure.

Literature Cited

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Agee, J. K. 1997. Fire management for the 21st century. Pages 191–201 in K. A. Kohm and J. F. Franklin, editors, Creating a forestry for the 21st century. Island Press, Washington, D.C.

Backer, D. M., S. E. Jensen, and G. R. McPherson. 2004. Impacts of fire-suppression activities on natural communities. Conservation Biology **18:**937–946.

Beyers, J. L. 2004. Postfire seeding for erosion control: effectiveness and impacts on native plant communities. Conservation Biology **18:**947–956.

Bureau of Land Management (BLM). 1996. Partners against weeds: an action plan for the Bureau of Land Management. BLM, Billings, Montana.

Cohen, J. D. 1999. Reducing the wildfire fire threat to homes: where and how much? General technical report PSW-GTR-173. U.S. Forest Service, Albany, California.

Cohen, J. D. 2000. Preventing disaster: home ignitability in the wildland-urban Interface. Journal of Forestry **98(3):**15–21.

DellaSala, D. A., and E. Frost. 2001. An ecologically based strategy for fire and fuels management in national forest roadless areas. Fire Management Today **61(2):**12–23.

Dombeck, M. P., C. A. Wood, and J. E. Williams. 2003. From conquest to conservation: our public lands legacy. Island Press, Washington, D.C.

General Accounting Office (GAO). 1999. Western national forests: a

cohesive strategy is needed to address catastrophic wildland fire threats. Report GAO/RCED–99–65. GAO, Washington, D.C.

General Accounting Office (GAO). 2001. The National Fire Plan: federal agencies are not organized to effectively and efficiently implement the plan. Report GAO–01–1022T. GAO, Washington, D.C.

Hann, W. J., et al. 1997. Landscape dynamics of the basin. Pages 337–1057 in T. M. Quigley and S. J. Arbelbide, technical editors. An assessment of ecosystem components in the Interior Columbia Basin and portions of the Klamath and Great Basins. General technical report PNW-GTR-405. U.S. Forest Service, Portland, Oregon.

National Interagency Fire Center (NIFC). 2003. Wildland fire statistics. NIFC, Boise, Idaho. Available from www.nifc.gov/stats/wildlandfirestats.html (accessed May 2004).

Odion, D. C., E. J. Frost, J. R. Strittholt, H. Jiang, D. A. DellaSala, and M.A. Moritz. 2004. Patterns of fire severity and forest conditions in the Western Klamath Mountains, California. Conservation Biology **18:**927–936.

Office of the President. 2002. Healthy forests: an initiative for wildfire prevention and stronger communities. Office of the President, Washington, D.C. Available from www.fireplan.gov/(accessed August 2003).

Pyne, S. J. 1982. Fire in America: a cultural history of wildland and rural fire. Princeton University Press, Princeton, New Jersey.

Pyne, S. J. 2001. Year of the fires: the story of the Great Fires of 1910. Viking Publishers, New York.

Quigley, T. M., and S. J. Arbelbide, technical editors. 1997. An assessment of ecosystem components in the Interior Columbia River Basin and portions of the Klamath and Great Basins. General technical report PNW-GTR-405. U.S. Department of Agriculture Forest Service, Portland, Oregon.

Siskiyou and Six Rivers National Forests. 2002. Biscuit Fire Burn Area Emergency Rehabilitation report. U.S. Forest Service, Medford, Oregon. Available online from www.biscuitfire.com/baer_index.htm (accessed May 2004).

U.S. Department of Agriculture Forest Service (USFS). 2000. National Fire Plan: managing the impact of wildfires on communities and the environment. USFS, Washington, D.C. Available from www.fireplan.gov/ (accessed May 2004).



Response to Comments on "Post-Wildfire Logging Hinders Regeneration and Increases Fire Risk"

D. C. Donato,[1]* J. B. Fontaine,[2] J. L. Campbell,[1] W. D. Robinson,[2] J. B. Kauffman,[3] B. E. Law[1]

We reported that postfire logging 2 to 3 years after the 2002 Biscuit Fire was associated with significant mortality in natural conifer regeneration and elevated potential fire behavior in the short term as a result of increased surface fuel loads. We underscore the strength of our study design and statistical conclusions, provide additional details of the research setting and scope, and address comments pertinent to forest development and fire ecology.

Although Newton *et al*. (*1*) and Baird (*2*) provide no compelling evidence to refute our findings, we are pleased with the opportunity for dialogue and to expand on our article (*3*). We respond by underscoring the strength of our study design, providing additional details of the research setting and scope, and addressing comments pertinent to forest development and fire ecology.

Study background. We reported that postfire logging (salvage) 2 to 3 years after the 2002 Biscuit Fire was associated with significant mortality in natural conifer regeneration and elevated potential fire behavior in the short term due to increased surface fuel loads (*3*). Our study design has robust inferential power (*4*), and the data strongly support these straightforward conclusions, as verified by independent statistical evaluations (*5*, *6*).

Our scope of inference (*3*) is the salvage of the Biscuit Fire [see (*4*) for study details]. Areas sampled were typical of portions of the Biscuit Fire designated for salvage (*4*). Responses to postfire logging may vary between and within fires, forest types, and technique/timing of logging. Similar patterns of seedling damage/reduction resulting from postfire logging operations have been documented across a range of conditions (*7*–*11*), which may be because postfire logging is often conducted under the presumption of negligible natural regeneration and is therefore not designed to protect it. The logging techniques on which we reported (handfelling with helicopter yarding >2 years postfire) occur on public lands throughout the western United States.

The hypothesis that prompt postfire logging could have different effects merits study. Currently, there are no data comparing effects of early versus delayed logging operations (*12*) and, to date, the few relevant studies of prompt postfire logging have also reported reductions in seedling densities (*7*, *8*). More field data are needed to elucidate the range of potential effects under different conditions and prescriptions.

Short-term data from well-designed studies, such as (*3*), are important in providing benchmarks for long-term studies and isolating the mechanisms through which management affects forest processes. To date, the few longer term studies of postfire logging (*13*) have been confounded by multiple postfire treatments (e.g., logging, fuel treatment, replanting). A review of postfire management studies (*12*) states, "when treatments involve logging as well as other site preparation measures, it is impossible to distinguish the specific causative factor behind any observed vegetation change." We maintain that research on postdisturbance management effects will be most valuable when each treatment is studied as a distinct variable [e.g., (*3*, *14*)].

Early regeneration. Although various reforestation practices after live tree harvest in southwest Oregon have been well studied (*1*, *15*), natural post-wildfire regeneration remains far less studied in the region. Postfire conditions differ substantially from conditions following live tree harvest in several important ways [e.g., (*16*, *17*)], including seedbed qualities, legacy structure, and stress seed crops. Thus, we caution against extrapolating knowledge from postharvest studies to natural post-wildfire regeneration.

Early regeneration data provide insight into important processes, including seed production, dispersal, germination, and early survival. The relation between short-term effects of postfire logging on these processes (*3*) and long-term recruitment patterns (*1*, *18*, *19*) is key to understanding the legacy of logging effects on stand development. Conifer regeneration following wildfires can be limited during two phases: (i) initial establishment due to seed source deficiency in large burned areas, and (ii) subsequent competition, survival, and release. We reported on the former, not the latter. This is important in light of uncertainties regarding the degree to which this first phase would occur in high-severity portions of the Biscuit Fire (*20*, *21*). We did not draw further conclusions about long-term effects of postfire logging (*3*). Relevant long-term data from replicated experiments do not exist (*12*).

Postfire succession in mixed-evergreen forests of the Klamath-Siskiyou region (which covers much of southwest Oregon and northwest California), is characterized by a period during which broadleaf vegetation forms a substantial overstory component (*19*). Several authors have suggested that, in the presence of shrub competition, early conifer establishment is especially important in attaining eventual conifer dominance (*15*, *20*, *22*). Alternatively, current studies indicate a variable, protracted conifer regeneration period in this region, with peak establishment generally within 5 years of fire and persistence in the presence of broadleaf species (*18*). Under either scenario, establishment of seedlings 2 to 3 years after fire represents an important period of succession in the Klamath-Siskiyou region. Subsequent competition from broadleaf vegetation has been shown to occur with or without postfire logging (*13*) and is therefore a related but separate issue from the results of our study (*3*).

With respect to regional stocking standards (*23*), we followed federal definition M, which states that a suitable tree (capable of meeting forest management objectives) "may qualify as a component of the stand by having survived at least one growing season in the field." The vast majority of seedlings we reported had been present for at least two growing seasons by 2005 (*24*). Regional stocking standards include prescriptions for density and distribution (*1*, *23*). We reported data pertinent to density standards, quantified at the hectare scale using an effective method (*4*) and assessed for variability at the treatment scale (across logging units) rather than within each logging unit. Traditional stocking surveys (*1*) were not our intent. We indicated that the median density we quantified exceeded that found in adequately stocked sites per the Biscuit management plan [since sites must be stocked at a minimum density (*23*)]. This was a benchmark for comparison and not a conclusion regarding stocking per se, which is quantified differently. Because much of the Biscuit salvage was planned in land use allocations for which very low densities and variable spacing were prescribed (*25*), we suggest that stand level density is an important parameter relative to other stocking standards.

Fuel dynamics. Although fuel composition, arrangement, and continuity are all important variables contributing to potential fire behavior, a predominant factor affecting behavior of the flame front is the mass of fine downed wood (*26*, *27*). We reported an increase by a factor of about 5 in fine downed wood as a result of postfire logging (*3*), which suggests that

[1]Department of Forest Science, [2]Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA. [3]Institute of Pacific Islands Forestry, USDA Forest Service, Pacific Southwest Research Station, 60 Nowelo Street, Hilo, HI 96720, USA.

*To whom correspondence should be addressed. E-mail: dan.donato@oregonstate.edu

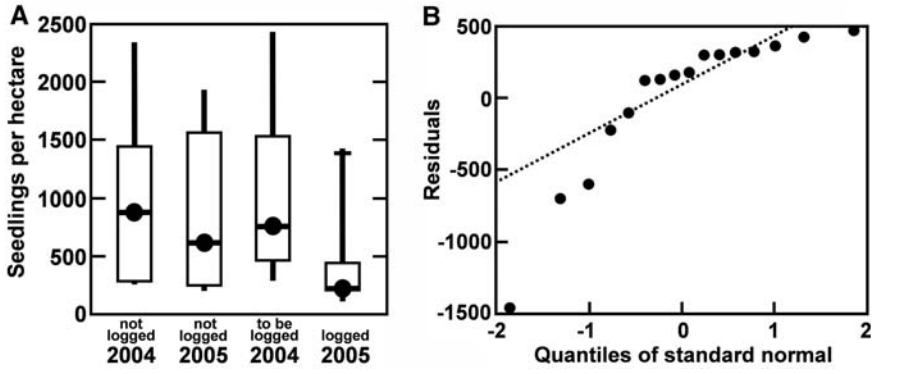


Fig. 1. (**A**) Box-and-whisker plots of Biscuit Fire seedling data (seedlings per hectare) from (*3*) and (**B**) residuals from parametric test [analysis of variance (ANOVA)] on interannual changes in untransformed seedling data, as in (*2*). (A) shows tendency toward positive skewness (typical for ecological count data) for all groups and unequal variance, as well as marked difference between the 2005-logged sample compared with other samples. Dot within box is the median; box edges are the 25th and 75th percentiles; whiskers represent the data range; points beyond 1.5 times the interquartile range from the quartiles are drawn as horizontal lines across the whisker. Shapiro-Wilk normality test (*32*) indicates lack of normality: W = 0.7173, $P = 0.0023$ for 2005-logged plots. (B) shows that parametric ANOVA tests on untransformed data, as in (*2*), are prone to spurious results for the seedling data due to substantial departure from normality (Shapiro-Wilk normality test: W = 0.7226, $P = 0.0026$ for annual change in density between years in logged plots). Analyses after data transformations or nonparametric analyses are highly preferred (*31*).

salvaged environments are predisposed to fires of greater intensity than unsalvaged sites in the near term. Fire behavior modeling of different salvage/fuel-treatment scenarios, parameterized with field data, will best characterize potential fire behavior in postfire settings. However, standard fire behavior models [e.g., (*26*)] do not include fuel continuity as an independent variable and therefore assume similar connections between fuel loads and fire behavior.

One of the primary purposes of the Biscuit management plan was to reduce the "risk" of high intensity and/or stand replacement fire (*21*); thus, we presented our results relative to this objective (*28*). Prescriptions also called for broad ranges of downed wood levels for soil function and habitat (*21*). Our observation was that downed wood levels following logging were variable relative to prescriptions, often as much a function of inherent, localized felling and handling practices as they were reflective of any specific prescription. Regardless, our research quantified higher postsalvage fuel loads, which are associated with higher potential fire behavior, thus adding empirical field data to what has only been modeled thus far (*29*).

Given the observed pulse of surface fuels after logging and its potential effects on surface fire behavior, our suggestion that leaving woody material (dead trees) standing could result in lower fire hazard is a reasonable hypothesis. Surface fuel loads derived from fire-killed trees are determined by the dynamic balance between inputs (from the canopy) and outputs (decomposition). As such, no scenario produces a larger pool of fine (up to 7.62 cm) and 1000-hour [7.62 to 20.32 cm (*19*)] fuels than a single one-time input from clearfelling shortly after a fire.

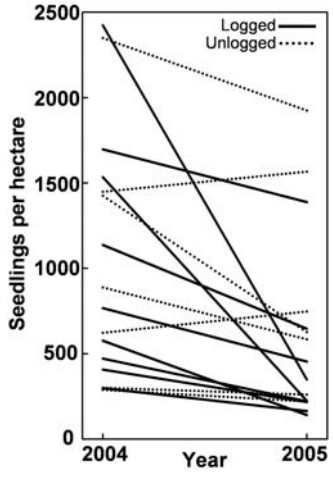


Fig. 2. Changes in seedling densities between 2004 and 2005 for logged and unlogged plots, with logging occurring between measurement periods. Equivocal variation between years can be seen in the unlogged plots (no consistent trend), whereas logged plots all show marked declines.

Long-term interactions between these inputs and live fuel succession are poorly understood, especially for the largest fuel size classes. As we stated in (*3*), hypotheses regarding long-term fire potentials merit study [see (*30*)].

Statistical analysis. All appropriate, conservative methods for analyzing our data yield robust, biologically and statistically significant effects (*3*, *5*, *6*). These methods employ either nonparametric analyses that do not require normality or equal variance, or a common transformation ($\log_e$) to more closely meet assumptions of parametric tests [Fig. 1 and (*31*)]. Parametric tests on untransformed data, as in (*2*), are prone to spurious results due to substantial departure from normality and unequal variance (Fig. 1).

Table 1. Seedling densities for each of the 16 burn plots before and after logging treatment. The following are test statistics and one-tailed *P* values from multiple analytical methods of testing the hypothesis that the reduction in seedling density in logged plots exceeded interannual variation in unlogged plots. Rank sum test on percentage change in each plot: W = 53, $P = 0.006$; rank sum test on untransformed (raw) changes: W = 60, $P = 0.045$; two-sample *t* test on percentage change in each plot: $t_{14} = 3.15$, $P = 0.004$; two-sample *t* test on changes in $\log_e$-transformed densities: $t_{14} = 2.70$, $P = 0.009$; two-sample *t* test on untransformed (raw) changes: $t_{14} = 1.52$, $P = 0.075$ [to our understanding this is equivalent to the analysis of Baird (*2*); see also Fig. 1B]. One-tailed tests are logically appropriate because, given the time frame of study as well as the timing of logging relative to the interannual and seasonal timing of regeneration, the immediate effect of logging on seedling densities (if different from zero) would be a reduction (*7*–*10*).

Plot	Seedlings per hectare 2004	Treatment	Seedlings per hectare 2005
1	298	logged	164
2	471	logged	221
3	767	logged	454
4	576	logged	141
5	407	logged	217
6	1534	logged	224
7	2423	logged	349
8	1697	logged	1388
9	1137	logged	646
10	288	unlogged	220
11	622	unlogged	747
12	300	unlogged	260
13	888	unlogged	584
14	1448	unlogged	1566
15	1425	unlogged	626
16	2349	unlogged	1924

Baird's (*2*) description of our analysis is misleading. Repeated measures are irrelevant because we did not assume independence of 2004 and 2005 measurements within each plot (Table 1). We intended to quantify annual change within plots. In addition, our descriptive estimate of the sample-wide change in logged plots between years was a 71% decline in the sample median, which does not arise from analysis of any particular plot. Rather, the median is a conservative measure of central tendency for the entire sample before and after logging, providing descriptive information at the broader, treatment-wide level.

Because the sample of unlogged plots showed no consistent or statistically significant pattern in changes in seedling density over time (Fig. 2 and Table 1) (*3*, *6*), and new in-seeding as well as mortality was occurring [see (*18*)], the statistically significant change in logged plots was attributed to logging. Analyses that include the

variation observed in the unlogged sample also yield findings of significant logging effects that differ only in the point estimate of effect magnitude (Table 1) (*5*, *6*).

Independent statistical evaluations of our data support the conclusions of significant effects of postfire logging on seedling regeneration and fuels (*5*, *6*). As stated in one such review, "Although there can be differences of opinion on methods of analysis, all reasonable methods will lead to congruent conclusions" (*5*).

The study design, results, and conclusions presented in (*3*) are strong, relevant, and straightforward. Newton *et al*. (*1*) and Baird (*2*) present different perspectives, but provide no data or evidence from other studies to contradict our findings and conclusions. A short-format paper such as ours is not intended to review or explore every angle but to present key data that will stimulate discussion and further research. We hope our research findings and comments provide direction for future studies and management.

References and Notes

1. M. Newton *et al.*, *Science* **313**, 615 (2006); www.sciencemag.org/cgi/content/full/313/5787/615a.
2. B. N. Baird, *Science* **313** 615 (2006); www.sciencemag.org/cgi/content/full/313/5787/615b.
3. D. C. Donato *et al.*, *Science* **311**, 352 (2006).
4. Materials and methods are available as supporting material on *Science* Online.
5. F. L. Ramsey, testimony submitted to U.S. House of Representatives, Committee on Resources, Subcommittee on Forests and Forest Health, Congressional Oversight Hearing, Medford, OR (2006); http://resourcescommittee.house.gov/archives/109/testimony/2006/ramsey_record.pdf
6. M. M. P. Huso, testimony submitted to U.S. House of Representatives, Committee on Resources, Subcommittee on Forests and Forest Health, Congressional Oversight Hearing, Medford, OR (2006); http://resourcescommittee.house.gov/archives/109/testimony/2006/huso_record.pdf
7. D. F. Greene, S. Gauthier, J. Noel, M. Rousseau, Y. Bergeron, *Front. Ecol. Environ.* **4**, 69 (2006).
8. J. J. Martinez-Sanchez, P. Ferrandis, J. Heras, J. M. Herranz, *For. Ecol. Manage.* **123**, 1 (1999).
9. D. F. Roy, California Forest and Range Exp. Sta., *For. Serv. Res. Note 107* (1956).
10. L. A. Isaac, G. S. Meagher, USDA Forest Service Pacific NW Forest and Range Exp. Sta. (USDA, Portland, OR, 1938).
11. Reference 8 in (*1*) does not pertain to postfire logging damage to regeneration. See Isaac and Meagher (*10*).
12. J. D. McIver, L. Starr, *West. J. Appl. For.* **16**, 159 (2001).
13. J. C. Stuart, M. C. Grifantini, L. Fox, III, *Forestry Sci.* **39**, 561 (1993).
14. S. L. Stephens, *For. Ecol. Manage.* **105**, 21 (1998).
15. S. D. Hobbs *et al.*, Eds., *Reforestation Practices in Southwestern Oregon and Northern California* (Oregon State Univ. Forest Res. Lab., Corvallis, OR, 1992).
16. J. F. Franklin *et al.*, *For. Ecol. Manage.* **155**, 399 (2002).
17. D. B. Tinker, D. H. Knight, *Ecosystems* **3**, 472 (2000).
18. J. Shatford, D. E. Hibbs, Cooperative Forest Ecosystem Research program, Oregon State Univ., *Progress Report* (2006).
19. J. K. Agee, Fire Ecology of Pacific Northwest Forests (Island Press, Washington, DC, 1993).
20. J. Sessions, P. Bettinger, R. Buckman, M. Newton, J. Hamann, *J. Forestry* **102**, 38 (2004).
21. USDA Forest Service, Biscuit Fire Final Environmental Impact Statement, www.fs.fed.us/r6/rogue-siskiyou/biscuit-fire/feis last accessed June 16, 2006.
22. L. A. Isaac, *J. Forestry* **38**, 716 (1940).
23. U.S. Department of the Interior Bureau of Land Management, Oregon State Office *Regeneration Stocking Surveys Handbook*, H-5705-1, Rel. 5-249 (USDI BLM, Portland, OR, 2003).
24. Such seedlings count toward meeting standards for density/distribution, even before a stand is "accepted" as beyond the juvenile stage [see definition P in (*23*)].
25. The management plan for Late Successional Reserves prescribes initial densities of 250 to 375 trees per hectare (eventual objective is 150 to 200 trees per hectare "free-to-grow") with variable, microsite-based spacing of 4.5 to 12 m (*21*). Low stocking rates would be possible even when stands are within this spacing prescription, which increases the relevance of stand level densities measured at broader scales.
26. P. L. Andrews, C. D. Bevins, R. C. Seli, USDA Forest Service Rocky Mt. Res. Sta. RMRS-GTR-106 (USDA, Ogden, UT, 2005).
27. R. C. Rothermel, USDA Forest Service, Intermountain Forest and Range Exp. Sta. Gen. Tech. Rep. INT-143 (USDA, Ogden, UT, 1983).
28. We maintained similar usage of the term "risk" (*21*) (although the term is also used to describe the probability of ignition) and clearly stated the affected parameters as those of potential fire behavior/effects (*3*).
29. J. K. Brown, E. D. Reinhardt, K. A. Kramer, USDA Forest Service Rocky Mt. Res. Sta. RMRS-GTR-105 (USDA, Ogden, UT, 2003).
30. M. D. Passovoy, P. Z. Fulé, *For. Ecol. Manage.* **223**, 237 (2006).
31. F. L. Ramsey, D. W. Schafer, *The Statistical Sleuth: A Course in Methods of Data Analysis.* 2nd ed. (Duxbury Press, Belmont, CA, 2002).
32. S. S. Shapiro, M. B. Wilk, *Biometrika* **52**, 591 (1965).

33. This manuscript benefited from reviews by statisticians L. L. Conquest, A. Gitelman, E. A. Housworth, M. M. P. Huso, P. Murtaugh, and F. L. Ramsey, as well as several colleagues and five anonymous reviewers. This work was supported by the Joint Fire Science Program and DOE grant DE-FG02-04ER63917. The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions or policies of the U.S. Government. Mention of trade names or commercial products does not constitute their endorsement by the U.S. Government.

Supporting Online Material

www.sciencemag.org/cgi/content/full/313/5787/615/DC1
Materials and Methods
References

20 March 2006; accepted 7 July 2006
10.1126/science.1126583

View publication stats

CSIRO PUBLISHING

International Journal of Wildland Fire
http://dx.doi.org/10.1071/WF12109

Fuel mass and forest structure following stand-replacement fire and post-fire logging in a mixed-evergreen forest

Daniel C. Donato[A,D,E], *Joseph B. Fontaine*[B], *J. Boone Kauffman*[C], *W. Douglas Robinson*[C] *and Beverly E. Law*[A]

[A]College of Forestry, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331, USA.
[B]School of Environmental Science, Murdoch University, 90 South Street, Perth, WA 6150, Australia.
[C]Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331, USA.
[D]Present address: Washington State Department of Natural Resources, PO Box 47016, Olympia, WA 98504, USA.
[E]Corresponding author. Email: donatod@onid.orst.edu

Abstract. Following severe wildfires, managing fire hazard by removing dead trees (post-fire logging) is an important issue globally. Data informing these management actions are relatively scarce, particularly how fuel loads differ by post-fire logging intensity within different environmental settings. In mixed-evergreen forests of Oregon, USA, we quantified fuel profiles 3–4 years after stand-replacement fire – assessing three post-fire logging intensities (0, 25–75, or >75% basal area cut) across two climatic settings (mesic coastal, drier interior). Stand-replacement fire consumed ~17% of aboveground biomass. Post-fire logging significantly reduced standing dead biomass, with high-intensity treatment leaving a greater proportion (28%) of felled biomass on site compared with moderate-intensity treatment (14%) because of less selective tree felling. A significant relationship between logging intensity and resulting surface fuels (per-hectare increase of 0.4–1.2 Mg per square metre of basal area cut) indicated a broadly applicable predictive tool for management. Down wood cover increased by 3–5 times and became more spatially homogeneous after logging. Post-fire logging altered the fuel profile of early-seral stands (standing material removed or transferred, short-term increase in surface fuels, likely reduction in future large fuel accumulation), with moderate-intensity and unlogged treatments yielding surface fuel loads consistent with commonly prescribed levels, and high-intensity treatment resulting in greater potential need for follow-up fuel treatments.

Additional keywords: biomass, Biscuit Fire, coarse woody debris, dead wood, fuel succession, Klamath–Siskiyou, legacy, logging intensity, post-fire management, salvage logging, snag.

Received 9 July 2012, accepted 6 November 2012, published online 15 February 2013

Introduction

Stand-replacing fires affect many forest ecosystems globally (Bond and Keeley 2005) and are key drivers of woody biomass dynamics (Spies *et al.* 1988; Everett *et al.* 1999; Pedlar *et al.* 2002; Hall *et al.* 2006). Following wildfires, managing fuels (biomass) is often a key concern, as the eventual fall of fire-killed trees may function as a positive feedback mechanism by providing fuel for subsequent fires, or 're-burns' (Brown *et al.* 2003). The widespread practice of post-fire logging (i.e. salvage) often carries an objective of reducing woody fuel loads and thus fire behaviour and effects in the event of a re-burn (e.g. McIver and Starr 2001; McGinnis *et al.* 2010). However, little empirical information exists to inform these management actions – in particular how post-fire fuel loads are affected by different post-fire logging intensities across different forest settings (McIver and Starr 2001; Peterson *et al.* 2009).

Although post-fire logging often aims to reduce future fire severity, the few empirical studies of actual fires occurring after post-disturbance logging have shown equivocal results, including reduced severity (Buma and Wessman 2011), increased severity (Hansen 1983; Thompson *et al.* 2007) and unchanged or mixed results (Kulakowski and Veblen 2007; Fraver *et al.* 2011). Mechanisms behind these varying observations remain unclear. Timber harvest in general is known to increase surface woody fuel loads by transferring non-merchantable branches and tree tops ('slash') to the surface, where most fires propagate (Snell and Brown 1980; Pyne *et al.* 1996; Stephens *et al.* 2009). Exactly how this premise extends to logging of dead trees has

Journal compilation © IAWF 2013

not been well quantified for most forest types. Recent studies indicate that surface fine fuel loads (<7.6-cm diameter) are indeed elevated following post-fire logging (Donato *et al.* 2006*a*; McIver and Ottmar 2007; Keyser *et al.* 2009; McGinnis *et al.* 2010) and empirical data and models suggest these elevated loads may persist for ~20 years in some settings (McIver and Ottmar 2007; McGinnis *et al.* 2010). Yet coarse woody fuels (>7.6-cm diameter) may accumulate less on the surface over the intermediate term (~10–50 years) if stems are removed, which could reduce potential fire effects such as soil heating (McIver and Ottmar 2007; Keyser *et al.* 2009; Monsanto and Agee 2008). Post-fire management can also influence live vegetation (Stuart *et al.* 1993), and this may further affect subsequent fire behaviour. To better identify relationships between post-fire fuels, management treatments and observed fire effects, data are needed on specific effects of individual activities such as logging, slash burning and vegetation management (McIver and Starr 2001; Donato *et al.* 2006*b*).

The quantity and distribution of fuels remaining after post-fire logging may vary widely by harvest method and biophysical setting. Treating slash fuels after felling of live trees is well known to be important for reducing total fuel loads and fire potentials (e.g. Weatherspoon and Skinner 1995; Graham *et al.* 2004; Agee and Skinner 2005). For fire-killed trees, however, the relative need for such follow-up treatments after differing levels of logging intensity has scarcely been reported, and no information exists on how this varies across forest types or settings. Such information is essential to informed post-fire decisions and meeting fuel management objectives (Peterson *et al.* 2009).

In this study, we investigated fuel dynamics in stand-replacement (high-severity) portions of the 2002 Biscuit Fire, a large wildfire in south-west Oregon, USA. Our objectives were to: (1) quantify aboveground biomass, composition and vertical distribution following stand-replacement fire relative to intact mature-to-old growth forest, including all material (fine and coarse, live and dead) in both the aerial and surface fuel strata and (2) quantify immediate changes in these profiles resulting from post-fire logging, as influenced by harvest intensity and biophysical setting (mesic coastal forest type *v.* drier inland forest type). We focussed on empirically measured fuel profiles rather than modelled fire behaviour because available models have not been calibrated or tested for post-fire environments, especially for the necessary custom fuel models (Passovoy and Fulé 2006; Cruz and Alexander 2010).

Methods

Study area

The study was conducted in the Klamath–Siskiyou Mountains, a coastal range in the state of Oregon, USA (Fig. 1), within the mixed-evergreen and *Abies concolor* zones (Franklin and Dyrness 1973). The region experiences a moist Mediterranean climate with warm, dry summers (mean maximum July temperature: 27°C) and cool, wet winters (mean minimum January temperature: 2°C) (Fontaine *et al.* 2010). Mean annual precipitation ranges from 140–500 cm over the burn area, with <15% falling from May–September (Daly *et al.* 2002; prismclimate.org). Forests are dominated by conifers, Douglas-fir (*Pseudotsuga menziesii*), white fir (*A. concolor*) and sugar pine (*Pinus lambertiana*); evergreen hardwoods, tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*) and canyon live oak (*Quercus chrysolepis*); and shrubs, greenleaf manzanita (*Arctostaphylos patula*) and snowbrush (*Ceanothus velutinus*). Fire regimes are complex, described as low- to mixed-severity with median return intervals ranging from 5–35 years in drier plant associations to 50–>100 years in higher elevation and wetter associations (Agee 1991; Agee 1993; Wills and Stuart 1994; Taylor and Skinner 1998; Stuart and Salazar 2000; USDA 2004). Stand-replacement fire effects (≥90% overstorey mortality) typically occur in variably sized patches as part of a burn mosaic (Donato *et al.* 2009*a*; Halofsky *et al.* 2011).

All sample areas were mature-to-old-growth (M/OG) Douglas-fir-dominated forests currently or before stand-replacement fire (see Thornburgh 1982; Agee 1993 for developmental and structural descriptions). Study areas were on steep slopes (generally >20°) between ~600 and 1300-m elevation, at mid-slope positions on a full range of aspects. Soils were derived from metasedimentary, metavolcanic and coarse-grained igneous parent materials (USDA 2004). We excluded conditions generally irrelevant to post-fire logging: extremely steep rocky areas, riparian zones, ultramafic soils (see Whittaker 1960), areas burnt with low or moderate severity (USDA 2004) and pre-existing plantations and shrub fields.

The Klamath–Siskiyou region is renowned for floristic diversity due in part to sharp topoedaphic and climatic gradients (Whittaker 1960); among the most important gradients are west-to-east trends in moisture and productivity. Western portions of the area (Fig. 1) receive greater maritime influence, experience less severe summer moisture deficits and have longer fire return intervals than do inland sites to the east (Daly *et al.* 2002; USDA 2004). As such, mesic western areas tend to support higher basal area and aboveground biomass than do drier eastern areas.

Study fire

The Biscuit Fire of 2002 burnt with mixed severity over 200 000 ha of the Klamath–Siskiyou Mountains. Relative proportions of low, mixed and high severity (as assessed by vegetation change) were respectively ~30, 27 and 43% (USDA 2004). The fire perimeter encompassed a broad range of biophysical conditions and spanned both western and eastern plant associations (Fig. 1). Following the fire, the Rogue River-Siskiyou National Forest implemented post-fire logging in limited areas of the burn. In addition to recouping economic value, stated objectives included reducing fire hazards associated with residual wood (USDA 2004).

Post-fire logging occurred mostly during the fall–spring of 2004–2005 (2–3 years post fire) with some additional logging during the winter–summer of 2005–2006 (3–4 years post fire). Logging occurred in stand-replacement patches ranging from ~4 to >1000 ha. Harvest units (spatially distinct logging parcels within timber sales) ranged from 1–70 ha in size (mean 8 ha). Trees were hand felled and de-limbed on site, generating slash in place. Logs were removed by cable or helicopter yarding. Prescriptions for down wood retention in severely burnt sites varied from 24 to 106 Mg ha^{-1} depending on plant association (USDA 2004). Slash treatment (prescribed burning of slash accumulations) occurred in <30% of sampled stands. All

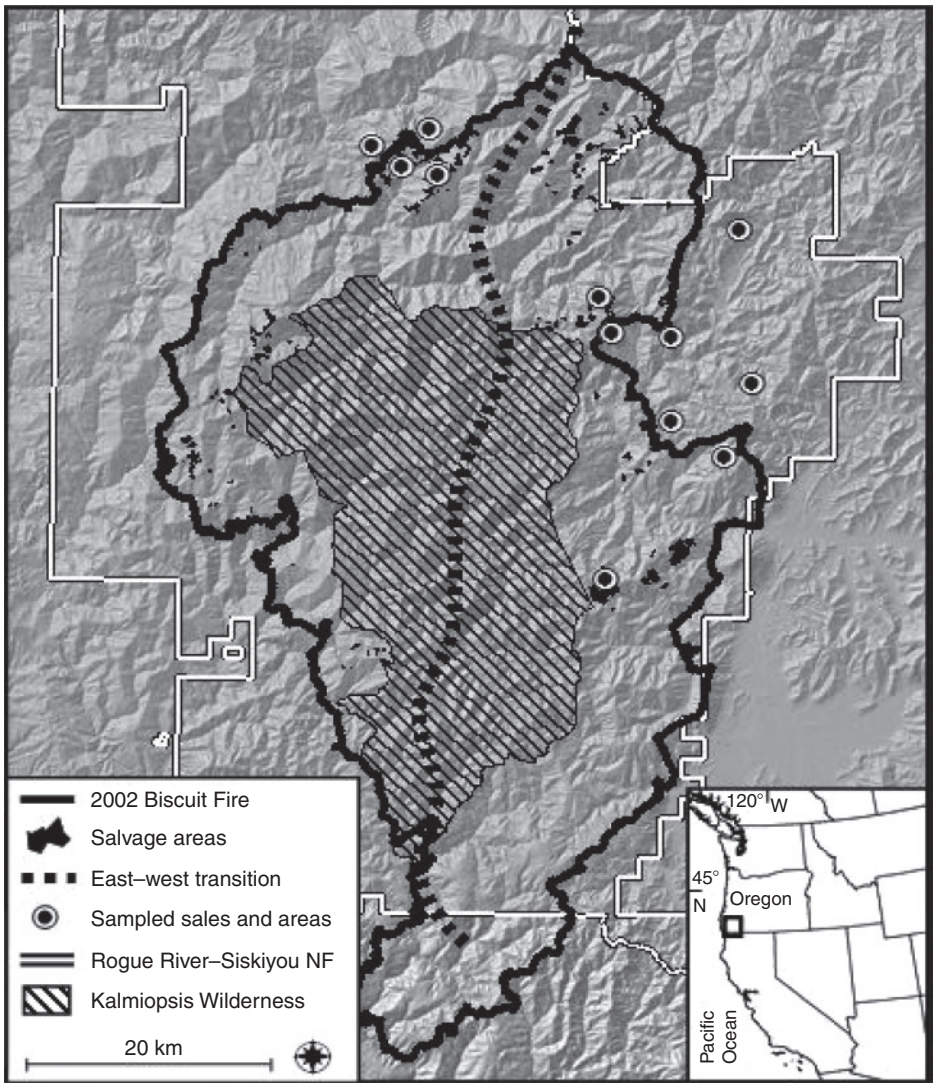


Fig. 1. Study area and sampling locations for quantification of fire and post-fire logging effects. Dots correspond to post-fire timber sales and adjacent unburnt areas in which sample stands were located (total $n = 38$ stands: 30 in the Biscuit Fire and 8 unburnt mature/old-growth stands). We sampled all large Biscuit Fire timber sales completed by late 2005, with one exception in the extreme west of the fire. Dashed line approximating transition zone between mesic westerly plant associations and drier easterly plant associations adapted from USDA (2004). Spatial data courtesy of Rogue River–Siskiyou National Forest.

post-logging data presented here from the Biscuit Fire reflect effects of tree harvest only (which was the only dead wood treatment in >70% of the stands), and not any subsequent treatments. Harvest prescriptions called for retention of 3–29 large (>41 cm) snags per hectare and variable retention of smaller (<41 cm) snags depending on merchantability (USDA 2004).

We categorised stands into three levels of treatment intensity: unlogged (U), logged at moderate intensity (M) and logged at high intensity (H). Moderate-intensity harvest units were helicopter yarded with 25–75% basal area cut at the hectare scale (mean 46% ± 5.5 s.e.); high-intensity harvest included a mix of cable and helicopter yarding with >75% basal area cut at the hectare scale (mean 89% ± 3.5 s.e.).

Data collection

We sampled all large Biscuit Fire timber sales completed by late 2005, with one exception in the extreme west of the fire due to access logistics. We sampled 26 stands in the eastern portion of the fire and 12 in the western portion (68% east, 32% west), corresponding to the distribution of Biscuit post-fire logging (67% east, 33% west by area). Study areas were identified *a priori* from Forest Service spatial data layers on proposed sale boundaries, burn severity and pre-fire forest cover and type. We interspersed treatment and control stands by sampling unlogged burn areas in and around each sampled sale. Unburnt M/OG stands were also sampled over a broad area corresponding to the distribution of sampled burn stands (Fig. 1). Study plots

(no more than one per harvest unit) were located randomly within harvest units and adjacent unlogged areas. Pre-treatment measurements occurred in the summer of 2004; post-treatment measurements (including re-measurement of control stands) occurred in the summers of 2005 and 2006, within 3–9 months of logging. The 26 eastern stands consisted of eight U stands, seven M stands, six H stands and five unburnt M/OG stands. The 12 western stands included three each of the four treatments.

We sampled each stand with a 1-hectare plot with a layout based on regional forest inventory protocols (USDA 2003*b*). All aboveground biomass pools were measured, partitioned by fuel stratum (*sensu* Pyne *et al.* 1996). Aerial biomass was defined as standing over- and mid-storey components (live and dead trees >10-cm diameter at breast height, DBH). Surface biomass was defined as standing understorey components (live and dead small trees, shrubs, forbs, grasses), down woody detritus, stumps and forest floor (litter and duff). Aerial and standing surface biomass were each measured in four regularly spaced circular subplots ranging from 2-m radius for the surface stratum to 17-m radius for the aerial stratum (surface and aerial subplots were concentric) (see USDA 2003*b*). For each tree we recorded species, DBH, total height, decay class (per Cline *et al.* 1980) and percentage of stem surface with bark and wood charring. For understorey hardwoods, shrubs, forbs and grasses we recorded percentage cover by species. Hardwoods and woody shrubs were further measured on an individual basis for live crown dimensions (length, width, height), basal diameter of live stems, and height and count of dead stems by 2-cm-basal diameter class. Forest floor mass was quantified by collecting eight systematically located 5.6-cm-diameter cores down to the mineral surface in each subplot (32 samples per plot), then separating litter and duff components, and drying at 70°C to constant mass.

We sampled down woody detritus by size class (see Agee 1993) along four 75-m planar intercept transects (Brown 1974; Harmon and Sexton 1996) radiating from plot centre in subcardinal directions. Coarse woody detritus (CWD; 7.63–20.32-cm and >20.32-cm classes) was surveyed along all 75 m of each transect and recorded for diameter, species, decay class and charring (Donato *et al.* 2009*b*). Fine woody detritus (FWD) was tallied by size class and char presence; survey lengths were, beginning from the distal end of transects: <0.62-cm class, 5 m; 0.63–2.54-cm class, 15 m; 2.55–7.62-cm class, 25 m.

Biomass computations

We computed stem mass for all trees using species- and region-specific allometric diameter-volume equations and wood densities (Walters *et al.* 1985; Means *et al.* 1994; Van Tuyl *et al.* 2005). Masses of tree foliage, bark, branch and unmerchantable tops were estimated directly from species-specific allometric equations (Means *et al.* 1994). Merchantable mass was defined as sound conifer stemwood >20-cm diameter (USDA 2004). All biomass components were adjusted for individual-specific metrics of bark and wood charring, top breakage and decay class status (Harmon and Sexton 1996; Appendix 1); as well as plot-specific ocular estimates of foliage and branch consumption (*sensu* USDA 2003*a*). Due to confounding of fire effects with definitions of decay class 1–2 characteristics (e.g. fine branch loss; Cline *et al.* 1980), recently fire-killed trees were assigned mean decay class 1–2 inputs. We computed biomass of surface-layer hardwoods and shrubs by empirically derived allometric equations (Donato *et al.* 2009*c*). Mass of forbs and low shrubs was estimated from regional equations relating cover to mass per area (Means *et al.* 1994). We computed mass of down woody detritus from line intercept data using standard geometric scaling and species- and decay-specific wood density values (Brown 1974; Harmon and Sexton 1996). Down wood was corrected on an individual piece basis for mass loss due to charring (Donato *et al.* 2009*b*).

Statistical analysis

Fire effects

To quantify apparent fire effects on aboveground biomass pools, we compared M/OG stands to three-year post-fire stands (unlogged). For this comparison we present means and 95% confidence intervals (CIs) by biomass category to evaluate magnitude of differences rather than obtain test statistics. Data for fire effects assessment were pooled across western and eastern stands because exploratory two-way analysis of variance (ANOVA; Ramsey and Schafer 2002) showed that fire effects did not differ strongly by forest type ($P > 0.05$ for all burn × forest type interaction terms).

Post-fire logging effects

To assess how post-fire logging effects varied by logging intensity and biophysical setting, we analysed fuel loads as a function of the three treatment levels (U, M, H); two forest types (mesic, drier); and a treatment × forest type interaction term in a two-way ANOVA. The forest type term allowed biomass levels in each treatment to vary between mesic *v.* drier stands, whereas the interaction term tested whether treatment effects varied by forest type. We analysed live and dead total biomass by stratum as well as fine and coarse down woody fuels. To provide management-relevant information on the implemented prescriptions, we also present trends in basal area and snag density among treatments.

Analysis of forest type and treatment differences was focussed on post-treatment comparisons ($n = 30$ burn stands (U = 11, M = 10, H = 9)). Because treatments were not implemented randomly (per the agency management plan), we also present results of a two-way ANOVA for the subset of stands for which we were able to collect before–after data ($n = 19$ (U = 8, M = 7, H = 4)) to assess whether strong differences among treatments existed before logging and whether the pre–post change was greater in treated stands than in controls. We could use only this subset for before–after analyses because 'reconstructing' stand density in logged stands for which we did not have pre-treatment data was precluded by the incidental felling, fragmentation and burial of an unquantifiable amount of small- and medium-sized stems. For all analyses, models were evaluated by residual-*v.*-fit plots using standard diagnostics (Ramsey and Schafer 2002). We $\log_e$-transformed basal area and snag density data to reduce heteroscedasticity. Biomass data were not transformed because the data were symmetrically distributed and showed no consistent pattern in residual spread. Specific treatment comparisons were performed by computing 95% CIs for each treatment within each forest type; lack of

Table 1. Mean (95% CI) aboveground biomass pools in mature-to-old-growth (M/OG) sites and 3 years after stand-replacement wildfire (Mg ha^{-1})

$n = 8$ M/OG stands and 11 burnt stands

Biomass category	M/OG		Post-fire	
Dead mass				
Aerial stratum				
Branch	1.4	(0.2–2.6)	69.0	(49.5–88.4)
Stem[A]	20.0	(5.8–34.2)	421	(288–555)
Total aerial dead	21.4	(6.1–36.6)	490	(352–628)
Surface stratum				
Stem + branch	2.4	(0.0–5.5)	3.7	(2.0–5.4)
Stumps	0.0	(0.0–0.0)	0.2	(0.0–0.4)
<0.62 cm fuels	1.1	(0.9–1.4)	0.3	(0.1–0.4)
0.62–2.54-cm fuels	1.9	(1.1–2.7)	0.8	(0.5–1.1)
2.54–7.62-cm fuels	3.8	(2.9–4.6)	1.1	(0.7–1.6)
7.63–20.32-cm fuels	3.0	(1.7–4.2)	1.6	(0.7–2.5)
>20.32-cm fuels	12.8	(5.0–20.5)	11.9	(0.0–24.2)
Forest floor (L+D)	27.2	(20.6–33.8)	1.1	(0.5–1.7)
Total surface dead	52.1	(43.2–61.1)	19.6	(6.1–33.0)
Live mass				
Aerial stratum				
Foliage	15.9	(10.2–21.6)	0.0	(0.0–0.0)
Branch	54.3	(22.9–85.7)	0.0	(0.0–0.0)
Stem	467	(248–685)	0.0	(0.0–0.0)
Total aerial live	537	(294–780)	0.0	(0.0–0.0)
Surface stratum				
Foliage	1.0	(0.2–1.7)	1.4	(0.9–1.9)
Stem + branch	3.3	(1.4–5.1)	2.2	(1.4–3.1)
Forbs and low shrubs	1.2	(0.0–2.5)	1.4	(0.6–2.3)
Total surface live	5.4	(2.9–7.9)	5.1	(3.6–6.5)
Grand total dead	73.5	(55.9–91.2)	510	(363–656)
Grand total live	542	(300–784)	5.1	(3.7–6.5)
Grand total biomass	616	(376–855)	515	(368–661)

[A]Stem masses include bark.

overlap of CIs with means of other groups was interpreted as evidence for differences (Ramsey and Schafer 2002).

Results

Fire effects

Most aboveground biomass persisted through stand-replacement fire. Mean residual dead mass after fire was 515 Mg ha^{-1}, 83% of the 616 Mg ha^{-1} in M/OG stands (Table 1). Aside from converting live biomass to dead (mean post-fire live : dead ratio = 1 : 99), the primary effect of fire was to consume the forest floor and fine fuels in the surface layer (Table 1). Mean forest floor mass after fire (1.1 Mg ha^{-1}) was 96% lower than in M/OG stands (27.2 Mg ha^{-1}) (Table 1). Mean surface wood mass was also lower in post-fire stands by 47–73% for all size classes except the >20.32-cm class, which was similar (Table 1). Live surface biomass (regenerating vegetation) 3 years post fire was already similar to that in M/OG stands (Table 1, Fig. 2).

Consumption of aerial biomass was minimal (Table 1, Fig. 3). Foliage consumption approached 100% but most aerial wood consumption was of twigs (needle-bearing and adjacent branchlets), which compose a small fraction of total mass.

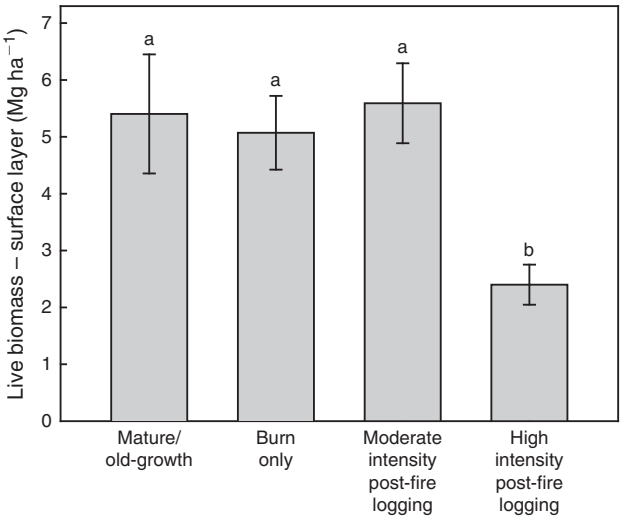


Fig. 2. Mean (±s.e.) live biomass in the surface layer (mid- and over-storey trees excluded). See Table 3 for statistical comparisons. Data are aggregated across the drier to mesic forest types because treatments effects were similar in both types (Table 3). Lower-case letters above bars denote significant differences based on the ANOVA at $\alpha = 0.05$; see Table 3 for full statistical outputs. Regenerating vegetation had already achieved similar biomass 3–4 years post fire as in mature/old-growth stands, and was lower after high-intensity logging.

Consumption of larger branches and stems was negligible (Table 1, Fig. 3, Donato 2008).

Following fire, mesic stands had higher residual biomass (mean 709 Mg ha^{-1}, 95% CI: 555–864) than did drier stands (mean 435 Mg ha^{-1}, 95% CI: 340–530). Tree biomass drove this difference, associated with larger mean snag diameter (44.9 *v.* 36.5 cm) and dead basal area (94.3 *v.* 68.1 m^2 ha^{-1}). Post-fire dead basal area averaged 83% Douglas-fir, 3% incense cedar and 3% white fir in mesic stands; and 65% Douglas-fir, 21% sugar pine and 6% white fir in drier stands. Hardwoods constituted a mean of 11% of total basal area in mesic stands (mainly tanoak) and 4% in drier stands (mainly Pacific madrone).

Post-fire logging effects

Pre-treatment comparisons

We detected no significant pre-existing differences among treatments in terms of basal area, stem densities, fine and coarse woody fuels or live and dead biomass (Table 2). Change magnitudes (post-treatment value minus pre-treatment value) were significantly greater in logged *v.* unlogged stands for all variables except live biomass and density of small snags (Appendix 2).

Post-treatment comparisons

Aerial dead biomass decreased monotonically with increasing harvest intensity in both forest types (Fig. 3, Tables 3, 4). Conversely, surface dead biomass increased monotonically with harvest intensity in both forest types, with treatment effects greater in mesic stands (Fig. 3, Table 3). Post-fire logging reduced standing dead basal area and large snag densities to a greater degree in mesic stands than in drier stands (Table 3).

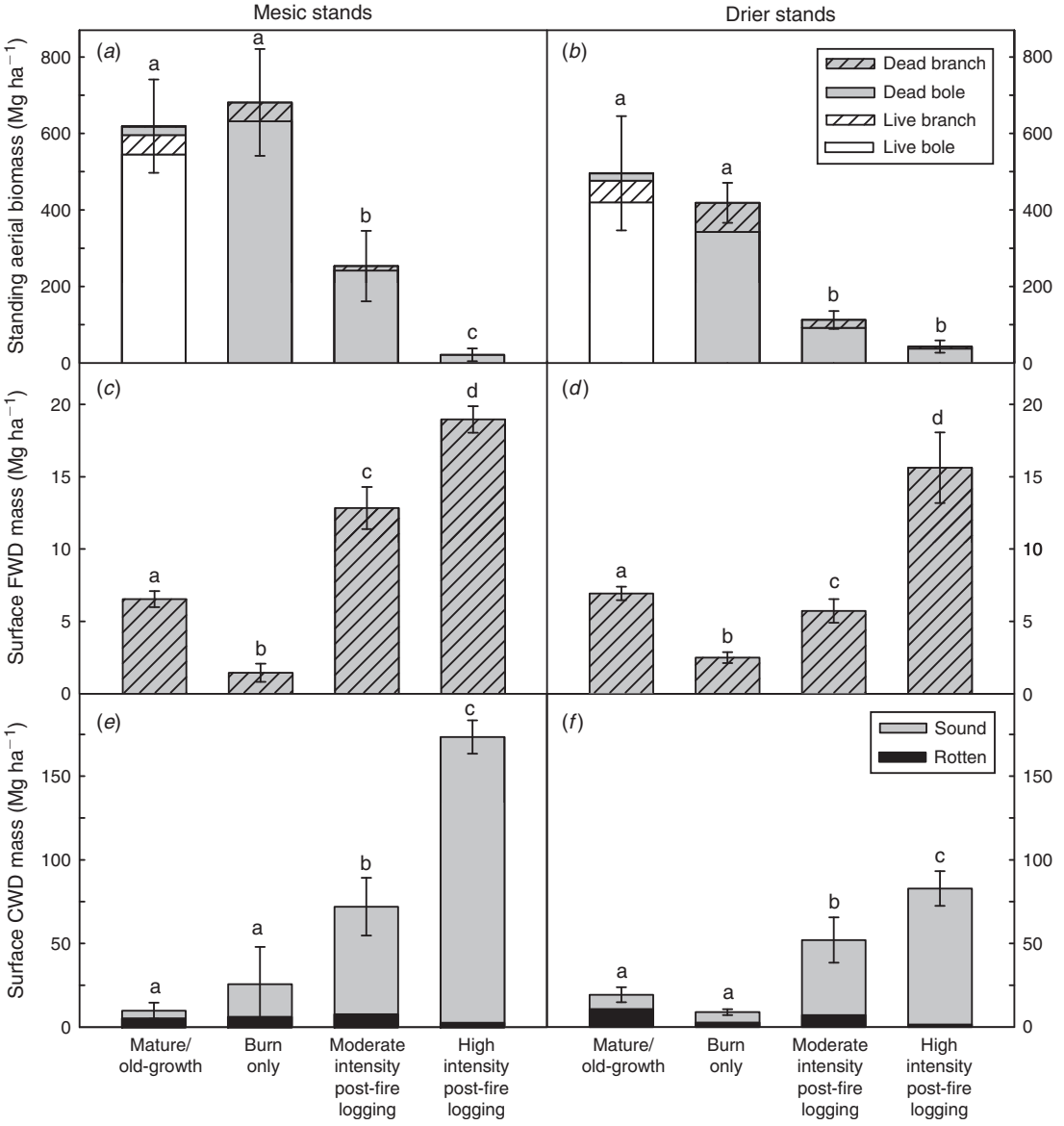


Fig. 3. Mean (±s.e.) aerial (*a–b*) and surface (*c–f*) wood biomass in mature/old-growth stands, and following stand-replacement fire and post-fire logging. Lower-case letters above bars denote significant differences based on the ANOVA at $\alpha = 0.05$; see Table 3 for full statistical outputs.

Live surface-layer biomass remained similar to unlogged stands after moderate-intensity logging, but was lower after high-intensity logging (Fig. 2).

In mesic sites, total biomass removal was estimated at 50 and 66% of post-fire biomass in M and H stands (Table 3). In drier sites, estimated total removal was 58 and 63% in M and H stands (Table 3). Total dead biomass remaining after logging did not differ strongly between moderate- and high-intensity logged stands in either forest type, with broadly overlapping confidence intervals (Table 3). Thus, with high-intensity harvest, more biomass was felled but not removed.

Surface woody fuel loads of all size classes increased following moderate- and high-intensity logging (Fig. 3, Tables 3, 4). Relative to drier stands, logging in mesic stands resulted in greater increases in both fine and coarse surface fuels (Fig. 3, Table 3). When harvest intensity was assessed as a continuous variable, post-logging surface fuel loads were significantly positively related to basal area cut (Fig. 4). As a reference, both moderate- and high-intensity logging resulted in surface fuel loads exceeding those in M/OG stands, except for in the smallest size class (Tables 1, 4).

Surface woody fuel loads became more spatially homogeneous following logging, whereas spatial patterns of live biomass remained similar. Mean surface cover of woody detritus was 6.3, 20.4 and 34.1% in U, M and H stands, compared with 14.5% in M/OG (Fig. 5*a*). Hectare-scale heterogeneity in CWD mass (coefficient of variation (CV%) among transects within a stand; Fraterrigo and Rusak 2008) decreased with logging

Table 2. Assessment of pre-treatment similarity for the subset of stands with before–after data ($n = 19$), by two-way ANOVA
Comparisons are results of Fisher's *F*-protected least significant difference comparisons with α set at 0.05 to aid interpretation (Ramsey and Schafer 2002). U, burnt, unlogged; M, burnt, moderate-intensity logged; H, burnt, high-intensity logged. *F* statistics and *P* values are shown for treatment effect only; for variables with significant mesic–dry differences, mesic stands had higher absolute amounts. See Appendix 2 for side and interaction terms, means and 95% CIs by treatment, and analysis of pre-post change values

Stand characteristic	Pre-treatment			
	Comparison	$F_{2,13}$	*P*	Mesic–dry differences
Standing dead basal area	U ≈ M ≈ H	1.81	0.203	Y
Snags ha^{-1} (>30-cm DBH)	U ≈ M ≈ H	3.24	0.072	N
Snags ha^{-1} (10–30-cm DBH)	U ≈ M ≈ H	3.19	0.077	N
Snags ha^{-1} (<10-cm DBH)	U ≈ M ≈ H	2.96	0.087	N
Dead biomass total	U ≈ M ≈ H	1.63	0.233	Y
Dead biomass aerial	U ≈ M ≈ H	1.93	0.184	Y
Dead biomass surface	U ≈ M ≈ H	0.56	0.587	Y
Fine woody detritus (<7.62-cm diameter)	U ≈ M ≈ H	0.16	0.851	N
Coarse woody detritus (>7.62-cm diameter)	U ≈ M ≈ H	0.55	0.590	Y
Live biomass total	U ≈ M ≈ H	1.30	0.306	N
Live biomass aerial[A]	U ≈ M ≈ H	n/a	n/a	N
Live biomass surface	U ≈ M ≈ H	1.30	0.306	N

[A]Live biomass aerial = 0 in all plots.

intensity, with a CV% respectively of 110.9, 56.7 and 40.3 in U, M and H stands, compared with 72.0 in M/OG stands (Fig. 5*d*). These effects were similar in each forest type.

Discussion

The effect of post-fire logging on fuel profiles and stand structures varied significantly with harvest intensity and among forest types. Our findings yield several inferences regarding post-disturbance biomass dynamics and for developing post-fire management prescriptions.

Fire effects

Our estimate of total biomass consumption by stand-replacement fire (17%) agrees well with literature estimates for Douglas-fir and mixed-conifer forests (16–24%) (Fahnestock and Agee 1983; Campbell *et al.* 2007; Meigs *et al.* 2009). Even active crown fires that kill nearly all trees tend to consume little aerial biomass – primarily leaves and small branches (Call and Albini 1997) – with most actual consumption occurring in the surface stratum.

Post-fire logging effects

Treatment effects by biophysical setting and intensity

As expected, post-fire logging removed some aerial biomass and transferred some to the surface, but these effects varied by biophysical setting and logging intensity. Surface fuel loads increased more with logging in mesic *v.* drier stands; mesic stands had more basal area standing, more basal area cut and thus larger increases in surface fuels. This was reflected in the positive relationship between the amount of basal area cut and resulting surface fuels (Fig. 4). This relationship likely has applicability across forest types, as the structural metric of basal area is generally a strong predictor of bole and branch biomass even as stand composition varies. For example, whereas post-fire logging in comparatively low-basal-area *P. ponderosa* forests resulted in much lower surface fuel loads than we report (McIver and Ottmar 2007; Keyser *et al.* 2009), the relationships between basal area cut and surface fuel accumulation in those studies correspond well to the association shown in Fig. 4. This predictive relationship could be used as a tool for post-fire management to anticipate ranges of surface fuel loads given different harvest intensities.

An important factor in post-disturbance stands is fuel continuity (Fraterrigo and Rusak 2008; Donato *et al.*, in press). In the case of fire, consumption of ground and surface fuels generally results in highly patchy residual fuel and low horizontal continuity. Re-burns are thus unlikely to carry through young stands initially. Post-fire logging decreased this spatial heterogeneity, resulting in more spatially continuous woody surface fuels (Fig. 5). In high-intensity logged stands, percentage cover of wood was higher, and stand-scale variation in CWD mass lower, than in burn-only or M/OG stands. The areal cover of live vegetation was little affected, however. Increased continuity of woody fuels may become important if it helps close the window of low fire spread capacity sooner, or if, in combination with other fuel components, post-harvest fuels contribute to meeting a threshold for fire propagation. In highly productive fire-prone regions such as the Klamath–Siskiyou, the low fire spread window may close relatively quickly as regenerating vegetation and new litter inputs accumulate on the surface, likely within 5–10 years (Table 1, Fig. 2; Hobbs *et al.* 1992; Stuart *et al.* 1993; Fontaine *et al.* 2009). Assessing the effects of changes in fuel continuity is difficult because common fire models do not adequately address stand-scale spatial heterogeneity (e.g. Stephens and Moghaddas 2005).

Relevance to follow-up treatments

These data indicate that with moderate-intensity logging, a mean of ~86% of felled tree biomass was actually removed from the site whereas ~14% remained on the ground as slash (6.1 : 1 ratio), compared with high-intensity logged

Table 3. Post-treatment stand characteristics (point estimate, 95% CI) and statistical comparisons of unlogged (U), moderate-intensity logged (M) and high-intensity logged (H) burn stands
$n = 8$, 7, 6 for U, M, H in drier stands; and 3 each for U, M, H in mesic stands. See Table 4 for standard errors and individual biomass pools. 95% CIs were derived from two-way ANOVA outputs. Trt, treatment (U, M, H), Ftype, forest type (mesic, drier)

Stand characteristic	Mesic stands			Drier stands			Two-way ANOVA result (*P*)		
	U	M	H	U	M	H	Trt (d.f. = 2,24)	Ftype (d.f. = 1,24)	Trt × Ftype (d.f. = 2,24)
Standing dead basal area ($m^2 ha^{-1}$)	94.3 (41.8–213)	41.5 (18.4–93.6)	2.5 (1.1–5.7)	68.1 (41.4–112)	23.7 (13.9–40.3)	9.7 (5.4–17.1)	<0.0001	0.586	0.019
Snags ha^{-1} (>30-cm DBH)	137 (50.8–368)	55.7 (20.7–150)	2.5 (0.9–6.7)	165 (90.1–303)	72.5 (37.9–139)	29.4 (14.6–59.3)	<0.0001	0.007	0.015
Snags ha^{-1} (10–30-cm DBH)	211 (69.5–640)	303 (99.8–918)	2.8 (0.9–8.5)	237 (120–468)	149 (71.9–308)	45.9 (20.9–101)	<0.0001	0.060	0.002
Snags ha^{-1} (<10-cm DBH)	124 (20.9–736)	334 (56.4–1981)	10.2 (1.7–60.7)	717 (241–2132)	622 (194–1994)	39.0 (11.1–137)	0.0005	0.049	0.733
Dead biomass total ($Mg ha^{-1}$)	709 (555–864)	355 (201–510)	244 (89.5–398)	435 (340–530)	182 (80.8–283)	161 (51.9–270)	<0.0001	0.002	0.336
Dead biomass aerial ($Mg ha^{-1}$)	681 (537–825)	253 (109–398)	21.2 (0.0–166)	419 (330–507)	113 (18.0–207)	43.0 (0.0–145)	<0.0001	0.015	0.076
Dead biomass surface ($Mg ha^{-1}$)	28.1 (0.0–63.1)	102 (66.9–137)	223 (188–258)	16.4 (0.0–37.8)	69.5 (46.6–92.4)	118 (93.4–141)	<0.0001	0.0003	0.010
Fine woody detritus ($Mg ha^{-1}$) (<7.62-cm diameter)	1.4 (0.0–5.1)	12.8 (9.1–16.5)	19.0 (15.3–22.7)	2.5 (0.2–4.8)	5.7 (3.3–8.1)	15.6 (13.0–18.2)	<0.0001	0.019	0.041
Coarse woody detritus ($Mg ha^{-1}$) (>7.62-cm diameter)	25.6 (0.0–56.8)	72.0 (40.8–103)	173 (142–205)	8.9 (0.0–28.0)	52.1 (31.7–72.5)	82.9 (60.8–105)	<0.0001	0.0005	0.013
Live biomass total ($Mg ha^{-1}$)	5.6 (3.4–7.8)	7.3 (5.1–9.5)	1.6 (0.0–3.8)	4.9 (3.5–6.3)	4.9 (3.4–6.4)	2.8 (1.2–4.4)	0.0008	0.385	0.170
Live biomass aerial ($Mg ha^{-1}$)	0	0	0	0	0	0	n/a	n/a	n/a
Live biomass surface ($Mg ha^{-1}$)	5.6 (3.4–7.8)	7.3 (5.1–9.5)	1.6 (0.0–3.8)	4.9 (3.5–6.3)	4.9 (3.4–6.4)	2.8 (1.2–4.4)	0.0008	0.385	0.170

stands in which the ratio averaged ~72 : 28% (2.6 : 1). In general, moderate-intensity logging on the Biscuit Fire occurred when only fire-killed trees deemed merchantable were felled, whereas high-intensity logging occurred when nearly all fire-killed trees were felled and only merchantable logs then yarded. This greater selectivity of moderate-intensity treatment suggests a more deliberate approach to post-fire wood management that is more likely to result in prescribed down wood levels, *v.* high-intensity treatment in which resulting levels become more dependent on timber decay status and merchantability, regardless of prescription (see Rickards 1989).

From a management perspective, optimum ranges of down wood in fire-prone forests aim to balance the ecological functions of dead wood with its contribution to fire potentials (Brown *et al.* 2003). Though not derived specifically for the Klamath–Siskiyou region, the range given for cooler forests (23–68 $Mg ha^{-1}$ of CWD) provides context for the post-logging fuel loads we measured. After moderate-intensity logging or no treatment, surface CWD loads were within or near this range (Fig. 2). High-intensity logging generated surface fuel loads well above these levels. This suggests that moderate-intensity logging or no treatment may result in acceptable (or even prescribed) fuel loads in the short term, whereas high-intensity logging may require additional treatments to mitigate short-term fire potentials.

Data following timber harvest alone provide insight as to when slash treatments may be warranted, and are relevant to operations in which slash is left on site (e.g. McIver and Ottmar 2007; and much of the Biscuit Fire). Studies in both young and mature unburnt stands have reported increased fire severity associated with untreated slash from logging and fuel-reduction treatments (e.g. Weatherspoon and Skinner 1995; Stephens 1998; Raymond and Peterson 2005; Stephens and Moghaddas 2005). Our empirical data suggest a potential need for follow-up slash treatments after dead tree (snag) removal as well, primarily after high-intensity logging, consistent with a modelling study conducted in the Sierra Nevada mountains of California, USA (Stephens 1998). Relatively few of our sampled stands from the Biscuit Fire received secondary treatments, precluding sufficient sample size or timing to assess their effects.

Influence of harvest timing

The time period between fire and logging may play a role in the amount of surface fuels generated (longer time → greater snag decay → lower merchantability → more material left on ground after felling). Our data suggest this was not a major driver in the case of the Biscuit fire because (1) no fine fuels have timber merchantability in any case and (2) nearly all coarse fuel increases could be accounted for by non-merchantable species and parts, pre-fire decay, and standard timber defect and breakage rates (Snell and Brown 1980). Based on our biomass data and allometries for merchantable boles (Means *et al.* 1994), we estimate that at least ~40% of post-fire biomass is not merchantable, even immediately post fire. This again highlights the importance of considering the non-merchantable component of post-fire wood (fine and fragmented or rotted coarse fuels) where management of early-seral fire potentials is an objective.

Table 4. Mean (s.e.) aboveground biomass pools (Mg ha^{-1}), separated by category, 3–4 years after stand-replacement wildfire and subject to three post-fire treatments: unlogged (U), moderate-intensity logged (M) and high-intensity logged (H)
$n = 8, 7, 6$ for U, M, H in drier stands; and 3 each for U, M, H in mesic stands

Biomass category	Mesic stands			Drier stands		
	U	M	H	U	M	H
Dead mass						
Aerial stratum						
Branch	49.4 (11.1)	11.4 (7.4)	0.0 (0.0)	76.3 (10.4)	20.6 (6.0)	5.4 (1.8)
Stem	632 (130)	242 (84.8)	21.2 (16.8)	342 (44.6)	91.8 (18.5)	37.6 (14.3)
Surface stratum						
Stem + branch	0.9 (0.4)	3.8 (1.7)	0.4 (0.3)	4.7 (0.7)	3.3 (1.0)	0.5 (0.3)
Stumps	0.2 (0.2)	13.3 (4.2)	29.9 (7.5)	0.2 (0.1)	8.4 (1.9)	19.2 (1.9)
<0.62-cm fuels	0.2 (0.0)	0.6 (0.2)	0.8 (0.1)	0.3 (0.1)	0.4 (0.1)	0.6 (0.2)
0.62–2.54-cm fuels	0.6 (0.2)	2.6 (0.5)	3.6 (0.1)	0.9 (0.1)	1.5 (0.2)	4.1 (0.6)
2.55–7.62-cm fuels	0.6 (0.4)	9.7 (0.8)	14.6 (0.9)	1.3 (0.2)	3.8 (0.6)	10.9 (2.0)
7.63–20.32-cm fuels	2.8 (1.2)	13.1 (4.1)	15.6 (3.6)	1.1 (0.2)	5.4 (1.1)	13.8 (2.0)
>20.32-cm fuels	22.9 (21.2)	58.9 (13.4)	158 (8.8)	7.8 (1.8)	46.7 (13.4)	69.1 (9.3)
Live mass						
Aerial stratum						
Stem + branch	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Surface stratum						
Foliage	1.0 (0.2)	2.5 (0.4)	0.2 (0.1)	1.6 (0.3)	1.7 (0.4)	0.6 (0.1)
Stem + branch	1.8 (0.2)	3.6 (0.5)	0.4 (0.2)	2.4 (0.5)	2.9 (0.5)	0.9 (0.1)
Forbs/low shrubs	2.9 (0.9)	1.2 (0.2)	1.0 (0.4)	0.9 (0.2)	0.3 (0.1)	1.3 (0.3)

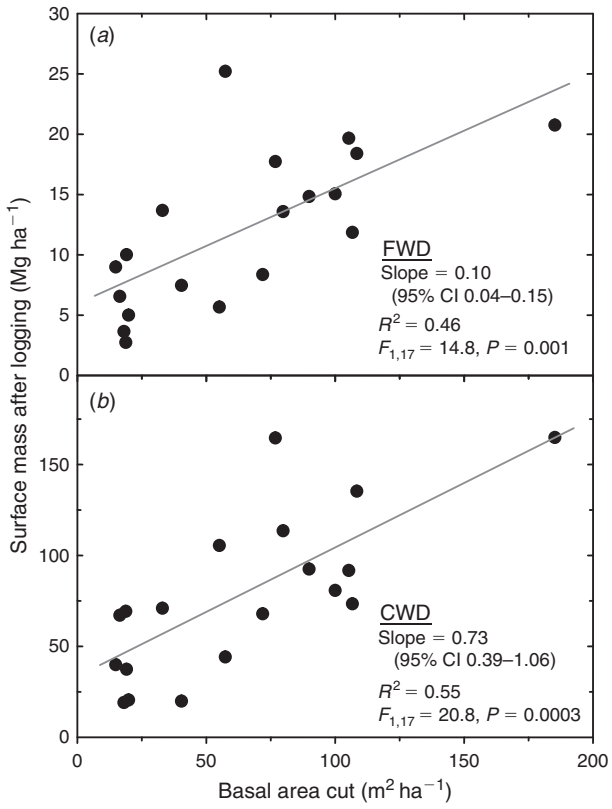


Fig. 4. Surface mass of fine (*a*) and coarse (*b*) woody detritus after post-fire logging as a function of total basal area cut.

Longer term considerations

These data provide information on immediate changes in fuel profiles with post-fire logging and are short term in nature. Over time, slash fuels left in place will decay and snags left in place will fragment and fall to the surface. Studies from dry continental-interior forest types (e.g. *P. ponderosa* or *P. contorta*) indicate that unlogged stands eventually accumulate greater surface fuel loads (Monsanto and Agee 2008; Keyser *et al.* 2009). McIver and Ottmar (2007), also working in interior dry forests, used models to project post-fire surface fuel loads and suggested that fine fuel loads remained greater in logged stands for ~20 years, but coarse fuel loads would be lower in logged stands from ~20–50 years post fire. Passovoy and Fulé (2006) concluded that, in the absence of management, CWD loads up to 27 years post fire in a ponderosa pine system remained within acceptable ranges outlined by Brown *et al.* (2003), and suggested that post-fire logging for fuel reduction appeared unnecessary. The need for and outcomes of management treatments may depend largely on forest type as well as yarding method and slash treatment, but the latter have not always been clear for studies of older fires and considerable uncertainties remain.

Initial studies in the Klamath–Siskiyou region suggest that unlogged stands may not have higher fuel loads until at least two to three decades after fire (Donato 2008). Longer-term snag dynamics are poorly understood for mixed-evergreen forests of the western USA, but forest inventory data suggest relatively rapid wood decay in this region (Hudiburg *et al.* 2009), which may lessen the surface accumulation of snag biomass. Consistent with this pattern is evidence of greatly diminished woody

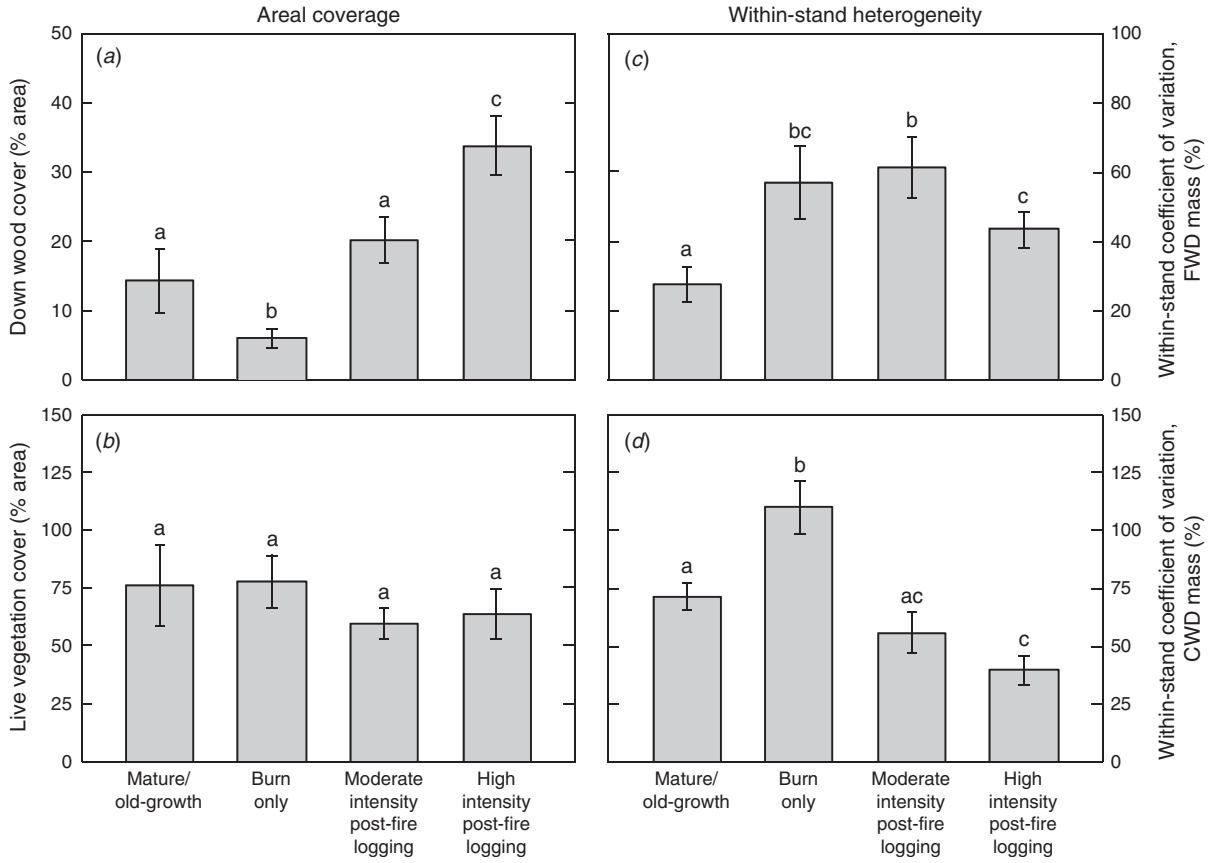


Fig. 5. Mean (±s.e.) cover and spatial variation in surface fuels. Lower-case letters above bars denote significant differences at $\alpha = 0.05$ based on the one-way ANOVA across all stands. Areal coverages are percentage of ground area of down wood (*a*) and live vegetation (*b*). Within-stand spatial heterogeneity is estimated by computing the coefficient of variation among transects within each sample stand, for fine down wood (*c*) and coarse down wood (*d*).

biomass in 18-year-old fires in this region and little to no difference in surface fuel loads between managed and unmanaged stands at that post-fire age (Donato 2008). Evidence also suggested rapid decay of snag and down wood biomass, with single-exponential decay constants (Harmon *et al.* 1986) of ~0.030 to 0.040 for all standing and down material combined; a value comparable with other studies in Douglas-fir forests (Sollins 1982; Agee and Huff 1987; Spies *et al.* 1988). Those findings agree well with observations 10 years after another fire in the region (56.5 *v.* 56.8 Mg ha^{-1} in logged *v.* unmanaged stands; Bureau of Land Management, Medford, OR, unpubl. data, 2003), as well as a recent study from the Sierra Nevada that reported higher dead fuel loads in post-fire logged stands up to 21 years after fire (McGinnis *et al.* 2010). In highly productive fire-prone systems, fast decay may reduce the contribution of residual post-fire wood to early-seral fire potentials, whereas the live component of regenerating vegetation, which accumulates biomass and continuity quickly (Hobbs *et al.* 1992), may be a much more important driver of fire potentials in young stands (Donato 2008).

Uncertainties and future research

An important research objective is better quantifying regional differences in snag decay rates, standing biomass and productivity within the context of post-fire fuel profile development. Remarkably few studies have quantified the overall decay rate of post-disturbance snags – integrating fragmentation, falling and mineralisation during both the standing and down phases (see Donato *et al.*, in press). We hypothesise that discrepancies in fuel loads between post-fire logged and unmanaged stands are greater for drier, continental interior forest types, and less so for mesic and coastal forest types, owing to higher rates of vegetation growth and wood decay in the latter systems.

Another seldom addressed issue for post-fire logging is that of fire regime context. Management of post-fire residual wood is often concerned with avoiding surface fuel loads deemed to be excessive with respect to fire potentials (Brown *et al.* 2003); however, pulses of dead wood are a characteristic feature of mixed- and high-severity fire regimes (e.g. Spies *et al.* 1988). Within the context of historic variation, therefore, the ecological basis for reducing post-fire fuels may be most pertinent in low-severity fire regimes where large pulses of fire-killed trees are considered outside the historic range of variation (see Monsanto and Agee 2008).

Although the applicability of common fire models to post-fire settings is not well established (Passovoy and Fulé 2006), known relationships between fuel loads and surface fire behaviour (Rothermel 1983) suggest that post-fire logging may

elevate fire potentials in the short term, other factors being equal. Exploratory analysis using the model BehavePlus 3.0 (Andrews *et al.* 2005) supported this inference, with predicted fire behaviour (e.g. rate of spread, surface flame length, soil heat flux) simply scaling upward with increased fine and coarse fuel loads in treated stands (Donato 2008). Slash from logging or fuel-reduction treatments has been associated with increased fire severity in both young and mature stands in various settings (e.g. Weatherspoon and Skinner 1995; Raymond and Peterson 2005; Stephens and Moghaddas 2005). Nevertheless, local fire behaviour depends on many factors such as fuel continuity, weather, etc., in addition to fuel load. Although we observed greater homogeneity in surface fuels after treatments, fuel continuity is poorly addressed in fire models (Stephens and Moghaddas 2005). Predicted effects could be lessened if fire cannot spread in very young stands due to low continuity, or amplified if post-logging fuels meet a threshold for fire propagation. Other uncertainties include the role of localised pockets of snag-fall (or slash) accumulation, and how the landscape context of post-fire logging units affects larger-scale fire spread.

Snags may contribute to fire behaviour by 'candling' and providing ember sources that can lead to spot fires. Oregon's 1933 Tillamook Burn, which re-burnt three times at 6-year intervals, is a commonly cited example of the fire contribution of snags since fires ceased to occur following extensive snag removal (Kemp 1967). However, the Tillamook Burn narrative is complicated by the fact that all three re-burns were started by post-fire logging operations and burnt through a mix of both logged and unlogged areas (Kemp 1967; Peterson *et al.* 2009). Surface or ground fuels are the primary carrier of wildfire and contribute most to soil heating and regeneration mortality (Pyne *et al.* 1996). The role of snags in fire behaviour has been the subject of little quantitative study, is not captured by available fire modelling frameworks and warrants future research.

Conclusions and management implications

Post-fire logging in this high-biomass, fire-prone system reduced standing fuel mass as expected, but the amount of material transferred to the surface varied by both environmental setting and treatment. Post-logging fuel loads were greater in higher basal-area mesic forests and with higher-intensity harvest. These findings suggest that reports of either increased or decreased fire severity following post-disturbance logging (Hansen 1983; Kulakowski and Veblen 2007; Thompson *et al.* 2007; Buma and Wessman 2011; Fraver *et al.* 2011) may stem in part from variation among studies in terms of harvest intensity and pre-disturbance forest structure. We also found that the efficiency of biomass removal (the proportion of biomass felled and removed versus felled and left on site) and the spatial heterogeneity of surface fuels both decreased with increasing harvest intensity. The general relationship we identified between harvest intensity (basal area cut) and resulting surface fuels likely has applicability across diverse forest types and could provide a useful predictive tool for developing post-fire management prescriptions.

Post-fire timber harvest is generally an economic rather than restorative undertaking (Peterson *et al.* 2009). From a fire management perspective, studies from several regions have reported inherently high fire potentials in early-seral stands, with limited efficacy of stand-level fuel treatments in reducing these potentials (Roloff *et al.* 2005; Stephens and Moghaddas 2005; McIver and Ottmar 2007; Thompson *et al.* 2007; McGinnis *et al.* 2010; but see Weatherspoon and Skinner 1995). As such, alternative or additional treatments may be necessary where objectives include reducing fire potentials, such as landscape fuel breaks (Agee *et al.* 2000) and managing for diverse vegetation structure (Donato *et al.* 2012). Where post-fire logging is conducted, our results suggest that moderate-intensity treatment results in surface fuel loads most consistent with prescribed levels when compared with high-intensity treatment, and may reduce the potential need for follow-up fuel treatments (e.g. slash piling, burning). Because moderate-intensity treatment leaves a greater proportion of snags standing, it may also be most compatible with objectives pertaining to the many other ecological roles of snags (e.g. wildlife habitat; Fontaine *et al.* 2009). Longer-term effects of post-fire logging on snag-fall inputs and coarse fuel loads remain an important research question. Finally, given the paucity of data on post-fire management effects, designing management projects with replication, pre-treatment data and controls as in this study will best clarify the tradeoffs of various post-fire interventions.

Acknowledgements

This research was supported by the Joint Fire Science Program and the Office of Science (BER), US Department of Energy (DOE, DF-FG02–04ER63917), and facilitated by the Siskiyou National Forest (Rogue River) and Bureau of Land Management (Medford, OR). The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions or policies of the USA Government. Mention of trade names or commercial products does not constitute their endorsement by the USA Government. We thank M. Huso for invaluable statistical advice; D. Peterson, G. Meigs, G. Riegel, J. Bailey, J. Campbell, J. Chamberlin, J. Jones, J. Thompson, M. Harmon and T. Spies for helpful reviews and discussions; and field crews for help with data collection.

References

Agee JK (1991) Fire history along an elevational gradient in the Siskiyou Mountains, Oregon. *Northwest Science* **65**, 188–199.

Agee JK (1993) 'Fire ecology of Pacific Northwest Forests.' (Island Press: Washington, DC)

Agee JK, Huff MH (1987) Fuel succession in a western hemlock/Douglas-fir forest. *Canadian Journal of Forest Research* **17**, 697–704. doi:10.1139/X87-112

Agee JK, Skinner CN (2005) Basic principles of forest fuel reduction treatments. *Forest Ecology and Management* **211**, 83–96. doi:10.1016/J.FORECO.2005.01.034

Agee JK, Bahro B, Finney MA, Omi PN, Sapsis DB, Skinner CN, van Wagtendonk JW, Weatherspoon CP (2000) The use of shaded fuelbreaks in landscape fire management. *Forest Ecology and Management* **127**, 55–66. doi:10.1016/S0378-1127(99)00116-4

Andrews PL, Bevins CD, Seli RC (2005) BehavePlus fire modeling system, version 3.0: users guide. USDA Forest Service, Rocky Mountain Research Station, General Technical Report GTR-RMRS-106. (Ogden, UT)

Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* **20**(7), 387–394. doi:10.1016/J.TREE.2005.04.025

Brown JK (1974) Handbook for inventorying downed woody material. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report GTR-INT-16. (Ogden, UT)

Brown JK, Reinhardt ED, Kramer KA (2003) Coarse woody debris: managing benefits and fire hazard in the recovering forest. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-105. (Ogden, UT)

Buma B, Wessman CA (2011) Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* **2**(5), art64. doi:10.1890/ES11-00038.1

Call PT, Albini FA (1997) Aerial and surface fuel consumption in crown fires. *International Journal of Wildland Fire* **7**(3), 259–264. doi:10.1071/WF9970259

Campbell J, Donato DC, Azuma D, Law B (2007) Pyrogenic carbon emission from a large wildfire in Oregon, United States. *Journal of Geophysical Research – Biogeosciences* **112**, G04014. doi:10.1029/2007JG000451

Cline SP, Berg AB, Wight HM (1980) Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *The Journal of Wildlife Management* **44**, 773–786. doi:10.2307/3808305

Cruz MG, Alexander ME (2010) Assessing crown fire potential in coniferous forests of western North America: a critique of current approaches and recent simulation studies. *International Journal of Wildland Fire* **19**, 377–398. doi:10.1071/WF08132

Daly C, Gibson WP, Taylor GH, Johnson GL, Pasteris P (2002) A knowledge-based approach to the statistical mapping of climate. *Climate Research* **22**, 99–113. doi:10.3354/CR022099

Donato DC (2008) Forest vegetation and fuel dynamics following high-severity fire, re-burn, and post-fire management in the Siskiyou Mountains, OR. PhD dissertation. Oregon State University, Corvallis, OR.

Donato DC, Fontaine JB, Campbell JL, Robinson WD, Kauffman JB, Law BE (2006*a*) Post-wildfire logging hinders regeneration and increases fire risk. *Science* **311**, 352. doi:10.1126/SCIENCE.1122855

Donato DC, Fontaine JB, Campbell JL, Robinson WD, Kauffman JB, Law BE (2006*b*) Technical Comment. *Science* **313**, 615c. doi:10.1126/SCIENCE.1126583

Donato DC, Fontaine JB, Campbell JL, Robinson WD, Kauffman JB, Law BE (2009*a*) Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath–Siskiyou Mountains. *Canadian Journal of Forest Research* **39**, 823–838. doi:10.1139/X09-016

Donato DC, Campbell JL, Fontaine JB, Law BE (2009*b*) Quantifying char in post-fire woody detritus inventories. *Fire Ecology* **5**, 104–115. doi:10.4996/FIREECOLOGY.0502104

Donato DC, Fontaine JB, Robinson WD, Kauffman JB, Law BE (2009*c*) Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. *Journal of Ecology* **97**, 142–154. doi:10.1111/J.1365-2745.2008.01456.X

Donato DC, Campbell JL, Franklin JF (2012) Multiple successional pathways and precocity in forest development: can some forests be born complex? *Journal of Vegetation Science* **23**, 576–584. doi:10.1111/J.1654-1103.2011.01362.X

Donato DC, Harvey BJ, Romme WH, Simard M, Turner MG Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. *Ecological Applications*, in press.

Everett R, Lehmkuhl J, Schellhaas R, Ohlson P, Keenum D, Riesterer H, Spurbeck D (1999) Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington State, USA. *International Journal of Wildland Fire* **9**, 223–234. doi:10.1071/WF00011

Fahnestock GR, Agee JK (1983) Biomass consumption and smoke production by prehistoric and modern forest fires in western Washington. *Journal of Forestry* **81**, 653–657.

Fontaine JB, Donato DC, Robinson WD, Law BE, Kauffman JB (2009) Bird communities following high-severity fire: response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. *Forest Ecology and Management* **257**, 1496–1504. doi:10.1016/J.FORECO.2008.12.030

Fontaine JB, Donato DC, Campbell JL, Martin JG, Law BE (2010) Effects of post-fire logging on forest surface air temperatures in the Siskiyou Mountains, Oregon, USA. *Forestry* **83**, 477–482. doi:10.1093/FORESTRY/CPQ030

Franklin JF, Dyrness CT (1973) Natural vegetation of Oregon and Washington. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW-GTR-008. (Portland, OR)

Fraterrigo JM, Rusak JA (2008) Disturbance-driven changes in the variability of ecological patterns and processes. *Ecology Letters* **11**, 756–770. doi:10.1111/J.1461-0248.2008.01191.X

Fraver S, Jain Y, Bradford JB, D'Amato AW, Kastendick D, Palik B, Shinneman D, Staonovick J (2011) The efficacy of salvage logging in reducing subsequent fire severity in conifer-dominated forests of Minnesota, USA. *Ecological Applications* **21**(6), 1895–1901. doi:10.1890/11-0380.1

Graham RT, McCaffrey S, Jain TB (2004) Science basis for changing forest structure to modify wildfire behavior and severity. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-120. (Fort Collins, CO)

Hall SA, Burke IC, Hobbs NT (2006) Litter and dead wood dynamics in ponderosa pine forests along a 160-year chronosequence. *Ecological Applications* **16**, 2344–2355. doi:10.1890/1051-0761(2006)016[2344:LADWDI]2.0.CO;2

Halofsky JE, Donato DC, Hibbs DE, Campbell JL, Donaghy-Cannon M, Fontaine JB, Thompson JR, Anthony RG, Bormann BT, Kayes LJ, Law BE, Peterson DL, Spies TA (2011) Mixed-severity fire regimes: lessons from the Klamath–Siskiyou ecoregion. *Ecosphere* **2**, art40. doi:10.1890/ES10-00184.1

Hansen SB (1983) The effects of the Baxter Park fire on the vegetation and soils of several coniferous stands. MSc thesis. University of Maine.

Harmon ME, Sexton J (1996) Guidelines for measurements of woody detritus in forest ecosystems. United States Long Term Ecological Research Network Office, University of Washington, Publication number 20. (Seattle, WA)

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* **15**, 133–302. doi:10.1016/S0065-2504(08)60121-X

Hobbs SD, Tesch SD, Owston PW, Stewart RE, Tappeiner JC, Wells GE (Eds) 1992. Reforestation practices in southwestern Oregon and northern California. Forest Research Laboratory, Oregon State University. (Corvallis, OR)

Hudiburg T, Law BE, Campbell JL, Donato DC, Duane M, Turner DP (2009) Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. *Ecological Applications* **19**, 163–180. doi:10.1890/07-2006.1

Kemp JL (1967) 'Epitaph for the Giants: the Story of the Tillamook Burn.' (Touchstone Press: Portland, OR)

Keyser TL, Smith FW, Sheppard WD (2009) Short-term impact of post-fire logging on regeneration, hazardous fuel accumulation, and understorey development in ponderosa pine forests of the Black Hills, SD, USA. *International Journal of Wildland Fire* **18**, 451–458. doi:10.1071/WF08004

Kulakowski D, Veblen TT (2007) Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology* **88**, 759–769. doi:10.1890/06-0124

McGinnis TW, Keeley JE, Stephens SL, Roller GB (2010) Fuel buildup and potential fire behavior after stand-replacing fires, logging fire-killed trees and herbicide removal in Sierra Nevada forests. *Forest Ecology and Management* **260**, 22–35. doi:10.1016/J.FORECO.2010.03.026

McIver JD, Ottmar R (2007) Fuel mass and stand structure after post-fire logging of a severely burnt ponderosa pine forest in northeastern Oregon. *Forest Ecology and Management* **238**, 268–279. doi:10.1016/J.FORECO.2006.10.021

McIver JD, Starr L (2001) A literature review on the environmental effects of post-fire logging. *Western Journal of Applied Forestry* **16**, 159–168.

Means JH, Hansen HA, Koerper GJ, Alaback PB, Klopsch MW (1994) Software for computing plant biomass–Biopak users guide. USDA Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-340. (Portland, OR)

Meigs GW, Donato DC, Campbell JL, Martin JG, Law BE (2009) Forest fire impacts on carbon uptake, storage, and emission: the role of burn severity in the eastern Cascades, Oregon. *Ecosystems* **12**, 1246–1267. doi:10.1007/S10021-009-9285-X

Monsanto PG, Agee JK (2008) Long-term post-wildfire dynamics of coarse woody debris after salvage logging and implications for soil heating in dry forests of the eastern Cascades, Washington. *Forest Ecology and Management* **255**, 3952–3961. doi:10.1016/J.FORECO.2008.03.048

Passovoy AD, Fulé PZ (2006) Snag and woody debris dynamics following severe wildfires in northern Arizona ponderosa pine forests. *Forest Ecology and Management* **223**, 237–246. doi:10.1016/J.FORECO.2005.11.016

Pedlar JH, Pearce JL, Venier LA, McKenney DW (2002) Coarse woody debris in relation to disturbance and forest type in boreal Canada. *Forest Ecology and Management* **158**, 189–194. doi:10.1016/S0378-1127(00)00711-8

Peterson DL, Agee JK, Aplet GH, Dykstra DP, Graham RT, Lehmkuhl JF, Pilliod DS, Potts DF, Powers RF, Stuart JD (2009) Effects of timber harvest following wildfire in western North America. USDA Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-776. (Portland, OR)

Pyne SJ, Andrews PL, Laven RD (1996) 'Introduction to Wildland Fire', 2nd edn. (Wiley: New York)

Ramsey FL, Schafer DW (2002) 'The Statistical Sleuth', 2nd edn, (Duxbury: Pacific Grove, CA)

Raymond CL, Peterson DL (2005) Fuel treatments alter the effects of wildfire in a mixed-evergreen forest, Oregon, USA. *Canadian Journal of Forest Research* **35**, 2981–2995. doi:10.1139/X05-206

Rickards L (1989) Wildlife reserve tree & large woody material – Silver Fire monitoring. Rogue River-Siskiyou National Forest. (Grants Pass, OR)

Roloff GJ, Mealey SP, Clary C, Barry J (2005) Evaluating risks associated with forest management scenarios in areas dominated by mixed-severity fire regimes in southwest Oregon. In 'Mixed Severity Fire Regimes: Ecology and Management'. (Eds L Taylor, J Zelnik, S Cadwallader, B Hughes) (Association for Fire Ecology: Spokane, WA)

Rothermel RC (1983) How to predict the spread and intensity of forest and range fires. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-143. (Ogden, UT)

Snell JAK, Brown JK (1980) Handbook for predicting residue weights of Pacific Northwest conifers. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report GTR-PNW-103. (Portland, OR)

Sollins P (1982) Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Canadian Journal of Forest Research* **12**, 18–28. doi:10.1139/X82-003

Spies TA, Franklin JF, Thomas TB (1988) Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* **69**, 1689–1702. doi:10.2307/1941147

Stephens SL (1998) Evaluation of effects of silvicultural and fuels treatments on potential fire behavior in Sierra Nevada mixed conifer forests. *Forest Ecology and Management* **105**, 21–35. doi:10.1016/S0378-1127(97)00293-4

Stephens SL, Moghaddas JJ (2005) Silvicultural and reserve impacts on potential fire behavior and forest conservation: twenty-five years of experience from Sierra Nevada mixed conifer forests. *Biological Conservation* **125**, 369–379. doi:10.1016/J.BIOCON.2005.04.007

Stephens SL, Moghaddas JJ, Edminster C, Fiedler CE, Haase S, Harrington M, Keeley JE, Knapp EE, McIver JD, Metlen K, Skinner CN, Youngblood A (2009) Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. *Ecological Applications* **19**, 305–320. doi:10.1890/07-1755.1

Stuart JD, Salazar LA (2000) Fire history of white fir forests in the coastal mountains of northwestern California. *Northwest Science* **74**, 280–285.

Stuart JD, Grifantini MC, Fox L, III (1993) Early successional pathways following wildfire and subsequent silvicultural treatment in Douglas-fir/hardwood forests, NW California. *Forest Science* **39**, 561–572.

Taylor AH, Skinner CN (1998) Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecology and Management* **111**, 285–301. doi:10.1016/S0378-1127(98)00342-9

Thompson JR, Spies TA, Ganio LM (2007) Re-burn severity in managed and unmanaged vegetation in a large wildfire. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 10 743–10 748. doi:10.1073/PNAS.0700229104

Thornburgh DA (1982) Succession in the mixed evergreen forests of northwestern California. In 'Forest Succession and Stand Development Research in the Northwest'. (Ed. JE Means) pp. 87–91. (Forest Research Laboratory: Corvallis, OR)

USDA (2003*a*) Annual inventory 2003 field guide supplement: fire effects and recovery. USDA Forest Service, Pacific Northwest Research Station. (Portland, OR)

USDA (2003*b*) Field instructions for the annual inventory of Washington, Oregon and California. USDA Forest Service, Pacific Northwest Research Station, Forest Inventory and Analysis Program. (Portland, OR)

USDA (2004) Biscuit Fire Recovery Project Final Environmental Impact Statement. USDA Forest Service, Pacific Northwest Region. (Medford, OR)

Van Tuyl S, Law BE, Turner DP, Gitelman AI (2005) Variability in net primary production and carbon storage in biomass across Oregon forests – an assessment integrating data from forest inventories, intensive sites, and remote sensing. *Forest Ecology and Management* **209**, 273–291. doi:10.1016/J.FORECO.2005.02.002

Walters DK, Hann DW, Clyde MA (1985) Equations and tables predicting gross total stem volumes in cubic feet for six major conifers of southwest Oregon. Oregon State University, Forest Research Laboratory, Research Bulletin 50. (Corvallis, OR)

Weatherspoon CP, Skinner CN (1995) An assessment of factors associated with damage to tree crowns from the 1987 wildfires in northern California. *Forest Science* **41**, 430–451.

Whittaker RH (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs* **30**, 279–338. doi:10.2307/1943563

Wills RD, Stuart JD (1994) Fire history and stand development of a Douglas-fir/hardwood forest in northern California. *Northwest Science* **68**, 205–212.

Appendix 1. Adjustments to tree mass computations for decay and fragmentation

Adjustments to tree mass components for decay status (e.g. wood density) were largely obtained from Harmon and Sexton (1996). For broken-topped trees, stem volume was computed using an equation for a tapered cylinder, $0.8\ \pi r^2 h$, and branch and bark masses were reduced proportional to amount of crown lost to breakage. Additional adjustments for branches and bark were adapted from several sources as shown in Table A1.

Table A1. Decay class adjustments to tree branch and bark computations
Estimates adapted from Cline *et al.* (1980), Harmon and Sexton (1996), Van Tuyl *et al.* (2005)

Characteristic	Decay class				
	1	2	3	4	5
Ratio of branch volume to original volume	1.00	0.80	0.40	0.00	0.00
Ratio of branch density to original density	1.00	0.78	0.67	0.38	0.37
Ratio of bark mass to original mass	1.00	1.00	0.20	0.00	0.00

Appendix 2. Means, 95% confidence intervals and two-way ANOVA outputs from assessment of pre-treatment similarity and pre-post change for subset of plots with before–after data

Table A2. Means, 95% CIs (in parentheses) and two-way ANOVA test statistics for pre-treatment comparisons for the subset of stands with before–after data ($n = 19$)
See text for treatment descriptions. Confidence intervals derived from two-way ANOVA. n (subset) = 5, 4, 2 for U, M, H in drier stands and 3, 3, 2 for U, M, H in mesic stands

Stand characteristic	Mesic stands			Drier stands			Two-way ANOVA result (P)		
	U	M	H	U	M	H	Trt (d.f. = 2,13)	Ftype (d.f. = 1,13)	Trt × Ftype (d.f. = 2,13)
Standing dead basal area ($m^2\ ha^{-1}$)	105 (67.0–164)	88.4 (56.5–138)	146.3 (84.6–253)	54.8 (38.7–77.5)	54.0 (36.6–79.5)	75.8 (43.8–131)	0.203	0.004	0.901
Snags ha^{-1} (>30-cm DBH)	152 (99.3–233)	114 (74.6–175)	172 (102–290)	124 (89.2–173)	143 (98.7–207)	271 (161–457)	0.072	0.360	0.287
Snags ha^{-1} (10–30-cm DBH)	194 (89.9–420)	428 (198–926)	43.5 (11.5–165)	243 (103–681)	247 (127–481)	265 (146–481)	0.077	0.161	0.061
Snags ha^{-1} (<10-cm DBH)	489 (131–1820)	1272 (342–4731)	195 (66.9–974)	1276 (461–3530)	1298 (416–4049)	340 (68.0–1701)	0.087	0.335	0.707
Dead biomass total ($Mg\ ha^{-1}$)	859 (540–1178)	914 (595–1232)	1303 (984–1622)	398 (202–593)	309 (100–518)	459 (234–685)	0.233	0.0002	0.501
Dead biomass aerial ($Mg\ ha^{-1}$)	817 (511–1123)	840 (533–1146)	1251 (945–1557)	364 (176–552)	282 (81.7–483)	444 (227–661)	0.184	0.0002	0.523
Dead biomass surface ($Mg\ ha^{-1}$)	42.3 (6.9–77.7)	74.1 (38.7–110)	51.5 (16.1–86.9)	33.7 (12.0–55.4)	26.6 (3.4–49.8)	15.2 (0.0–40.3)	0.587	0.043	0.439
Fine woody detritus ($Mg\ ha^{-1}$)	1.2 (0.1–2.3)	2.0 (0.9–3.1)	2.0 (0.9–3.1)	1.9 (1.2–2.6)	1.3 (0.6–2.0)	1.7 (0.9–2.5)	0.852	0.818	0.293
Coarse woody detritus ($Mg\ ha^{-1}$)	35.1 (3.3–66.9)	60.3 (28.5–92.1)	47.1 (15.3–78.9)	18.4 (0.0–37.9)	17.1 (0.0–37.9)	1.7 (0.0–24.2)	0.590	0.014	0.542
Live biomass total ($Mg\ ha^{-1}$)	4.3 (1.6–7.0)	5.3 (2.6–8.0)	3.1 (0.4–5.8)	4.2 (2.5–5.9)	3.8 (2.0–5.6)	1.8 (0.0–3.7)	0.306	0.356	0.806
Live biomass aerial ($Mg\ ha^{-1}$)	0	0	0	0	0	0	n/a	n/a	n/a
Live biomass surface ($Mg\ ha^{-1}$)	4.3 (1.6–7.0)	5.3 (2.6–8.0)	3.1 (0.4–5.8)	4.2 (2.5–5.9)	3.8 (2.0–5.6)	1.8 (0.0–3.7)	0.306	0.356	0.806

Table A3. Means, 95% confidence limits (in parentheses) and two-way ANOVA test statistics of pre–post change comparisons for the subset of stands with before–after data (n = 19)

Pre–post change: post-treatment minus pre-treatment value. See text for treatment descriptions. 95% CIs are from ANOVA output. n (subset) = 5, 4, 2 for U, M, H in drier stands and 3, 3, 2 for U, M, H in mesic stands

Stand characteristic	Mesic stands			Drier stands			Two-way ANOVA result (P)		
	U	M	H	U	M	H	Trt (d.f. = 2,13)	Ftype (d.f. = 1,13)	Trt × Ftype (d.f. = 2,13)
Standing dead basal area (m^2 ha^{-1})	−9.7 (−42.8, 23.4)	−50.1 (−83.2, −17.0)	−154 (−195, −113)	3.9 (−21.8, 29.6)	−23.0 (−51.7, 5.7)	−60.0 (−101, −19)	0.0001	0.004	0.077
Snags ha^{-1} (>30-cm DBH)	−16.5 (−40.7, 7.7)	−49.3 (−73.5, −25.1)	−175 (−205, −145)	5.0 (−13.8, 23.8)	−45.1 (−66.1, −24.1)	−190 (−220, −160)	<0.0001	0.704	0.342
Snags ha^{-1} (10–30-cm DBH)	24.4 (−42.2, 91.0)	−130 (−196, −63.2)	−21.8 (−103, 59.8)	21.9 (−29.7, 73.5)	24.5 (−33.2, 82.2)	−162 (−243, −80.2)	0.009	0.883	0.002
Snags ha^{-1} (<10-cm DBH)	−255 (−1518, 1009)	−1224 (−2488, 40)	−597 (−2145, 951)	−444 (−1422, 535)	−263 (−1357, 831)	−266 (−1814, 1281)	0.754	0.468	0.576
Dead biomass total (Mg ha^{-1})	−150 (−417, 117)	−559 (−825, −292)	−1072 (−1399, −746)	12.3 (−194, 219)	−123 (−354, 108)	−262 (−588, 64.6)	0.002	0.0006	0.083
Dead biomass aerial (Mg ha^{-1})	−136 (−425, 153.5)	−586 (−876, −297)	−1246 (−1601, −892)	27.5 (−197, 252)	−149 (−399, 102)	−374 (−729, −19.8)	0.0006	0.0008	0.082
Dead biomass surface (Mg ha^{-1})	−14.1 (−49.3, 21.1)	27.8 (−7.4, 63.0)	174 (131, 217)	−15.2 (−42.5, 12.1)	25.3 (−5.2, 55.8)	113 (69.5, 156)	<0.0001	0.137	0.212
Fine woody detritus (Mg ha^{-1})	0.3 (−2.4, 2.9)	10.8 (8.2, 13.4)	17.6 (14.4, 20.8)	0.3 (−1.7, 2.4)	3.4 (1.2, 5.7)	9.3 (6.1, 12.5)	<0.0001	0.0002	0.007
Coarse woody detritus (Mg ha^{-1})	−9.5 (−37.8, 18.9)	11.7 (−16.6, 40.0)	125 (89.8, 159)	−7.9 (−29.8, 14.0)	17.3 (−7.2, 41.8)	93.5 (58.8, 128)	<0.0001	0.484	0.426
Live biomass total (Mg ha^{-1})	1.4 (−0.3, 3.0)	2.0 (0.3, 3.6)	−1.3 (−3.3, 0.8)	1.9 (0.6, 3.2)	1.5 (0.1, 2.9)	1.0 (−1.0, 3.0)	0.087	0.261	0.297
Live biomass aerial (Mg ha^{-1})	0	0	0	0	0	0	n/a	n/a	n/a
Live biomass surface (Mg ha^{-1})	1.4 (−0.3, 3.0)	2.0 (0.3, 3.6)	−1.3 (−3.3, 0.8)	1.9 (0.6, 3.2)	1.5 (0.1, 2.9)	1.0 (−1.0, 3.0)	0.087	0.261	0.297

CONSERVATION OF AQUATIC AND FISHERY RESOURCES IN THE PACIFIC NORTHWEST:

Implications of New Science for the Aquatic Conservation Strategy of the Northwest Forest Plan

Frissell, Christopher A.

Baker, Rowan. J.

DellaSala, Dominick A.

Hughes, Robert M.

Karr, James R.

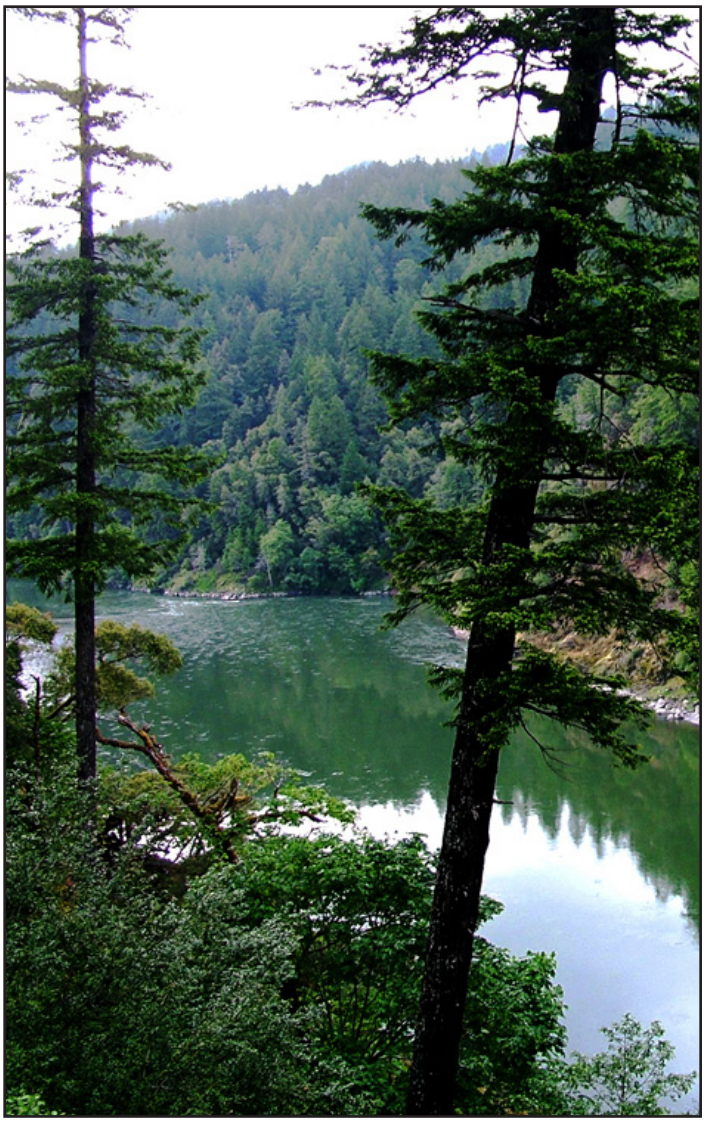
McCullough, Dale A.

Nawa, Richard. K.

Rhodes, Jon

Scurlock, Mary C.

Wissmar, Robert C.



FINAL REPORT
July 30, 2014

Copyright © 2014 Coast Range Association

CONSERVATION OF AQUATIC AND FISHERY RESOURCES IN THE PACIFIC NORTHWEST:

Implications of New Science for the Aquatic Conservation Strategy of the Northwest Forest Plan

ABSTRACT

Twenty years have elapsed since a major science synthesis and planning effort led to adoption of the Aquatic Conservation Strategy (ACS) of the Northwest Forest Plan (NFP) in 1994. Their purpose was to protect and restore riparian and aquatic ecosystems on Pacific Northwest federal forest lands and to ensure that forest management plans achieved legally required and socially desired multiple use objectives, including water quality, aquatic and wildlife resources. In this paper, we review relevant science emerging since 1993 to assess whether proposed changes to the ACS, including reduced riparian reserve protections and a substantially lowered burden of proof for watershed-disturbing activities, are scientifically justified. Observed and anticipated effects of climate change, and of cumulative anthropogenic stressors operating in the nonfederal lands surrounding NFP lands strongly indicate the need to strengthen, not weaken key ACS protections. Roads and ground disturbance associated with mechanical thinning and fuels reduction activities, especially within Riparian Reserves, cause adverse environmental impacts that generally offset or exceed presumed restorative benefits. Headwater streams warrant wider riparian forest buffers than current ACS provisions to ensure effective retention of sediment and nutrients derived from upslope logging, fire, and landslides. Widespread and sustained ecological harm caused by roads is now widely recognized, and ACS measures should be strengthened to more effectively arrest and reduce road impacts in all catchments. Grazing, mining, post-disturbance logging (e.g., fire salvage), water withdrawal, and aerial application of toxic chemicals can cause both acute and chronic harm to aquatic ecosystems. Existing ACS standards and guidelines would need to be strengthened to more effectively control these impacts. A more thorough and current scientific review and synthesis by federal agencies to inform a future ACS is long overdue. Unfortunately, no such review has occurred, while recent agency and legislative proposals would substantially reduce protective provisions of the ACS and NFP by increasing the extent of logging and other mechanized forest management, such as fuels treatments.

Introduction: Origins of the Aquatic Conservation Strategy

In 1994, region-wide social protest over logging old-growth forests, court injunctions on federal forest timber sales, and a rare presidential "roundtable" summit, led to sweeping changes the management of federal forest lands in the U.S. Pacific Northwest. The federal agencies with primary land management responsibilities, the U.S. Department of Agriculture's Forest Service (USFS) and U.S. Department of Interior's Bureau of Land Management (BLM), jointly adopted a new, regional conservation and management framework now known as the Northwest Forest Plan (hereinafter referred to as the NFP, or the "Plan"). The NFP was designed to meet President Clinton's call for an approach that would (1) satisfy federal courts and lift the injunctions, (2) protect the environment, and (3) help stabilize the regional economy (GAO 1999). The Plan's Record of Decision (USDA and USDI 1994) offered a "scientifically sound, ecologically credible, and legally responsible" long-term management strategy for federal lands within the range of the northern spotted owl (*Strix occidentalis cauria*). The NWP region encompasses over 99,000 square km (24.5 million acres) within the highly productive forest zones of western Washington and Oregon and northern California. In addition to spotted owls and other wildlife species dependent on late seral forests, these federal lands also harbor sensitive, declining, and federally listed salmon species (FEMAT 1993; USDA and USDI 1994). Declines in once-abundant salmon and other fish assemblages, amphibians and invertebrates (e.g., river mussels) indicate substantial and persistent loss of aquatic ecosystem integrity (Hughes et al. 2004; Kaufmann and Hughes 2006).

To ensure that the new plan had the sound scientific basis necessary to withstand legal scrutiny, the federal agencies convened an interagency and interdisciplinary panel of scientists (Forest Ecosystem Management Assessment Team, FEMAT 1993) to develop the rationale and options for conservation provisions of the Plan. Recognizing that terrestrial and freshwater species fundamentally share the same landscape, FEMAT scientists developed a system of terrestrial reserves and conservation provisions and a separate but overlapping Aquatic Conservation Strategy ("ACS").

Since the NFP was adopted, social and political pressure have mounted to significantly recast or eliminate the Plan (e.g., Johnson and Franklin 2012), including key elements of its ACS. In late 2013, two bills were introduced in Congress (S.1784 and H.R.1526) that would substantially reshape management on approximately 8000 square km (roughly 2 million acres) managed by the BLM in western Oregon. Separately, the BLM has initiated an administrative planning process intended to result in a decision to replace the NFP policies. These efforts appear principally motivated by the goal of increasing commercial timber production (Blumm and Wigington 2013, DellaSala et al. 2014). Meanwhile, the Forest Service has adopted guidance that would permit substantial alteration of key elements of the ACS in future revisions of its National Forest Management Plans in the Pacific Northwest.

Both agency and congressional proponents of significant alterations of the NFP and its ACS have referred generally to "new science" as a basis for many proposed changes. However, we find that post-1993 scientific findings relevant to the ACS have not been synthesized and addressed in a systematic manner. In this paper we review the key ACS elements, briefly discuss several proposed modifications, and identify concerns about the likely consequences of proposed modifications. Finally we identify needed improvements in the protective measures in the ACS as indicated by new and emerging scientific knowledge, and suggest the form future revisions of ACS provisions might take if they are to be responsive and robust to recent scientific advances.

Core Design Elements of the Aquatic Conservation Strategy

FEMAT (1993) articulated the ACS with two spatial and two programmatic components for managing watersheds and riparian areas: (1) *Key Watersheds,* a land allocation comprising hydrologically discrete areas that putatively contain much of the remaining higher-quality aquatic habitat and offer the greatest potential protection for recovering at-risk fish species. These watersheds are priorities for active restoration, ARE subject to a "no net increase" mandate for road density and watershed analysis mandate for major land use activites.

TABLE 1.
The nine narrative ACS Objectives describing watershed functions and processes and which apply landscape-wide (USDA and USDI. 1994. Record of Decision, p.B-11).

Forest Service and BLM-administered lands within the range of the northern spotted owl will be managed to:

1. *Maintain and restore the distribution, diversity, and complexity of watershed and landscape-scale features to ensure protection of the aquatic systems to which species, populations and communities are uniquely adapted.*
2. *Maintain and restore spatial and temporal connectivity within and between watersheds. Lateral, longitudinal, and drainage network connections include floodplains, wetlands, upslope areas, headwater tributaries, and intact refugia. These network connections must provide chemically and physically unobstructed routes to areas critical for fulfilling life history requirements of aquatic and riparian-dependent species.*
3. *Maintain and restore the physical integrity of the aquatic system, including shorelines, banks, and bottom configurations.*
4. *Maintain and restore water quality necessary to support healthy riparian, aquatic, and wetland ecosystems. Water quality must remain within the range that maintains the biological, physical, and chemical integrity of the system and benefits survival, growth, reproduction, and migration of individuals composing aquatic and riparian communities.*
5. *Maintain and restore the sediment regime under which aquatic ecosystems evolved. Elements of the sediment regime include the timing, volume, rate, and character of sediment input, storage, and transport.*
6. *Maintain and restore in-stream flows sufficient to create and sustain riparian, aquatic, and wetland habitats and to retain patterns of sediment, nutrient, and wood routing. The timing, magnitude, duration, and spatial distribution of peak, high, and low flows must be protected.*
7. *Maintain and restore the timing, variability, and duration of floodplain inundation and water table elevation in meadows and wetlands.*
8. *Maintain and restore the species composition and structural diversity of plant communities in riparian areas and wetlands to provide adequate summer and winter thermal regulation, nutrient filtering, appropriate rates of surface erosion, bank erosion, and channel migration and to supply amounts and distributions of coarse woody debris sufficient to sustain physical complexity and stability.*
9. *Maintain and restore habitat to support well-distributed populations of native plant, invertebrate, and vertebrate riparian-dependent species.*

(2) Riparian Reserves, a land allocation of varying widths along streams and lakes where aquatic and riparian objectives receive primary emphasis and where management is constrained according to activity-specific standards and guidelines. (3) *Watershed Analysis* is an assessment procedure designed to recommend how to tailor management priorities and actions to the biophysical limitations and perceived restoration needs of individual watersheds. (4) *Watershed Restoration*, a long-term program of somewhat unspecified scope and content, but which may include such wide-ranging provisions as road decommissioning, instream habitat alterations, and other measures (ROD 1994).

Late Successional [forest] Reserves, Congressionally designated reserves, and administratively withdrawn areas are land allocations outside of the specific components of the ACS, but they provide additional protection for portions of watersheds, riparian and aquatic ecosystems, particularly in terms of how they regulate landscape-wide management disturbances. In turn, aspects of the ACS also help provide habitat and connectivity for terrestrial wildlife species (ROD 1994, p.7). Many birds, mammals, amphibians, and invertebrates benefit from roadless areas (Trombulak and Frissell 2000); require large trees or wood debris for nesting or other uses; or rely on riparian forests for refuge, foraging, or dispersal (Pollock and Beechie 2014).

Beyond land allocations, the ACS imposes constraints on habitat-degrading management activities in two other ways: 1) It provides binding *standards and guidelines* that explicitly constrain numerous potential management activities within riparian reserves and key watersheds. 2) It requires all management activities on surrounding federal forestlands to be consistent with maintaining and restoring watershed functions and processes that are described in nine narrative ACS objectives (Table 1). The activity-specific standards and guidelines were intended to "prohibit and regulate activities in Riparian Reserves that retard or prevent attainment of the [ACS] objectives" (USDA and USDI 1994). The precaution that management activities may not retard recovery is a potent requirement. In order to ensure an action does not retard or prevent attainment of recovery, managers must ascertain the net effects of any proposed action on natural recovery processes at site-specific areas and larger spatial scales. This requirement addresses the observation (FEMAT, 1993) that past ecological degradation caused by numerous incremental harms often is not recognized. Cumulative effects across the landscape commonly offset gains from those passive or active management measures claimed to benefit ecological conditions and aquatic resource values.

Although it is beyond the scope of this paper to enumerate the many activity-specific standards and guidelines that comprise the ACS, some specific examples will be discussed because they are conspicuously affected by new or emerging scientific knowledge. The nine over arching ACS objectives also have binding force and constitute forest-wide standards and guidelines themselves (ROD 1994). This approach was explicitly intended to constrain activities in geomorphically, hydrologically, and ecologically sensitive areas and to limit the cumulative impacts of activities throughout a watershed (FEMAT 1993, V-29). The identified goal was to maintain conditions within a broadly conceived "range of variability" across multiple spatial and temporal scales, by evaluating, avoiding, or reversing ecologically harmful management at watershed and site-specific scales. The science of ecological restoration broadly recognizes that avoidance of adverse impacts is far more effective than post-hoc remediation of impacts (Kauffman et al. 1997, Karr et al. 2004, Roni et al. 2008), and this principle is codified in the Plan's Standards and Guidelines for watershed restoration (guideline WR-3 clearly states: "*Do*

not use mitigation or planned restoration as a substitute for preventing habitat degradation.") During the mid-1990s, some federal agencies argued that site-specific failure to meet ACS objectives was broadly acceptable if unacceptable outcomes were not expected to be observed at larger scales. However, courts have validated that the conservation burdens delineated in the ACS apply to both site- or project-specific as well as larger scales, such as a watershed, planning area, or national forest.[1] The guiding language in the nine narrative objectives directs managers to "maintain and restore" specifically identified ecological conditions and functions. Hence management activities that will affect aquatic ecosystems may be pursued only under a reasonable assurance that they are restorative or protective in nature. It is not sufficient that management activities produce acceptably small adverse impacts, or cause harms that might potentially be mitigated by other measures.

Courts have ruled that FEMAT (1994) embodies the best available scientific information pertaining to the impacts of forestry activities on salmon and their habitat in the Pacific Northwest federal forests and that the Plan adequately integrates FEMAT's scientific representations[2]. Several scientific reviews (e.g., Spence et al. 1996, DellaSala and Williams 2006, Reeves et al. 2006a, Everest and Reeves 2006) have broadly concluded that while a great deal of new information has been published, the fundamentals and rationale of FEMAT and the ACS remain consistent with available scientific information. However, no interagency scientific panel comparable to the scope of FEMAT has been reconvened to formally address the broad question of how new scientific information may affect the validity of the ACS and how that might in turn affect Endangered Species Act (ESA) consultations, Clean Water Act (CWA) compliance, or NEPA, NFMA, and other relevant project level planning processes.

Because the ACS is incorporated into agency land use management plans, it is directly enforceable by third parties pursuant to the over arching resource planning statutes of the USFS and BLM. While the majority of distribution of salmon species in the Pacific Northwest lies downstream of federal forest watersheds, the federal lands provide important high-quality refugia for many populations (Burnett et al. 2006), and federal forests confer regional hydrologic benefit to water quality and ecosystem integrity downstream. Implementation of the ACS on federal forests has become a foundational baseline component for attainment of salmonid recovery under the Endangered Species Act and of water quality standards under the Clean Water Act. For example, federal ESA salmon recovery plans in Oregon and California rely heavily on Plan implementation (e.g., NMFS 2007, pp. 402-403, NMFS 2012, pp. 3-48, 49). Furthermore, because of the extent to which ACS implementation is widely assumed to represent the federal contribution to aquatic ecosystem conservation, changes have regulatory implications for nonfederal lands. For example, the underlying analyses of Habitat Conservation Plans granted to nonfederal landowners in the Pacific Northwest under the ESA, with assurances extending 40-50 years, explicitly rest on full ACS implementation on surrounding federal lands. (See e.g. WA DNR 2005). Similar expectations

---

1 See e.g. Pac. Fed'n of Fishermen's Ass'ns et. al. v. Nat'l Marine Fisheries Serv., 71 F. Supp. 2d 1063 (W.D. Wash. 1999) ("PCFFA II")(finding that the Plan requires a determination of consistency with the ACS objectives at the project scale); Pac. Fed'n of Fishermen's Ass'ns et. al. v. Nat'l Marine Fisheries Serv. 265 F.3d 1028 (9th Cir. 2001) ("PCFFA III") (finding NMFS' biological opinions on 23 timber sales affecting then-listed Umpqua cutthroat trout and Oregon Coast coho salmon failed to assess site-level impacts).

2 See e.g. Seattle Audubon Soc'y v. Lyons, 871 F. Supp 1291, 1303 (W.D. Wash. 1994), aff'd sub nom., Seattle Audubon Soc'y v. Moseley, 80 F.3d 1401 9th Cir. 1996) (finding adequate scientific support in the plan's decision record and "unprecedented thoroughness" of the agencies' effort to meet "the legal and scientific needs of forest management").

undergird the state of Oregon's restoration plan for salmon and water quality.[3] In basins where water quality standards are not being met, state and federal regulators routinely consider the ACS to be an adequate implementation plan for BLM and Forest Service managers. Substantive alteration and weakening of the ACS threatens to upset a complicated web of region-wide conservation planning that is explicitly and implicitly dependent on the future habitat quality and recovery rate that the ACS is designed to achieve.

3 http://www.oregon.gov/OPSW/archives/ocsri_mar1997/ocsri_mar1997ex.pdf *(identifying NFP implementation as a critical element of Oregon's salmon recovery plan)*

Changes to the ACS Proposed by Administrative and Legislative Efforts

ACS Riparian Reserves. Based on the nested set of ecological rationales considered in FEMAT (1993), the ACS specified a set of "default" widths of the Riparian Reserve land allocation to be a) at least two site-potential tree heights (*ca*. 100 m or 330ft) on either side of fish-bearing streams, and b) at least one tree height (*ca*. 50 m or 160 feet) on non-fish bearing streams. Within these reserves, the conservation of aquatic and riparian-dependent terrestrial resources receives primary emphasis. Beyond these default delineations, Riparian Reserves must be drawn to protect areas susceptible to channel erosion and mass wasting. The Riparian Reserve widths were based on ecosystem process considerations (FEMAT 1993, Olson et al. 2007) and broadly specified population viability and habitat considerations for seven groups of salmonids and many terrestrial and avian species. Various sources (e.g., Johnson et al. 2012) have estimated that based on the high stream densities prevailing over much of the region, roughly 40% of total acres within the Plan area are located within the "default" Riparian Reserve system. However, only about 11% of the Plan area lies in Riparian Reserves associated with those areas (often referred to as "Matrix lands") where commercial logging is expected to be concentrated, and where the Riparian Reserve allocation most directly restricts potential logging activity and other management-related disturbances. Very few of the many completed watershed analyses offered a scientific rationale for reducing default Riparian Reserve areas in any location; a larger number identified site-specific reasons to expand Riparian Reserves beyond the specified default widths (Pacific Rivers Council 2008).

Proposed Changes to the ACS and Riparian Reserves. The BLM's 2008 Western Oregon Plan Revisions (WOPR) proposed a new regime of management for the "Oregon and California (O&C) Lands, distributed widely across western Oregon (Blumm and Wigington 2013). The WOPR proposed greatly reducing default Riparian Reserve widths, primarily arguing that ACS default delineations include some upland or "non-riparian" vegetation and that summer stream shade and large wood recruitment to fish-bearing streams could be maintained with narrower reserve widths. Narrative objectives and standards and guidelines were also reduced or eliminated, allowing commercial timber harvest in Riparian Reserves for pervasive "safety and operational" reasons. The analyses and rationale underlying the WOPR were withdrawn by BLM in 2009 in significant part because they were deemed unlikely to survive consultations with ESA enforcement agencies (the National Marine Fisheries Service and US Fish and Wildlife Service). In a recent regional planning document, BLM (2013) argued again that "Riparian Reserve boundaries extend out beyond the water influence zone and are wider than necessary for water quality protection" but provided few or no specific scientific citations to support these claims. BLM has provided little scientific rationale or empiri-

cal validation for their decision to selectively focus on hydrophilic vegetation, proximate stream shade, and large wood recruitment as the only ecological considerations dictating riparian reserve delineation—in contrast to the much more comprehensive set of biophysical functions considered in FEMAT and the NFP ACS. (Note, as detailed later in this text, we also disagree with BLM's specific simplifying assumptions about effect of Riparian Reserve width on maintenance of shade and wood recruitment, and further conclude that other functions, such as nutrient retention, implicate much wider and less-disturbed reserves.)

A similar extremely constricted perspective on riparian ecological functions appears to underlie two Congressional bills for BLM lands in western Oregon (the "O&C" Lands), one of which (H.R. 1526, http://defazio.house.gov/issues/bipartisan-oc-forests-plan) would reallocate some 675,000 ha (1,667,000 acres) to an "O&C Trust"," the primary purpose of which is timber management (Blumm and Wigington 2013). Areas equivalent to Riparian reserves in the Trust would be designated at about half the width of the current ACS default requirement for steams (with extremely limited buffers for springs, seeps, wetlands, and unstable landscapes). A U.S. Senate bill introduced in 2013 (S.1786) would allocate about 50% of O&C lands to so-called "forestry emphasis areas," cut default Riparian Reserve areas by half across all stream types, with further narrowing if watershed analysis deems them "not ecologically important." The bill would provide for potentially extensive commercial logging in the rubric of thinning riparian areas where stands are younger than 80 years of age; only stands older than 120 years would be protected from logging. These older stands remain in scattered small patches across O&C lands but are important ecologically given high levels of timber cutting on surrounding nonfederal lands (DellaSala et al. 2013). Environmental review at the project level would also be curtailed from current requirements, including but not limited to eliminating the requirement for project-level determinations of consistency with ACS objectives.

Meanwhile the USFS—which manages the majority of federal forestlands in the three state NWP area, has focused on incrementally replacing the ACS with new provisions in upcoming revisions of individual National Forest Plans. In 2008 the Forest Service adopted new regional planning guidance (USDA 2008) that generally mirrors the NFP default riparian area widths and key watersheds allocations, but altered the narrative ACS Objectives, Watershed Analysis, and other NFP direction for management within reserve areas. This guidance stakes a claim for expanded agency discretion to undertake a broader range of vegetation and ground-disturbing management activities within riparian reserves, including but not limited to thinning and other commercial logging and livestock grazing. The 2008 Forest Service regional guidance, if implemented in future revised Forest Plans, would allow actions that alter riparian reserve resources and goals, as long as managers can present a general argument that impacts would be offset by other, beneficial actions or naturally-occurring improvements dispersed or averaged across time or space. The apparent intent of these changes is to reduce the burden for analysis of environmental impacts associated with such projects, which would, for example, streamline approval of more aggressive implementation of mechanized and commercial thinning and other vegetation- and ground-disturbing actions within Riparian Reserves. We are concerned that the 2008 USFS planning guidance has not been subject to rigorous external or scientific review, and if implemented could have harmful consequences for riparian and aquatic resources that have not been adequately evaluated or disclosed.

Weakening of the Northwest Forest Plan ACS will impact numerous listed fish, wildlife and plant species by changing the range of acceptable on-the-ground outcomes from management actions. Across the Pacific Northwest,

reduced protections for listed species and water quality via changes in the ACS would likely necessitate reconsideration of many existing agency programs and initiatives that have been premised on implementation of the 1994 ACS measures.

ACS Watershed Restoration. The ACS intended watershed restoration to be strategically identified and prioritized through *Watershed Analysis*, with particular emphasis on improving ecological conditions in *Key Watersheds*. Protection through passive restoration (Kauffman et al. 1997) of existing high-quality habitat is explicitly prioritized over active instream rehabilitation. To be effective, instream habitat-improvement projects rely on concurrent long-term riparian and catchment-scale protection and rehabilitation measures, and these must be programmatically tiered to management plans affecting each watershed. Hence site-specific active measure, such as instream habitat structures or riparian tree planting, should not be claimed to mitigate for ongoing or future harmful and degrading management actions (Frissell and Nawa 1992, Frissell and Bayles 1996, Roni et al. 2008).

Proposed Changes in Watershed Restoration Policy. In contrast, the current Senate Bill would simply allocate $1 million annually for instream wood placement and $5 million for road removal or "improvement" across the BLM's O&C land area, and apparently exclude such activities from environmental analysis under NEPA. In doing so this bill would decouple active restoration measures from land management decisions. The bill would also alter the programmatic approach to watershed restoration, as discussed in the next section.

Proposed changes to ACS Key Watershed allocations. The Senate and the House bills and the BLM (2013) call for revising Key Watershed allocations in place for the past 20 years under the NFP and ACS. Many current Key Watersheds would apparently be dropped from the allocation under the House bill, with the consequences for conservation planning and species at risk unevaluated; the Senate Bill calls for a revised watershed classification to accommodate new land allocations.

Certain revised Key Watershed delineations might in theory benefit particular populations of species such as ESA-listed coho salmon. However, the concept of prioritizing conservation efforts in Key Watersheds is undermined when watershed-scale priorities are upended and reshuffled on a time frame that is decades shorter than the amount of time expected for significant watershed restoration to occur. Effective watershed restoration requires a sustained commitment to aquatic resource protection and restoration, coupled with appropriately conditioned and scaled land management and effectiveness monitoring extending for decades to centuries (FEMAT 1993). Critical components of the ROD for the ACS include requirements for no road construction within inventoried roadless areas within Key Watersheds, and no net increase in road density within each Key Watershed. These protections for Key Watersheds would apparently be lost under the Congressional proposals, at least for those Key Watersheds that would be de-designated. Although the 2013 Senate bill would retain a process it refers to as "Watershed Analysis" its purpose appears to be inverted: it would not focus on watershed restoration, but on identifying ecological changes due to increase commercial logging over that which might occur under the default prescriptions specified in the bill.

CHANGES IN TERRESTRIAL LAND ALLOCATIONS ALSO AFFECT WATERSHED INTEGRITY

Land allocations within the NFP and other authorities, but outside of the ACS, including Late Successional Reserves, Wilderness, other congressionally designated or "administratively withdrawn" lands, and inventoried roadless areas, can confer additional protection to watersheds. These land allocations can prevent or retard road network expansion, and other disturbances, allowing natural ecosystem maintenance and natural recovery processes to proceed. They limit the spatial extent of disturbances across watershed and stream networks, and reduce the incidence or likelihood of adverse cumulative impacts. Many Key Watersheds are closely associated with such specially designated lands, though unfortunately few are largely or entirely nested such within such conservation delineations (Frissell and Bayles 1996). As a consequence, when new proposals strip away the protection conferred by Late Successional Reserves, roadless areas, or other administrative designations, watersheds are placed at greater risk of impact from forestry activities. Land disturbance from roads, logging, grazing, or other actions can undermine the benefits of restoration and land protection elsewhere in the same watershed (Espinosa et al. 1997), depending on the geography of the watershed in question. The trade-offs of cumulative risk and potential harm to watersheds and sensitive or listed aquatic species from changes in land allocation have not been rigorously assessed in the Congressional and administrative proposals. Such trade-offs amount to a wholesale re-casting of NFP land allocations for the region that includes and surrounds the O&C lands. Each of the 2013 Congressional bills proposes to substantially re-allocate protection of older forests, generally by focusing protection on older stands rather than the more expansive Late Successional Reserves of the present NFP. Moreover the Congressional bills make special provision for thinning under nearly all land allocations, with guidelines allowing for agency-determined findings of need and some minimal requirements for tree retention. Although the NFP did not prohibit thinning or salvage logging in these areas, the legislative bills favor more extensive and intense logging and increasing fragmentation by logging roads than have previously occurred in areas now classified as Late Successional Reserves.

NEW SCIENCE THAT INFORMS AQUATIC CONSERVATION STRATEGY AND PRACTICES

In the following section we discuss some relevant new science published since the convening of FEMAT (1993). We provide selected citations and briefly summarize our view of major implications for the purpose of developing and improving an effective aquatic conservation framework. While our interpretations and recommendations focus on the ACS, many of the citation sources and their implications are derived from studies of other regions and ecosystem types out of necessity because of limited research done in the Pacific Northwest. Just as in FEMAT (1993), relevant scientific information that is critical to define and frame topics of crucial conservation concern sometimes originates from other similar regions, and often spans a variety of disciplines.

In this paper we were not able to comprehensively address all areas of scientific advancement concerning forest management, water quality and aquatic conservation. Some topics await further elaboration. For example, we do

not comprehensively discuss the literature on impacts of logging and roads on streamflow patterns (e.g., Moore and Wondzell 2005), and subsequent effects on stream geomorphology, habitat, and biota. However, we do consider known effects of forest management and climate change on streamflows as a contributing concern under several topic headings. Most importantly, we also do not assess new science pertinent to non-aquatic and amphibian wildlife species in this report. This important work remains to be done.

Management after Wildfire, Disease, and Other Disturbances. Salvage logging of dead or dying trees after fires, insect outbreaks, and other disturbances in Pacific Northwest forests continues to be undertaken in the region, and its effects are a recurring ecological concern (see review by Lindenmayer and Noss 2006). Soon after the NFP was adopted in 1994, the scientific community began to weigh in on the inadvisability of post-disturbance logging. Scientists have catalogued the critical importance of large standing live trees, snags, and downed wood from fallen trees in the post-disturbance recovery of natural forests, including stand successional pathways, watershed processes, and wildlife and fish habitat (e.g., Gresswell 1999, Minshall 2003). Numerous scientific syntheses provided precautionary advice against post-fire logging on a wide range of causal grounds (e.g., Beschta et al. 2004, Karr et al. 2004, Lindenmayer et al. 2004, Lindenmayer and Noss 2006, Donato et al. 2006, Noss et al. 2006). More recent work has identified the potential importance of pulses in trophic energy following high-severity wildfire (Malison and Baxter 2010) for persistence and recovery of aquatic and riparian species. This new information builds on a more longstanding recognition that wildfire, that among its many other effects, plays an important long-term role in the generation of complex wood debris structures in streams (Minshall 2003). Other reviews focused on plant and landscape ecology broadly call into question the effectiveness of salvage logging insect-infested trees to control insect outbreaks (e.g., Black et al. 2013, Six et al. 2014). Similar concerns about the consequences of salvage logging curtailing natural ecosystem recovery processes pertain to salvaging of stands affected by any natural mortality agent, such as windthrow or volcanism.

However, post-disturbance logging was not expressly ruled out in the NFP and ACS, and the political demand for salvage logging remains high, so large post-fire salvage logging projects have been pursued by the USFS and BLM in many areas, including on occasion within Key Watersheds, Riparian Reserves, Late Successional Forest Reserves, and designated critical habitat of listed species (see DellaSala et al. 2014). Scientific consensus on the inadvisability of post-disturbance logging largely emerged in the years just after FEMAT, hence the ACS should be strengthened to reflect such sources as the recommendations in Beschta et al. (2004), Karr et al. (2004), and Black et al. (2013).

We conclude that for maintenance of forest ecosystem integrity*, post-disturbance logging should be prohibited in Riparian Reserves, Key Watersheds, Late Successional Reserves, and other areas where conservation is a dominant emphasis. Post-disturbance actions should prioritize road decommissioning or systemic road drainage improvements, and suspension of livestock grazing to reduce harm under the increased hydrological stresses expected in post-fire forests and their aquatic and riparian habitats and biota.*

Forest Thinning Intended to Reduce Tree Density or Wildfire Fuels. Current ACS language allows the agencies to "apply silvicultural practices for Riparian Reserves to control stocking, reestablish and manage stands, and acquire desired vegetation characteristics needed to attain…objectives." The agencies carry a project-specific burden to establish

the need for thinning and that outcomes are ecologically restorative. Recently the USFS and BLM have pressed to increase in the average size of thinning projects apparently to reduce the number and cost of site-specific environmental analyses by broadening their scope. Agency initiatives presume extensive use of mechanical harvesting methods in conjunction with commercial timber sales to thin trees in Riparian Reserves and other areas where conservation values are given highest priority. In wetter forest types, the primary claim that thinning is restorative rests on the assumption that the growth rate and vigor of those trees left alive after thinning will likely improve, thereby hastening the future development of larger-sized trees in the stand. In drier forests, the primary rationale is that thinning is needed to promote a generalized reduction in fuel loads, thereby presumably reducing the risk, or severity, or rate of spread, of wildfire and that thinning can increase fire resistance of selected individual trees.

Regardless of silvicultural intent, mechanized treatments in Riparian Reserves can disturb vegetation and soils in close proximity to surface waters, where the risk of sediment delivery and other impacts is demonstrably high (Rashin et al. 2006, Dwire et al. 2010). Logging activity that disturbs soils within riparian buffers can also reduce the buffer's effectiveness to retain sediment and nutrients delivered from upslope sources. Thinning or other disturbance of coniferous or deciduous trees and shrubs within riparian and wetland areas can cause decades of diminished summer low flows (after an initial few years during which low flows may increase), as a consequence of increased water demand by rapidly re-growing vegetation (Hicks et al. 1991, Moore and Wondzell 2005). In addition, thinning and yarding of logs from near-stream areas requires or encourages the construction of roads in close vicinity to streams, where the likelihood of sediment delivery and other impact from roads is increased (Luce et al. 2001). Bryce et al. (2010) found that for sediment-sensitive aquatic vertebrates and macroinvertebrates, minimum-effect levels for percentage fines were 5% and 3%, respectively, meaning that even small increases in fines can adversely affect salmonids and their prey.

Mechanized thinning and fuels operations usually require higher-density road access to be feasibly implemented. Mechanical treatments for fuels reduction are particularly problematic because recurring entries at roughly 10-year intervals are necessary to sustain the desired conditions (Martinson and Omi 2013); such a forest management regime strongly favors, if not requires, a permanent, high-density road network. Many thinning projects involve road and landing construction and reconstruction, as well as elevated haul and other use of existing roads, all of which significantly contribute to watershed and aquatic degradation. Even if constructed roads and landings are deemed "temporary," their consequent impacts to watersheds and water bodies are long lasting or permanent. The hydrological and ecological disruptions of road systems and their use (Jones et al. 2000, Trombulak and Frissell 2000, Gucinski et al. 2001, Black et al. 2013), exacerbated by other effects of vehicle traffic, will likely outweigh any presumed restorative benefit to streams and wetlands accruing from thinning and fuels reduction. In recent years, the prospect of future thinning or fuels reduction projects often has become the basis for the USFS or BLM to avoid or delay decommissioning environmentally harmful roads, even when fiscal resources were available for the work. Prescribed fire without extensive mechanical treatment is of much less concern, as it is more feasible to apply in sparsely-roaded wildlands, entails far less soil disturbance, and if conducted in proper times and places it can more adequately mimic the ecological effects of natural wildfire.

Substantial questions remain about the putative ecological benefits of thinning and

fuels reduction. This is critical because agency proponents commonly argue that the desired ecological benefits outweigh the adverse environmental effects of logging and fuels treatments. Dispute among federal agencies about claimed ecological benefits of thinning in moister, Douglas-fir-dominated forest types (widespread in the Pacific Northwest) led to an interagency scientific review in 2012-2013 (Spies et al. 2013). That panel concluded that increased tree growth might be better obtained from thinning very young, high-density stands--which very seldom produces commercially saleable logs. They further concluded that thinning produces unusually low-stem-density forests and causes long–term depletion of snag and wood recruitment that is likely detrimental in most Riparian Reserves (Spies et al. 2013, and see Pollock et al. 2012, Pollock and Beechie 2013). Further depletion of wood recruitment in headwater streams can adversely affect the behavior of debris flows in Pacific Northwest watersheds in ways that further reduce residual wood debris and its important functions over extensive portions of streams and rivers (May and Gresswell 2002), where present-day wood abundance is decimated compared to historical conditions (Sedell et al. 1988, Pollock and Beechie 2014). Finally, recent reviews also raise compelling, unanswered questions about the effectiveness of thinning forests for attempted control of insect outbreaks (Black et al. 2013, Six et al. 2014).

The effect of thinning on fire behavior and effects within riparian areas has been little studied. For western North American forests in uplands the literature is replete with ambiguous and conflicting results regarding the effects of thinning and other mechanical fuels treatments on fire severity, rate of spread, and recurrence. Moreover, the probability of a fire burning through a treated stand within the limited time window of potential effectiveness of a fuels treatment has been shown to be very small (Lydersen et al. 2014, Rhodes and Baker 2008). Any presumed benefit is even less persistent in Riparian Reserve areas where woody vegetation regrows rapidly after treatment, and where in moister forest types fire tends to recur with lower frequency. Equally important, we question whether managers should be striving to reduce fire severity in riparian areas as a rule, considering that high-severity fire plays a natural and historical role in shaping riparian and stream ecosystems (Gresswell 1999, Minshall 2003, Benda et al. 2003, Malison and Baxter 2010). Other natural forest disturbances, including windthrow, insect outbreaks, and landslides on forested slopes, appear to play a similarly important role in generating pulses of wood debris recruitment to streams, establishing a long-lasting source of ecological and habitat complexity.

Considering the difficult-to-justify costs and recognized inherent risks of adverse impact associated with such operations in sensitive areas, balanced against the uncertainty in intended benefits, we conclude the following: *Thinning and fuels reduction by means of mechanized equipment or for commercial log removal purposes should be generally prohibited in Riparian Reserves and Key Watersheds. Any thinning or fuels treatment that does occur as a restorative treatment in Riparian Reserves (e.g., to remove non-native tree species from a site) should retain all downed wood debris on the ground. Thinning projects that involve road and landing (including those deemed "temporary") construction and/or reconstruction of road segments that have undergone significant recovery through non-use should also be prohibited, due to their long term impacts on critical watershed elements and processes.*

Road Networks and Their Management. Roads are ecologically problematic in any environment because they affect biota, water quality, and a suite of biophysical processes through many physical, chemical, and biological pathways (Trombulak and Frissell 2000, Jones et al. 2000, Al-Chokhachy et al. 2010).

The magnitude of existing road impacts on watersheds and streams in the Plan may equal or exceed the effect of all other activities combined. Firman et al. (2012) reported that density of spawning coho salmon across coastal Oregon streams was negatively associated with road density. Kaufmann and Hughes (2006) found that road density in Coast Range streams was associated negatively with 25-50% of the variability in condition of aquatic vertebrate assemblages. More recently, Meredith et al. (2014) showed that the abundance of habitat-forming wood in Columbia Basin streams declined with proximity to roads, and the effect was roughly the same magnitude as that of natural climate and vegetation differences or long-term livestock grazing.

Roads are necessary to support logging, mining, grazing, and motorized recreation, but the existing federal forest road system far outstrips the extent of those demands. The number and poor condition of USFS and BLM roads, the agencies' inability to prevent current roads from deteriorating and harming streams, and the pervasive effects of roads on the physical and biological environments were recognized in FEMAT (1993). In addition, forest roads have been the subject of high-profile national dialogue and policy reviews since the development of the Plan (Gucinski et al. 2001, Pacific Rivers Council 2008). The ACS's primary means of protecting streams from roads and encouraging effective restoration are twofold: First, ASC objectives discouraged locating roads within Riparian Reserves, and second, roadless areas were to be maintained and overall road density reduced in Key Watersheds. For a small number of Key Watersheds where road network reduction has been pursued, agency monitoring efforts have reported improvements of certain instream habitat conditions, a response not detected elsewhere (Gallo et al. 2005, Reeves et al. 2006a). Often overlooked is that proposals to reduce the size of Riparian Reserves could provide more free rein for the construction of roads and landings in closer proximity to streams, markedly increasing the likelihood of sediment delivery and alteration of near-stream hydrology.

How to substantially reduce road density in critical watersheds and improve road drainage, stream crossings, and other factors that affect streams and aquatic biota, while maintaining sufficient roads for other forest uses, remain central challenges to forest planning and management. The ACS and other operative policies have lacked sufficient means and impetus to accomplish this in the past 20 years. We therefore suggest five policy changes to achieve needed road reductions: 1) *Prohibit the construction of new permanent and "temporary" roads*, except in limited instances were construction of a short segment of new road is coupled with and necessary for the decommissioning of longer and more damaging segments of existing road. 2) *Allow no net increase in road density in any watershed*. New "temporary" roads and landings should be considered to be roads and counted towards road density levels for at least several decades after decommissioning. 3) *Strengthen road density restrictions for Key Watersheds and establish unambiguous standards and metrics for net road density reduction, which include adequate accounting for landings and the impacts of so-called "temporary" and decommissioned roads and landings*. 4) *Improve the system of classification (e.g., road type, use) and inventory (e.g., whether a road is active or decommissioned), and mapping (i.e., update maps to reflect current conditions)* to ensure that agency bookkeeping of road miles corresponds with actual field conditions. This provision is necessary because at present many roads "disappear" when dropped from the inventory, but they in fact remain on the landscape causing watershed impacts. Also, lax road mapping programs and narrow definitions of what constitutes a road can significantly under represent the actual road densities. 5) *Require each proposed forestry and other development project to meet a target of incremental reduction of the road system* in

all watersheds affected by the project. Road density redution should be required until road density in the affected watershed is lower than the target established on the basis of biological response.[4] Finally, 6) *roads for which there are not adequate funds for maintenance and upkeep should be decommissioned*.

Riparian Reserves for Protecting Stream Temperature. Conservation (including restoration) of natural thermal regimes of streams and rivers was but one of many factors considered when ACS default riparian reserve widths were determined in the initial design of the ACS. In recent years the land management agencies and others have commonly assumed shade from riparian vegetation is the predominant proximate control on stream temperature, and some research has suggested that trees within 30 m or so of the stream margin contribute over 90 percent of the effective shade (e.g., Reeves et al. 2013). Furthermore, it has been suggested that headwater streams that do not carry water in summer should presumably not need shade to conserve summer thermal maxima in downstream waters. These two premises have become a primary rationale for proposals by BLM and in congressional bills to reduce default Riparian Reserve widths for some stream types, with the intent of increasing the area of Matrix land or equivalent that is subject to commercial logging. From the perspective of temperature protection, we have four concerns with this rationale for shrinking Riparian Reserves.

First, *redundancy*: most current analyses rest on a static view of riparian stand structure and function—that is, shade is modeled as a nearest single layer function of the existing standing trees only. The tree nearest to the stream margin is attributed as the contributor to shade, even though one or more trees standing behind it, slightly farther from the stream, may contribute shade as well. But when trees fall or die in the so-called "inner zone," then the "outer zone" trees become a replacement source of shade. Obviously, if the outer zone trees have been logged, that functional redundancy is lost and any riparian disturbance, man-made or natural, may lead to incrementally reduced stream surface shade—and an increase in stream temperatures.

Second, *density*: whereas we measure canopy shade with fixed-resolution instruments, little is known about how measurements of shade translate to actual solar penetration. In the coarsest sense, a canopy densiometer is used to visually estimate canopy cover with only 17 sample points that are irrespective of solar path. Even more quantitative instruments, such as the Solar Pathfinder or SunEye have the tendency to overlook the value of small canopy gaps or multiple canopy thickness in reducing light intensity reaching the stream, as does the densiometer. "Redundant" tree canopies create a shade structure that is dense compared to that of a single tree, and this may substantially affect the actual solar energy reaching the water surface in ways that we that we seldom adequately measure.

Third, *groundwater*: thermal response is affected in numerous ways by near-surface groundwater, which affects both surface streamflow rate and the temperature of water at the point of delivery. After initial increases in base flow following logging, summer base flow can decline for many years as a consequence of rapidly re-growing second-growth vegetation and its evapotranspiration demand (Hicks et al. 1991, Moore and Wondzell 2005). Logging in the outer areas of Riparian Reserves or forest-

4 E.g., 1 mile per square mile (0.62 km per square km) for watersheds with Pacific salmon, steelhead and cutthroat trout (Lee et al. 1997, Thompson and Lee 2000, Carnefix and Frissell 2009), and 0.5 miles per square mile for watersheds supporting bull trout (USFWS 1999; Baxter et al. 2000, see Fig 5 and Appendix, showing that population growth remained negligible in streams with higher road densities; and Ripley et al. 2005, Fig. 5 showing that probability of bull trout occurrence in Alberta tributary streams dropped by half where road densities exceeded about 0.6 miles per square mile).

ed wetlands can contribute to or conceivably magnify this effect. Accordingly, in some Pacific Northwest watersheds, stream temperature is more strongly associated with catchment-wide logging than with streamside vegetation cover (Pollock et al. 2009). Stream warming in such watersheds (often containing gently sloping or hilly terrain and numerous forested wetlands) could be influenced by reduced canopy shade over large areas of near-surface groundwater. Warming also could be influenced by changes in shallow groundwater flux rates and the level of the water table (Poole et al 2008). Hence, stream temperatures in some circumstances can become warmer at their point of origin (in spring, summer and fall) following watershed logging. Other research has established the importance of the hyporheic flow exchange in determining surface water thermal regime (Poole and Berman 2001, Baxter and Hauer 2001, Poole et al. 2008). The hyporheic zone may include extensive areas of shallow subsurface flow within montane alluvial valleys. In summer this subsurface pool may be dominated by spring snowmelt or cool rain runoff that cools surface streams when it discharges in midsummer (Poole and Berman 2001, Wondzell 2011). The extent of hyporheic storage and exchange bears a somewhat uncertain relationship to surface landforms, and until the decades after FEMAT, land management agencies lacked both the methods and incentive to accurately map these critically important areas (Torgersen et al. 1999, Baxter and Hauer 2001, Ebersole et al. 2003, Poole et al. 2004, Poole et al. 2008, Torgersen et al. 2012). Sediment accumulation in streambeds, or loss of step pools and other structures contributing to channel complexity—often formed by stable large wood—is thought to reduce entrainment of surface flows into, hence flow exchange with, the hyporheic zone (Moore and Wondzell 2005, Poole et al. 2008).

Given these uncertainties, and the increased importance of such groundwater source areas under future climate changes, any management change that increases the areal extent of logging in watersheds poses a risk of contributing to undesired stream warming. Notably, winter and spring stream temperatures can be of comparable importance to summer temperatures in meeting the habitat needs of species. In particular, temperatures of seasonably intermittent streams (even though they may be non-fish-bearing in summer or support salmonids only in early summer) can be important for salmon and other species in winter and spring (Wigington et al. 2006), and are directly and indirectly influenced by riparian canopy shade, thermal insulation, and other forest conditions that mediate water temperature fluctuations.

Fourth, *channel migration*: over time, stream channels migrate and even small streams have secondary channels that may flow only during the rainy season. However, existing side channels and backwaters provide important rearing and refuge habitat for salmonids, and they are commonly unmapped or mapped poorly. In addition, if riparian buffers are narrowed, some of these channels may migrate outside the narrowed buffer and be exposed to direct sunlight and substantially warmed. For instance, the sources of LWD are impaired during channel migration where outer zones have been harvested. Washington state and private forest practices rules have included criteria designed to identify and protect channel migration zones for many years (Brummer et al. 2006); in the ACS, explicit rules for their delineation are left to watershed analysis.

Considering the multiple ecological factors and processes that affect stream temperature and considering that temperature conservation is but one of many significant functional factors influenced by streamside forests, we *find no sufficient scientific support for reducing current ACS Riparian Reserve default widths for any stream type. In many watersheds and stream segments, larger areas of forest protection are warranted to prevent warming of*

shallow groundwater, particularly given likely trends future climate change, and the expectation of increased influence of wildfire and other "unmanaged" forest disturbances (Westerling et al. 2006).

Riparian Reserves and Nutrient Retention. The role of forested riparian buffers in retaining nutrients mobilized by upslope disturbance, or delivered to watersheds in precipitation and fertilization, is globally recognized. Forested buffer zones are commonly prescribed to reduce nutrient delivery to streams in agricultural landscapes (Sweeney and Newbold 2014). Logging and fuels management treatments that disturb green vegetation generate increased nitrogen leaching from forest soils that enters streams and wetlands by both surface and subsurface flow paths (Wenger 1999, Gomi et al. 2002, Kubin et al. 2006). Any ground-disturbing activity or condition (such as a road network) tends to mobilize phosphorus in association with soil erosion. Logging disturbs vegetation and soils over large areas, and scaled over large landscapes or river basins, initial disturbance of forested lands tends to generate larger net increases in nutrient loading than repeat disturbances of already-altered agricultural or urban lands (Wickham et al. 2008; note this observation is from a large population of monitoring sites and remains true even though agricultural lands are commonly more heavily fertilized than forest lands). Over time, nutrient loading to headwater streams transfers downstream, where nutrients accumulate in rivers, lakes, estuaries, and nearshore marine ecosystems (Freeman et al. 2007). For all of these reasons, forestry operations have been identified as a major contributor to nutrient loading, eutrophication, and associated impairment of water quality in Pacific Northwest lakes (Blair 1994, Dagget et al. 1996, Oregon DEQ 2007), rivers and estuaries (Oregon DEQ 2007).

Cumulative nutrient impairment of downstream receiving waters can occur without violation of nutrient standards in headwater streams, simply as a consequence of sustained increases in loading from storm water runoff from forest roads and periodic logging. In effect, logging alters the entire regime of nutrient and sediment export, and nutrient losses to surface waters are endemic and widespread consequences of logging and other disturbance of forested watersheds.

The question of what role Riparian Reserves play in nutrient retention has received insufficient consideration in the Pacific Northwest. Research on the nutrient retention efficiency of various forested buffer widths from the Upper Midwest and other regions (Nieber et al. 2011, Sweeney and Newbold 2014) suggests that average phosphorus and nitrogen retention is around 80% for undisturbed buffer zones of 30 m (100 feet) wide. Extrapolation suggests that buffers of 45 m (150 feet) or greater might be necessary to attain 90-99 percent retention of nutrients mobilized by upslope disturbance. These distances are likely too small for Pacific Northwest forests, where slopes are steeper, soils tend to be more porous, and macropores or channeled flow from uplands are more common than in the Midwest (all factors identified in Nieber et al. [2011] as reducing retention efficiency).

By virtue of their high density of surface channels across most mountainous landscapes, headwater streams with seasonal flow receive a large portion of the nutrients mobilized by up-slope disturbance (Gomi et al. 2002, Freeman et al. 2007). Therefore, full protection of wide Riparian Reserves along even the smallest stream channels (and surface-connected wetlands) is likely necessary for effective nutrient retention when surrounding uplands are disturbed. Channel network expansion from gully erosion (Reid et al. 2010) or roads (Wemple and Jones 2002) and channel simplification through loss of woody debris or sediment increases also reduces retention efficiency of nutrients, sediment, and organ-

ic matter in headwater systems. Moreover, thinning or other disturbance of vegetation or soils within the Riparian Reserve could short-circuit the benefit of riparian forest buffers, by creating a near-stream source of nutrients that is not fully mediated by the retention capacity of the default-width riparian zone.

Although more research is needed in the Pacific Northwest on nutrient retention, current scientific knowledge is sufficient to justify three recommendations. 1) *Continuous, no-cut Riparian Reserves exceeding 50 m (160 feet) along all streams and wetlands are generally needed to mitigate the effects of up-slope logging on nutrient loading to both freshwater ecosystems and downstream marine environments.* 2) *Cessation of livestock grazing in Riparian Reserves, road network reduction, and reconfiguration of remaining roads to reduce their hydrologic connectivity to surface waters are needed to reduce downstream nutrient loading.* 3) *Analysis of the effects of management actions on nutrient loading to immediate downstream receiving waters, including lakes, wetlands, reservoirs, mainstem rivers, estuaries, and the nearshore marine, are needed in environmental assessments, environmental impact statements, watershed analyses, and ESA consultations for aquatic species.*

Livestock Grazing. Whereas forestry predominates in the Northwest Forest Plan area, grazing affects a significant portion of the area as well; for example, 22 percent of BLM lands were subject to livestock grazing in the early 2000s (BLM 2008). A larger area was affected by historic grazing, where soil impacts may persist. Livestock grazing has large impacts on streams (Al-Chokhachy et al. 2010) because livestock tend to concentrate in streams, floodplains and alluvial valleys (see Beschta et al. 2013 for a recent synthesis). Besides direct disruption of wetlands and streambeds, and the suppression of woody vegetation, soil compaction by grazing in both riparian and upland areas degrades runoff quality and adversely alters flow regimes and watershed functions such as soil water storage and nutrient retention.

In addition to these direct impacts, new research shows that managing for livestock can indirectly alter ecosystem trophic cascades. For example, livestock depredation on open range led to programs to extirpate large native carnivores. Reduced numbers of carnivores release native ungulates and other herbivores from predation, leading to declines of riparian vegetation and stream conditions even outside of livestock-grazed areas (Beschta and Ripple 2012). Removing livestock grazing from federal lands has high potential to increase the resilience of watersheds and streams to environmental stresses, including climate change (Beschta et al. 2013, 2014). Measures to reduce the ecological impacts of livestock grazing, primarily by fencing streamside areas and moving cattle frequently from site to site, have met with variable success (Rhodes et al. 1994). Implementation of these methods is limited by the high capital cost of building and maintaining extensive fencing, the wages of field personnel to manage herds, and the cost of necessary environmental review and monitoring. Livestock grazing in forests is a commercial use that is not restorative, and often is marginal economically. We conclude that *livestock grazing should be excluded from Riparian Reserves, Key Watersheds, and other lands where conservation is the primary management objective.*

Chemical Use in Forests. Only very recently has science begun to directly tackle the difficult questions of fate, effects, and toxicity of pesticides and other chemicals associated with forestland uses on stream biota. Toxic contaminants come from various sources, including storm water runoff from roads (particularly those that discharge directly to surface waters pipes and ditches) (McCarthy et al. 2008, Feist et al. 2011). Herbicides are applied to tree plantations and roadsides to

control unwanted vegetation. Until recently these activities were limited by court order on BLM and USFS lands, but now they are increasing in extent and frequency, as well as continuing on adjacent private forest lands. The NMFS is reviewing the science concerning potential harm to listed species of Pacific salmon from application of commonly used pesticides. For example, use following label restrictions of the herbicide 2,4-D was determined to jeopardize Pacific salmon (NMFS 2011). Forest fire retardants that are aerially dropped in large quantities during wildfire suppression operations often reach surface waters, where they may be toxic to salmonids (Buhl and Hamilton 1998, Gaikowski et al. 1996).

While the science on toxic chemicals is certainly advancing, we have five interim recommendations based on existing knowledge: 1) *Minimize application of chemicals for forest management purposes in time and space;* for example, hand-application should be favored over aerial application when there is no feasible alternative to pesticide use. 2) *Weigh the full range of environmental trade-offs between the perceived benefits of chemical use and its possible harms in each case before a decision is made to use chemicals in forest management.* 3) *Implement wide, un-thinned forested buffers in Riparian Reserves to help reduce exposure of fish and aquatic life to toxic chemicals.* Thinned or narrow buffers can allow greatly increased aerosol penetration (chemical) from slopes to streams, and narrower buffers may also allow more transport of toxins in runoff. 4) *Reduce road density and the hydrologic connectivity of roads to surface waters to help control toxins* that originate from road use and maintenance, as well as those that are applied up-slope but find their way to streams via surface runoff. 5) *Analyze the possible effects of management actions in affecting the delivery of toxic chemicals to streams in every NEPA document and ESA consultation.*

Climate Change: Consequences and Adaptation. Anticipated climate change will alter the way we expect ecosystems to respond to forest management actions (Dale et al. 2001, Mote et al. 2003). In general for this region, hydrologic model predictions stepped-down from regional and global circulation models project increased stream and lake warming (varying magnitude across the seasons); more intense winter precipitation events, including flood and wind disturbance of riparian forests; earlier snow pack melting except for the highest elevation watersheds; and likely increased intensity and duration of droughts (Battin et al. 2007, Dalton et al. 2013). In very general terms, most climate change scenarios suggest larger and higher severity wildfires than seen in recent decades, and generally elevated evapotranspiration that could further reduce low summer streamflows. Luce and Holden (2009) documented a widespread pattern of declining summer streamflow over recent decades at gauging stations across the Pacific Northwest.

Climate changes will likely exacerbate existing (ongoing) trends in watershed degradation by affecting key processes or factors (stream thermal regimes, surface flows, groundwater and floodplain connectivity, landslide rates, fuels, fire, invasive species, and post disturbance human responses, to name but a few). Most climate change adaptation strategies call for strategic removal of non-climate stressors, because these will likely be more tractable or remediable than climate stressors (ISAB 2007, Furniss et al. 2010). No formal review of the ACS has apparently been conducted by the USFS or BLM to determine what, if any, science-based changes to the ACS best address future climate scenarios. It seems unlikely, however, that even a cursory review of the climate literature would lend support to proposals to remove or diminish currently protective provisions of the ACS.

The current ACS requirements are integral to assuring streams, wetlands, and other water bodies have the best possible resilience in the face of increasing climate stress. Extensive forested north-facing slopes can moder-

ate some climate influence on watersheds, and localized springs, and extensive shallow alluvial aquifers that store water seasonally can moderate summer streamflows and both summer and winter temperatures (Poole and Berman, 2001, Isaak et al. 2010, Wondzell 2011). Complex natural riparian vegetation communities and natural accumulations of large wood (resulting in concentrations of stored sediment) in and near floodplains are instrumental in creating and maintaining conditions that support hyporheic flow exchange. Wide Riparian Reserves provide not only shade, but essential protection and support for the natural processes that maintain and regenerate the suite of hydrologic and geomorphic elements that help buffer streams against climate forcing.

Intact watersheds are often seen to be less vulnerable to storms, floods, droughts, wildfire, and other extreme events, and are expected to be more resilient to future climate change than highly altered watersheds. Streams and rivers affected by reduced alluvial groundwater storage and diminished hyporheic buffering, fragmentation and loss of biological habitat connectivity, and a less intact native biota, are likely to respond more quickly and with greater volatility to climate change, as are engineered systems such as roads and dams. Watershed resilience in the face of climate change can best be maintained by protecting and restoring the suite of natural processes and conditions that characterize natural forested riparian areas and floodplains (Seavy et al. 2009, Furniss et al., 2010). This is exactly what the ACS was originally designed to accomplish. Whittling away riparian protections on the basis of narrowed, single-factor considerations such as proximate stream shade undermines the comprehensive protection of stream and riparian processes that the ACS was designed to maintain and restore. Finally, under changing climate, some management practices that seemed to produce desirable outcomes in the past may not do so in the future. For example, the putative effectiveness of forest thinning at altering fire behavior could become even more uncertain if weather extremes become more of a top-down driver of fire behavior (see Martinson and Omi 2013) in future climates (Dale et al. 2001, Westerling et al. 2006).

Our overall recommendation is that 1) *ACS protections for Riparian Reserves should be sustained and strengthened to better protect and restore natural ecosystem processes that confer resilience to climate change,* as detailed in our other recommendations. In addition, 2) *an interagency scientific conservation design effort is needed to expand and reconfigure some present Key Watersheds to ensure they better encompass specific areas that are likely to be topographic and hydrologic buffers to future climate change impacts.* Finally, we recommend that 3) *the direct and indirect effects of management actions on the integrity and capacity of stream and watershed ecosystems for resilience to climate change be analyzed in every environmental assessment, environmental impact statement, watershed analysis, and ESA consultation.*

Monitoring and Adaptive Management.

Environmental monitoring data often prove to be useful, but we cannot always anticipate how those data will be useful. Monitoring can be especially valuable when coupled with available data from historical records and time series sampling (such as streamflow gauging and temperature recorder data strings) (Wissmar 1993, Wissmar and Beschta 1988). Substantial progress has been made in the past 20 years on sampling design and methods of data collection for monitoring streams, watersheds and regions of watersheds (Steel et al. 2010). Twenty years after FEMAT, there are greatly expanded technological capabilities for spatially explicit data reporting and analysis, and numerous and increasingly robust methods to integrally evaluate considerations of ecological scale, geographical context, spatial and temporal continuity, and biological connectivity in data design and analysis.

The Northwest Forest Plan designated large

Adaptive Management Areas where alternative means of management and conservation might be implemented and closely monitored. For many reasons this option failed. Public involvement was required, but in most cases the public could not agree on the need for trial and testing of specific management hypotheses (Gray 2000). Managers and scientists also sometimes disagreed on hypotheses to test or what practices should be implemented. Lacking coherent large-scale experimental proposals drawing broad social support, funding never materialized. These failures are by no means endemic to the NFP—they characterize many, if not most aspirational attempts at formalized, large-scale adaptive management (Walters 1997).

We note, however, that ongoing management across multiple ownerships and with a multitude of natural background conditions creates a broad array of natural experiments that already exist on the landscape. Scientists can probably continue to learn much of what we need to know by creative monitoring of extant natural experiments. However imperfect they may be, natural experiments are more beneficial than waiting for planned, large-scale experiments that have proven exceedingly difficult to execute (and are almost always far from ideal themselves in terms of design and resources).

The existing monitoring program for aquatic resources in the Northwest Forest Plan area (Aquatic and Riparian Effectiveness Monitoring Program, AREMP, http://www.reo.gov/monitoring/reports/watershed/aremp/aremp.htm) in our view is constrained by certain design and sampling protocols that limit AREMP's capacity for drawing inferences about changes in habitat condition, living system condition, and biophysical processes over time. Whereas AREMP is intended by design to detect trends in some riparian or stream conditions over large areas, interpreting causal relations for responses requires information about changes in physical conditions and biota at specific locations over time. Further, AREMP design is based on delineated hydrologic units some of which do not represent hydrographically complete watersheds; this confounds identifying linkages between watershed condition and stream biotic and physical responses (Omernik 2003). Considering the scope of natural and man-caused variability in the field, Anlauf et al. (2011) suggested that AREMP incorporates a statistically insufficient number of sites to yield useful confidence intervals needed for reliable assessments of many measures of stream condition. Effectiveness monitoring generally fails when the design or data preclude process or cause-effect inferences, or when assumed fundamental relationships between habitat indices and biological populations and assemblages remain untested. Outside of the specific confines of AREMP, some useful new understanding has emerged from regionally extensive monitoring programs on federal lands in the Pacific Northwest (e.g., Hough-Snee et al. 2014, Meredith et al. 2014). In our view, these studies, far more specifically than AREMP, focus on iterative explicit hypotheses about cause-and-effect relations to inform the query and analysis of field survey data

We recommend three policy shifts in how monitoring is employed under the ACS. First, as a standard management practice, require *some form of effectiveness monitoring and expert review of stream and watershed responses for every forestry, range, mining, recreation development, or active management project.* Every project that could potentially affect watershed and stream conditions should integrally include collection of a field data set that sheds some light on key post-project biophysical conditions influenced by the project. Agency actions should help to increase the certainty of outcomes at particular sites. Agencies should first engage experts that could check collective awareness of the reliability of conventional assumptions about the effects of manage-

ment actions. Expert's perspectives would and increase the likelihood of the agencies identifying unanticipated outcomes that warrant broader study and management consideration. Expert review of project outcomes is needed to discourage the institutional habitat of assuming *a priori* that project outcomes are more certain and unequivocally beneficial than they often are.

Secondly, agencies should review existing programs of comprehensive regional and watershed-scale effectiveness monitoring programs, and develop comprehensive monitoring strategies to optimize return on the capital investment in monitoring. *We call for an interagency scientific panel to review the status and effectiveness of trend monitoring efforts, and identify data sets that could be useful in drawing inferences for improved monitoring programs.* New monitoring programs should be capable of assessing the effects of management actions and climate change on aquatic ecosystems and biological resources associated with BLM and USFS lands. They should be robust to both anticipated and unanticipated environmental changes.

Third, agency-driven improvements in monitoring programs should include *increased emphasis on tracking ecological conditions, including explicit biological condition measures, and the ability to establish with some certainty that trends in Key Watersheds result from specific management actions or choices (which may include deferral of active management).* Key Watersheds are especially critical for the medium- and long-term conservation success of the ACS, and may be disproportionately important to the survival and recovery of ESA-listed and other sensitive species. The special need to focus sustained time-trend effectiveness monitoring in Key Watersheds again raises the concern that re-delineation of Key Watersheds with each new piece of legislation or management planning cycle could disrupt long-term monitoring efforts. Pursuant to our third recommendation, we also recommend that agencies retain some degree of flexibility in allocation of monitoring resources to allow for occasional more directed and intensive investigation where assessments indicate that surprising and ecologically important outcomes have occurred.

CONCLUSIONS

In this report we examine selected new and emerging science that is relevant to the future of the ACS, and touch on concepts that should be integral to whatever might replace the ACS in the future. We believe more exhaustive consideration of the topics we raised--and a broadened consideration of others, including the functions of riparian and watershed reserves for conservation of terrestrial wildlife species--will only strengthen our conclusion that the founding rationale, basic architecture, and core conservation elements of the ACS remain sound. We also maintain that some specific improvements in ACS protection and conservation provisions are warranted.

New science raises many concerns about the adequacy of implementation of the ACS by the federal agencies. These issues include including post-fire and other logging after disturbances, logging and fuels treatments in riparian areas, the degree of riparian protection for headwater streams, the adequacy of past efforts for road system downsizing and remediation, the adequacy of conservation priorities for and delineations of Key Watersheds, the effectiveness of grazing management, and whether current monitoring is as useful as it should be.

This report raises concerns about anticipated climate change. While climate change does not fundamentally alter the basic facts of good conservation and responsible management, it both theoretically and materially raises the level of concern about many specific management issues, including the potential effective-

ness of restoration actions, the effectiveness of riparian areas as stream buffers, and implications for the burden of proof for management actions that balance known environmental problems against presumed restorative benefits. Most watersheds in the region are of mixed federal and other ownership. Because progress in protection and restoration on private lands has been limited (Stout et al. 2012), federal lands will likely continue to be the focus of watershed protection and aquatic habitat conservation, and related climate change initiatives for the foreseeable future.

Finally, an improved monitoring program will be necessary to ascertain that conservation of aquatic ecosystems and resources is in fact occurring, especially in the face of increasing physical and biotic stresses imposed by changing climate and human population growth. It will be of continued or increasing importance to evaluate the degree to which Riparian Reserves can serve as effective buffers against the cumulative effects of logging, roads, and other disturbances on forest lands catchment-wide. This question has assumed greater importance as research in disturbed ecosystems worldwide has demonstrated that watershed condition can sometimes affect fish assemblages more strongly than does riparian condition (Roth et al. 1996; Wang et al. 2003; 2006; Sály et al. 2011; Marzin et al. 2012).

We conclude that attempts to reduce protections to watershed, riparian, and freshwater ecosystems by weakening major components of the ACS and other related conservation elements of the Northwest Forest Plan are not justified by new and emerging science. Improved ecosystem protections--and better monitoring of outcomes--are warranted across all land ownerships, including federal forest lands, if freshwater ecosystems and their biota, including salmon and other sensitive species are to be effectively conserved in an era of increased ecological stress and changing climate.

LITERATURE CITED

Al-Chokhachy, R., B.B. Roper, and E.K. Archer. 2010. Evaluating the status and trends of physical stream habitat in headwater streams within the interior Columbia River and upper Missouri River Basins using an index approach. *Transactions of the American Fisheries Society* 139:1041-1059.

Anlauf, K.J., W. Gaeuman, and K.K. Jones. 2011. Detection of regional trends in salmonid habitat in coastal streams, Oregon. *Transactions of the American Fisheries Society* 140:52-66.

Battin, J., M.W. Wiley, M.H. Ruckelshaus, R.N. Palmer, E. Korb, K.K. Bartz, and H. Imaki. 2007. Projected impacts of climate change on salmon habitat restoration. *Proceedings of the National Academy of Sciences of the United States of America* 104:6720–6725.

Baxter, C.V. and F.R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (Salvelinus confluentus). *Canadian Journal of Fisheries and Aquatic Sciences* 57: 1470-1481.

Benda, L., D. Miller,., P. Bigelow, , and K. Andras, 2003. Effects of post-wildfire erosion on channel environments, Boise River, Idaho. *Forest Ecology and Management*, 178(1):105-119.

Beschta, R.L., J.J. Rhodes, J.B. Kauffman, R.E. Gresswell, G.W. Minshall, J.R. Karr, D.A. Perry, F.R. Hauer, and C.A. Frissell. 2004. Postfire management on forested public lands of the Western United States. *Conservation Biology* 18: 957–967.

Beschta, R.L., D.L. Donahue, D.A. DellaSala, J.J. Rhodes, J.R. Karr, M.H. O'Brien, T.L. Fleischer, and C. Deacon-Williams. 2013. Adapting to climate change on western public lands: Addressing the ecological effects of domestic, wild, and feral ungulates. *Environmental Management* 51:474–491.

Beschta, R.L., D.L. Donahue, D.A. DellaSala, J.J. Rhodes, J.R. Karr, M.H. O'Brien, T.L. Fleischer, and C. Deacon-Williams. 2014. Reducing livestock effects on public lands in the western United States as climate changes: A reply to Svejcar et al. *Environmental Management*, in press.

Beschta, R.L. and W.J. Ripple. 2012 The role of large predators in maintaining riparian plant communities and river morphology. *Geomorphology* 157-158: 88-98.

Black, S.H., D. Kulakowski, B.R. Noon, and D. DellaSala. 2013. Do bark beetle outbreaks increase wildfire risks in the Central U.S. Rocky Mountains: Implications from recent research? *Natural Areas Journal* 33:59-65.

Blair, M.S. 1994. Oregon coastal lake study: Phosphorus loading and water quality implications. M.S. Thesis, Oregon State University, Corvallis, OR. 114 pp.

BLM (Bureau of Land Management). 2008. Final Environmental Impact Statement for the Revision of the Resource Management Plans of the Western Oregon Bureau of Land Management Districts. Portland, OR. Available online at http://www.blm.gov/or/plans/wopr/final_eis/

Blumm, M.C., and T. Wigington. 2013. The Oregon and California Railroad Grant Lands' sordid past, contentious present, and uncertain future: a century of conflict. *40 Boston College Envvironmental Affairs Law Review* 40:1 (2013). http://lawdigitalcommons.bc.edu/ealr/vol40/iss1/2/

Brummer, C.J., T.B. Abbe, , J.R. Sampson, , and D.R. Montgomery, 2006. Influence of vertical channel change associated with wood accumulations on delineating channel migration zones, Washington, USA. *Geomorphology* 803:295-309.

Bryce, S.A., G.A. Lomnicky, and P.R. Kaufmann. 2010. Protecting sediment-sensitive aquatic species in mountain streams through the application of biologically based streambed sediment criteria. *Journal of the North American Benthological Society* 29:657-672.

Buhl, K.J. and S.J. Hamilton. 1998. Acute toxicity of fire-retardant and foam-suppressant chemicals to early life stages of Chinook salmon (*Oncorhynchus tshawytscha*). Environmental Toxicology and Chemistry 17(8):1589-1599.

Burnett, K. M., G.H. Reeves, D.J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. *Ecological Applications* 17(1), 66-80.

Carnefix, G. and C. A. Frissell. 2009. Aquatic and other environmental impacts of roads: The case for road density as indicator of human disturbance and road-density reduction as restoration target, a concise review. Pacific Rivers Council Science Publication 09-001. Pacific Rivers Council, Portland, OR and Polson, MT. http://pacificrivers.org/science-research/resources-publications/road-density-as-indicator/download

Carpenter, S.R., N.F. Caraco, D.L. Correll, R.W. Howarth, A.N. Sharpley, and V.H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8:559–568. http://dx.doi.org/10.1890/1051-0761(1998)008[0559:NPOSWW]2.0.CO;2

Cover, M.R., C.L. May, W.E. Dietrich, and V.H. Resh. 2008. Quantitative linkages among sediment supply, streambed fine sediment, and benthic macroinvertebrates in northern California streams. *Journal of the North American Benthological Society* 27(1):35-149. http://csmres.jmu.edu/geollab/May/Web/Research/Reprints/cover%20et%20al%202008%20jnabs.pdf

Daggett, S.G., A.H. Vogel, and R.R. Petersen. 1996. Eutrophication of Mercer, Munsel, and Woahink Lakes, Oregon. *Northwest Science* 70 (Special Issue 2):28-38.

Dale, V.H., L.A. Joyce, , S. McNulty, , R.P. Neilson, , M.P. Ayres, , M.D. Flannigan, , ... and M.B. . Wotton. 2001. Climate Change and Forest Disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience* 51(9):723-734.

Dalton, M.M., P.W. Mote, and A.K. Snover. 2013. *Climate Change in the Northwest Implications for Our Landscapes, Waters, and Communities*. Island Press, Washington DC. 271 pp.

DellaSala, D.A. 2013. Ecological Importance of Bureau of Land Management O&C and Coos Bay Wagon Road Holdings in Western Oregon with Special Attention to Surface Water Source Areas. Geos Institute, Ashland, OR, 19 pp.

DellaSala, D. A., R.G. Anthony, M.L. Bond, Monica, E.S. Fernandez, C.A. Frissell, Chris, C.T. Hanson, and R. Spivak. 2014. Alternative Views of a Restoration Framework for Federal Forests in the Pacific Northwest. *Journal of Forestry* 111(6):420-429.

DellaSala, D.A. and J. Williams. 2006. Northwest Forest Plan ten years later – how far have we come and where are we going. *Conservation Biology* 20:274-276.

DellaSala, D.A., J.R. Karr, and D.M. Olson. 2011. Roadless areas and clean water. *Journal of Soil and Water Conservation* 66:78A-84A.

Donato, D.C., J.B. Fontaine, J.L. Campbell, W.D. Robinson, J.B. Kauffman, and B.E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science 311: 352.

Dwire, K.A, C.C. Rhoades, and M.K. Young. 2010. Potential effects of fuel management activities on riparian areas. pp. 175–205 In W.J. Elliot et al., (eds.), Cumulative watershed effects of fuel management in the western United States. USDA Forest Service General Technical Report RMRS-GTR-231, Rocky Mountain Research Station, Ft. Collins, CO. ftp://frap.fire.ca.gov/pub/incoming/TAC/Contractor%20final%20lit%20review%20docs/lit%20review_water/Dwire%202006.pdf

Ebersole, J.L., W.J. Liss, and C.A. Frissell. 2003. Cold water patches in warm streams: Physicochemical characteristics and the influence of shading. *Journal of the American Water Resources Association* 39:355-368. (Published online 8 June 2007).

Espinosa, Jr., F.A., J.J. Rhodes, and D.A. McCullough. 1997. The failure of existing plans to protect salmon habitat in the Clearwater National Forest in Idaho. *Journal of Environmental Management* 49(2): 205-230.

Estes, J.A. 2011. Trophic downgrading of planet Earth. *Science* 333. 15 July 2011

Everest, F.H. and G.H. Reeves. 2006. Riparian and aquatic habitats of the Pacific Northwest and southeast Alaska: ecology, management history, and potential management strategies. Gen. Tech. Rep. PNW-GTR-692. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 130 p.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, and H.W. Li. 2000. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52(6):1-16.

Feist, B.E., E.R. Buhle, P. Arnold, J.W. Davis, and N.L. Scholz. 2011. Landscape ecotoxicology of coho salmon spawner mortality in urban streams. *PLoS ONE* 6(8): e23424. doi:10.1371/journal.pone.0023424. http://www.plosone.org/article/info:doi%2F10.1371%2Fjournal.pone.0023424

FEMAT (Forest Ecosystem Management and Assessment Team). 1993. Forest Ecosystem Management: An ecological, economic and social assessment. USDA Forest Service, BLM, USFWS, NOAA, EPA and National Park Service, Portland, Oregon. 1039 p.

Firman, J.C., E.A. Steel, D.W. Jensen, K.M. Burnett, K. Christiansen, B.E. Feist, Blake E., D.P. Larsen, and K. Anlauf. 2011. Landscape models of adult coho salmon density examined at four spatial extents. *Transactions of the American Fisheries Society* 140:440-455.

Freeman, M.C., C.M. Pringle, and C.R. Jackson. 2007. Hydrologic connectivity and the contribution of stream headwaters to ecological integrity and regional scales. *Journal of the American Water Resources Association* 43(1):5-14. DOI: 10.1111/j.1752-1688.2007.00002.x. http://www.energy.vt.edu/ncepstudy/pub/nature/regionalscaleinfluence.pdf

Frissell, C.A. and D. Bayles. 1996. Ecosystem management and the conservation of aquatic biodiversity and ecological integrity. *Water Resources Bulletin* 32:229-240.

Furniss, M.J., B.P. Stabb, S. Hazelhurst, C.F. Clifton, K.B. Roby, B.L. Ilhadrt, E.B. Larry, A.H. Todd, L.M. Reid, S.J. Hines, K.A. Bennett, C.H. Luce, and P.J. Edwards. 2010. Water, climate change, and forests: watershed stewardship for a changing climate. USDA Forest Service General Technical Report PNW-GTR-812, Portland, Oregon, 75pp. http://www.fs.fed.us/pnw/pubs/pnw_gtr812.pdf

Franklin, J.F. and K.N. Johnson. 2012. A restoration framework for federal forests in the Pacific Northwest. *Journal of Forestry* 110: 429-439.

Frissell, C.A. and R.K. Nawa. 1992. Incidence and causes of failure of artificial habitat structures in streams of western Oregon and Washington. *North American Journal of Fisheries Management* 12:182-197.

Gaikowski, M.P., S.J. Hamilton, K.J. Buhl, S.F. McDonald, and C.H Summers. 1996. Acute toxicity of three fire-retardant and two fire-suppressant foam formulations to the early life stages of rainbow trout (*Oncorhynchus mykiss*). *Environmental Toxicology and Chemistry* 15(8):1365-1374.

Gallo, K., S.H. Lanigan, P. Eldred, S.N. Gordon, and C. Moyer. 2005. Northwest Forest Plan—the first 10 years (1994–2003): Preliminary assessment of the condition of watersheds. Gen. Tech. Rep. PNW-GTR-647. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 133 p.

GAO (Government Accountability Office). 1999. Ecosystem Planning: Northwest Forest and Interior Columbia River Basin Plans Demonstrate Improvements in Land-Use Planning (Letter Report, 05/26/99, GAO/RCED-99-64). http://www.gpo.gov/fdsys/pkg/GAOREPORTS-RCED-99-64/html/GAOREPORTS-RCED-99-64.htm

Gomi, T., R.C. Sidel, and J.S. Richardson. 2002. Understanding processes and downstream linkages of headwater streams. *BioScience*52:905-916.

Gray, A.N. 2000. Adaptive ecosystem management in the Pacific Northwest: a case study from coastal Oregon. *Conservation Ecology* 4(2):6. [online] http://www.consecol.org/vol4/iss2/art6/

Gresswell, R.E. 1999. Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Association* 128:193–221.

Gucinski, H., M.J. Furniss, R.R. Ziemer, and M.H. Brookes. 2001. Forest roads: a synthesis of scientific information. Gen. Tech. Rep. PNWGTR-509. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR. http://www.fs.fed.us/pnw/pubs/gtr509.pdf

Hicks B.J., R.L. Beschta, and R.D. Harr. 1991. Long-term changes in streamflow following logging in western Oregon and associated fisheries implications. *Water Resources Bulletin* 27(2): 217- 226.

Hough-Snee, N., A. Kasprak, B.B. Roper, and C.S. Meredith. 2014. Direct and indirect drivers of instream wood in the interior Pacific Northwest, USA: decoupling climate, vegetation, disturbance, and geomorphic setting. *Riparian Ecology and Conservation* 2(1): 2299-1042. DOI: 10.2478/remc-2014-0002

Houlahan, J.E. and C.S. Findlay. 2003. The effects of adjacent land use on wetland amphibian species richness and community composition. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1078–1094

Hughes, R.M, S. Howlin, and P.R. Kaufmann. 2004. A biointegrity index for coldwater streams of western Oregon and Washington. *Transactions of the American Fisheries Society* 133:1497-1515.

ISAB. (Independent Scientific Advisory Board). 2007. Climate change impacts on Columbia River basin fish and wildlife. Northwest Power and Conservation council, Portland, OR. 136 pp. http://www.nwcouncil.org/media/31247/isab2007_2.pdf

Issak, D.J., C.H. Luce, B.E. Rieman, D.E. Nagel, E.E. Peterson, D.L. Horan, S. Parkes, and G.L. Chandler. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications* 20:1350–1371.

Johnson, K.N. 2010. Water, climate change, and forests: watershed stewardship for a changing climate. USDA Forest Service General Technical Report PNW-GTR-812. Portland, Oregon, 75pp. http://www.fs.fed.us/pnw/pubs/pnw_gtr812.pdf

Johnson, K.N. and J.F. Franklin. 2012. Increasing Timber Harvest Levels on the BLM O&C Lands While Maintaining Environmental Values (Revised). Testimony before the Senate Committee on Energy and Natural Resources , June 25, 2013. Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR. Online at http://fes.forestry.oregonstate.edu/sites/fes.forestry.oregonstate.edu/files/PDFs/Johnson_June%202013.pdf

Jones, J.A., F. J. Swanson, B.C. Wemple, and K.U. Snyder. 2000. Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. *Conservation Biology* 14:76-85.

Karr, J.R., J.J. Rhodes, G.W. Minshall, F.R. Hauer, R.L. Beschta, C.A. Frissell, and D.A. Perry. 2004. The effects of postfire salvage logging on aquatic ecosystems in the American West. *BioScience*54:1029-1033.

Kauffman, J.B., R.L. Beschta, N. Otting, and D. Lytje. 1997. An ecological perspective of riparian and stream restoration in the western United States. *Fisheries* 22(5):12-24.

Kaufmann, P.R. and R.M. Hughes. 2006. Geomorphic and anthropogenic influences on fish and amphibians in Pacific Northwest coastal streams. pp. 429-455. In R.M. Hughes, L. Wang, and P.W. Seelbach (eds.). *Landscape influences on stream habitat and biological assemblages*. American Fisheries Society, Symposium 48.

Klein, R.D., J. Lewis, and M.S. Bufflben. 2012. Logging and turbidity in the coastal watersheds of northern California. *Geomorphology* 139-140:136-144. http://www.sciencedirect.com/science/article/pii/S0169555X11005277

Kubin, E. 2006. Leaching of nitrogen from upland forest-regeneration sites into wetland areas. Pp. 87-94 In Krecek, J. and M. Haigh (eds.) *Environmental Role of Wetlands in Headwaters*. Springer, The Netherlands.

Labbe T.R. and K.D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications* 10: 1774–1791.

Lee, D.C., J.R. Sedell, B.E. Rieman, R.F. Thurow, J.E. Williams, and others. 1997. Broadscale assessment of aquatic species and habitats. Pp. 1057-1496 in S.J. Arbelbide (editor). An assessment of ecosystem components in the Interior Columbia Basin and portions of the Klamath and Great Basins: Vol. III. USDA Forest Service General Technical Report PNW-GTR-405.

Lindenmayer, D.B., D.R. Foster, , J.F. Franklin, , M.L Hunter,., R.F. Noss,., F.A. Schmiegelow, , and D. Perry, 2004. Salvage harvesting policies after natural disturbance. *Science (Washington)* 303(5662):303.

Lindenmayer, D.B. and R.F. Noss. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. *Conservation Biology* 20(4): 949–958.

Lowe, W.H. and G.E. Likens. 2005. Moving headwater streams to the head of the class. *BioScience* 55:196-197.

Luce, C.H., B.E. Rieman, J.L. Dunham, J.G. King, & T.A. Black, 2001. Incorporating aquatic ecology into decisions on prioritization of road decommissioning. Water Resources Impact 3(3):8-14.

Luce, C.H. and Z.A. Holden. 2009. Declining annual streamflow distributions in the Pacific Northwest United States, 1948–2006. *Geophysical Research Letters* 36, L16401, doi:10.1029/2009GL039407, 2009.

Lydersen, J.M., M.P. North, and B.M. Collins. 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. Forest Ecology and Management 328:326-334. DOI:10.1016/j. Foreco.2014.06.005.

Malison, R.L. and C.V. Baxter. 2010. The “fire pulse:” wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. *Canadian Journal of Fisheries and Aquatic Sciences* 67(3):570-579.

Martinson, E.J. and P.N. Omi. 2013. Fuels treatments and fire severity: A meta-analysis. Research Paper RMRS-RP-103WWW. USDA Forest Service, Fort Collins, CO. 38 pp. http://www.fs.fed.us/rm/pubs/rmrs_rp103.pdf

Marzin, A.P., P. Verdonschot, and D. Pont. 2012. The relative influence of catchment, riparian corridor and local anthropogenic pressures on fish and macroinvertebrate assemblages in French rivers. *Hydrobiologia* 704: 375–388.

McCarthy S.G., J.P. Incardona, and N.L. Scholz. 2008. Coastal storms, toxic runoff, and the sustainable conservation of fish and fisheries. American Fisheries Society Symposium 64:1-21.

McCullough, D.A. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids, with special reference to Chinook salmon. EPA 910-R-99-010. Prepared for the United States Environmental Protection Agency, Region 10, Seattle, Washington. 279 p.

Meredith, C., B. Roper, and E. Archer. 2014. Reductions in instream wood in streams near roads in the interior Columbia River Basin. *North American Journal of Fisheries Management* 34(3):493-506.

Minshall, W. 2003. Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management* 178:155-161.

Minshall, G.W., C.T. Robinson, and D.E. Lawrence. 1997. Postfire response of lotic ecosystems in Yellowstone National Park U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2509-2525.

Montgomery, D.R. 1995. Input- and output-oriented approaches to implementing ecosystem management. *Environmental Management* 19(2): 183-188.

Montgomery, D.R., G.E. Grant, and K. Sullivan. 1995. Watershed analysis as a framework for implementing ecosystem management. *Water Resources Bulletin* 31(9):369-386.

Moore, R.D. and S.M. Wondzell. 2005. Physical hydrology and the effects of forest harvesting in the Pacific Northwest: A review. *Journal of the American Water Resources Association* 41(4):763-784. DOI: 10.1111/j.1752-1688.2005.tb03770.x

Mote, P.W., E.A. Parson, A.F. Hamlet, W.S. Keeton, D. Lettenmaier, N. Mantua, E.L. Miles, D.W. Peterson, D.L. Peterson, R. Slaughter, and A.K. Snover. 2003. Preparing for climatic change: the water, salmon, and forests of the Pacific Northwest. *Climatic Change* 61: 45–88.

Newcombe, C.P. and J.O.T. Jensen. 1996. Channel suspended sediment and fisheries: a synthesis for quantitative assessment of risk and impact. *North American Journal of Fisheries Management* 16(4):693-719

NMFS (National Marine Fisheries Service). 2007. Puget Sound Salmon Recovery Plan. Pacific Northwest Region, Seattle, WA. 472 pp. http://www.westcoast.fisheries.noaa.gov/publications/recovery_planning/salmon_steelhead/domains/puget_sound/chinook/pugetsoundchinookrecoveryplan.pdf

NMFS (National Marine Fisheries Service). 2011. Biological Opinion: Environmental Protection Agency Registration of Pesticides 2,4-D, Triclopyr BEE, Diuron, Linuron, Captan, and Chlorothalonil. June 30, 2011. 970 pp. + appendices. http://www.nmfs.noaa.gov/pr/pdfs/consultations/pesticide_opinion4.pdf

NMFS (National Marine Fisheries Service). 2012. Recovery Plan Volume 1 for the Southern Oregon Northern California Coast Evolutionarily Significant Unit of coho salmon (*Oncorhynchus kisutch*). Southwest Regional Office, Arcata, CA. http://www.westcoast.fisheries.noaa.gov/publications/recovery_planning/salmon_steelhead/domains/southern_oregon_northern_california/soncc_plan_draft_2012_entire.pdf

NOAA-NMFS and USFWS (National Marine Fisheries Service and US Fish and Widllife Service). 2006a. Final Environmental Impact Statement for the Proposed Issuance of Multiple Species Incidental Take Permits or 4(d) Rules for the Washington State Forests Habitat Conservation Plan (January 2006).

NOAA-NMFS and USFWS (National Marine Fisheries Service and US Fish and Widllife Service). 2006b. Endangered Species Act Section 7 Consultation Biological Opinion and Section 10 Statement of Findings And Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat Consultation (June 5, 2006). 337 pp.

Noss, R.F., J.F. Franklin, W.L. Baker, T. Schoennagel, and P.B. Moyle. 2006. Managing fire-prone forests in the western United States. Frontiers in Ecology and the Environment 4:481-487.

Olson, D.H., P.D. Anderson, C.A. Frissell, H.H. Welsh, Jr., and D.F. Bradford. 2007. Biodiversity management approaches for stream-riparian areas: perspectives for Pacific Northwest headwater forests, microclimates, and amphibians. *Forest Ecology and Management* 246(1):81-107.

Omernik, J.M. 2003. The misuse of hydrologic unit maps for extrapolation, reporting and ecosystem management. *Journal of the American Water Resources Association* 39:563–573.

Oregon DEQ. 1994. Coquille River and estuary water quality report, Total Maximum Daily Load program. Oregon Department of Environmental Quality. Portland, OR. 48pp. http://www.deq.state.or.us/wq/tmdls/docs/southcoastbasin/coquille/CoquilleRiverTMDL.pdf

Oregon DEQ. 2007. Tenmile Lakes Watershed Total Maximum Daily Load (TMDL). Oregon Department of Environmental Quality. Portland, OR. 167 pp. http://www.deq.state.or.us/wq/tmdls/docs/southcoastbasin/tenmile/tmdl.pdf

Pacific Rivers Council. 2008. Comments on BLM WOPR DEIS. Portland, Oregon. [Jan. 11, 2008]. http://pacificrivers.org/conservation-priorities/land-management/federal-forest-planning/western-oregon-plan-revisions/prcs-comprehensive-comments-on-the-draft-eis

Pacific Rivers Council (Wright, B. and C. Frissell). 2010. Roads and rivers II: An assessment of national forest roads analyses. Report for the Pacific Rivers Council, Portland, OR. [online] http://pacificrivers.org/science-research/resources-publications/roads-and-rivers-ii/download

Pollock, M.M. and T.J. Beechie. 2014. Does riparian forest thinning enhance biodiversity? The ecological importance of large wood. *Journal of the American Water Resources Association* 50(3):543-559. DOI: 10.1111/jawr.12206

Pollock, M.M., T.J. Beechie, M. Liermann, and R.E. Bigley. 2009. Stream temperature relationships to forest harvest in western Washington. *Journal of the American Water Resources Association* 45(1):141-156.

Pollock, M.M., T.J. Beechie, and H. Imaki. 2012. Using reference conditions in ecosystem restoration: an example for riparian conifer forests in the Pacific Northwest. *Ecosphere* 3(11) Article 98: 1-23. http://dx.doi.org/10.1890/ES12-00175.1

Poole, G.C. and C.H. Berman. 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. *Environmental Management* 27(6):787–802.

Poole, G.C., S.J. O'Daniel, K.L. Jones, W.W. Woessner, E.S. Bernhardt, A.M. Helton, J.A. Stanford, B.R. Boer, and T.J. Beechie. 2008. Hydrologic spiralling: the role of multiple interactive flow paths in stream ecosystems. *River Research and Applications* 24(7):1018-1031.

Rashin, E.B., C.J. Clishe, A.T. Loch, and J.M. Bell. 2006. Effectiveness of timber harvest practices for controlling sediment. *Journal of the American Water Resources Association* 42:1307-1347.

Reeves, G.H., L.E. Benda, K.M. Burnett, P.A. Bisson, and J.R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. *In* J. Nielsen (editor), Proceedings of the American Fisheries Society Symposium on Evolution and the Aquatic Ecosystem, Bethesda, Maryland. Pp. 334–349.

Reeves, G.H., J.E. Williams, K. Gallo, and K.M. Burnett. 2006a. The aquatic conservation strategy of the Northwest Forest Plan. *Conservation Biology* 20: 319-329.

Reeves, G.H, P.A. Bisson, B.E. Reiman, and L.E. Benda. 2006b. Postfire logging in riparian areas. *Conservation Biology* 20:994-1004.

Reeves, G.H., B.R. Pickard, and K.N. Johnson. 2013. Alternative Riparian Buffer Strategies for Matrix Lands of BLM Western Oregon Forests that Maintain Aquatic Ecosystem Values. REVIEW DRAFT. January 23, 2013.

Reid, L.M., N.J. Dewey, T.E. Lisle, and S. Hilton. 2010. The incidence and role of gullies after logging in a coastal redwood forest. *Geomorphology* 117: 155-169. [online] http://naldc.nal.usda.gov/download/40745/PDF

Reid, L.M. and S. Hilton. 1998. Buffering the buffer. In: Proceedings of the Conference on Coastal Watersheds: The Caspar Creek Story. U.S.D.A. Forest Service, Pacific Southwest Forest and Range Experiment Station, Redwood Sciences Lab, Arcata, CA. http://www.fs.fed.us/psw/publications/documents/gtr-168/08reid.pdf

Rhodes, J.J. and W.L. Baker. 2008. Fire probability, fuel treatment effectiveness and ecological trade-offs in western U.S. public forests. *The Open Forest Science Journal* 1:1-7.

Rhodes, J.J., D.A. McCullough, and F.A. Espinosa. 1994. A coarse screening process for evaluation of the effects of land management activities on salmon spawning and rearing habitat in ESA consultations. Columbia River Inter-Tribal Fish Commission, Technical Report 94-4. Portland, OR. 245pp.

Roni, P., K. Hanson, and T. Beechie, 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North American Journal of Fisheries Management*, 28(3):856-890.

Roth, N.E., J.D. Allan, and D.L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology* 11:141–156.

Sály, P., P. Takács, I. Kiss, P. Bíró and T. Erós. 2011. The relative influence of spatial context and catchment- and site-scale environmental factors on stream fish assemblages in a human-modified landscape. *Ecology of Freshwater Fish* 20: 251–262.

Seavy, N.E., T. Gardali, G.H. Golet, F.T. Griggs, C.A. Howell, R. Kelsey, S.L. Small, J.H. Viers, J. F. Weigand. 2009. Why climate change makes riparian restoration more important than ever: recommendations for practice and research. *Ecological Restoration* 27(3): 330-338. http://er.uwpress.org/content/27/3/330.full.pdf+html

Sedell, J.R., P.A. Bisson, , F.J. Swanson, , and S.V. Gregory, (1988).What we know about large trees that fall into streams and rivers. Pp. 83-112 In *From the forest to the sea, a story of fallen trees*, Maser, C., Tarrant, R.F., Trappe, J.M., and Franklin, J.F., tech eds. USDA Forest Service General Technical Report GTR-PNW-229, Pacific Northwest Res. Sta., Portland, OR. http://andrewsforest.oregonstate.edu/pubs/pdf/pub871.pdf

Spence, B.C., G.A. Lomnicky, R.M. Hughes, and R.P. Novitzki. 1996. An ecosystem approach to salmonid conservation. Funded jointly by the U.S. EPA, U.S. Fish and Wildlife Service and National Marine Fisheries Service. TR-4501-96-6057. ManTech Environmental Research Services Corp., Corvallis, OR.

Spies, T., M. Pollock, G. Reeves, and T. Beechie. 2013. Effects of riparian thinning on wood recruitment: A scientific synthesis. Science Review Team, Wood Recruitment Subgroup, Forestry Sciences Laboratory, Corvallis, OR, and Northwest Fisheries Science Center, Seattle, WA. 28 January 2013. 46pp. http://www.mediate.com/DSConsulting/docs/FINAL%20wood%20recruitment%20document.pdf

Steel, E.A., R.M. Hughes, A.H. Fullerton, S. Schmutz, J.A. Young, M. Fukushima, S. Muhar, M. Poppe, B.E. Feist, and C. Trautwein. 2010. Are we meeting the challenges of landscape-scale riverine research? A review. *Living Reviews in Landscape Research* 4(2010):1. http://www.livingreviews.org/lrlr-2010-1.

Stout, H.A., P.W. Lawson, D.L. Bottom, T.D. Cooney, M.J. Ford, C.E. Jordan, R.G. Kope, L.M. Kruzic, G.R. Pess, G.H. Reeves, M.D. Scheuerell, T.C. Wainwright, R.S. Waples, E. Ward, L.A. Weitkamp, J.G. Williams, and T.H. Williams. 2012. Scientific conclusions of the status review for Oregon coast coho salmon (*Oncorhynchus kisutch*). U.S. Dept. Commerce, NOAA Tech. Memo.NMFS-NWFSC-118, 242 p.

Sweeney, B.W. and J.D. Newbold, 2014. Streamside Forest Buffer Width Needed to Protect Stream Water Quality, Habitat, and Organisms: A Literature Review. *Journal of the American Water Resources Association* (JAWRA):560-584.

Thompson, W.L. and D.C. Lee. 2000. Modeling relationships between landscape-level attributes and snorkel counts of chinook salmon and steelhead parr in Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1834–1842. doi:10.1139/cjfas-57-9-1834

Torgersen, C.E., Price, D.M., Li, H.W., and McIntosh, B.A. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. *Ecological Applications*, 9(1):301-319.

Torgersen, C.E., J.L. Ebersole, and D.M. Keenan. 2012. Primer for Identifying Cold-Water Refuges to Protect and Restore Thermal Diversity in Riverine Landscapes. EPA 910-C-12-001, U.S. Environmental Protection Agency, Seattle, Washington. p. 91.

Trombulak, S.C. and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18-30.

USDA/USDI 1994. ROD (Northwest Forest Plan Record of Decision). FSEIS and ROD for the Amendment of Planning Documents and Management of Habitat for Late-Successional Old-growth Forest Related Species within the Range of the Northern Spotted Owl. Portland, OR. http://www.blm.gov/or/plans/NFPnepa/FSEIS-1994/NFPTitl.htm

USDA Forest Service Pacific Northwest Region. 2008. Aquatic and Riparian Conservation Strategy (ARCS), August 13, 2008. 31 pp.

USFWS (USDI Fish and Wildlife Service). 1999. Endangered and Threatened Wildlife and Plants; Determination of Threatened Status for Bull Trout in the Conterminous United States. Final Rule. Federal Register 64:58909-58933.

Walters, C. 1997. Challenges in adaptive management of riparian and coastal ecosystems. *Conservation Ecology* 1(2):1. [online] http://www.consecol.org/vol1/iss2/art1/

Wang, L.Z., J. Lyons, P. Rasmussen, P. Seelbach, T. Simon, M. Wiley, P. Kanehl, E. Baker, S. Niemela, and P.M. Stewart. 2003. Watershed, reach, and riparian influences on stream fish assemblages in the Northern Lakes and Forest Ecoregion, USA. Canadian Journal of Fisheries and Aquatic Sciences 60: 491–505.

Wang, L., P.W. Seelbach, and J. Lyons. 2006. Effects of levels of human disturbance on the influence of catchment, riparian, and reach-scale factors on fish assemblages. Pages 199–219 In R.M. Hughes, L. Wang, and P.W. Seelbach, editors. Landscape influences on stream habitats and biological assemblages. American Fisheries Society Symposium 48, Bethesda, Maryland.

WDNR (Washington Department of Natural Resources). 2005. Forest Practices Habitat Conservation Plan. Olympia, WA. http://www.dnr.wa.gov/businesspermits/topics/forestpracticeshcp/pages/fp_hcp.aspx

Wemple, B.C. and J.A. Jones. 2003. Runoff production on forest roads in a steep, mountain catchment. *Water Resources Research* 39(8):1220, doi:10.1029/2002WR001744.

Wenger, S. 1999. A review of the scientific literature on riparian buffer width, extent, and vegetation. Office of Public Service and Outreach, Institute of Ecology, University of Georgia, Athens, Georgia, USA. http://www.cc.utexas.edu/law/centers/cppdr/services/Improving%20Streams%20web/Work%20Groups/Public%20Lands/Wegner_1999_Review_of_buffer_width.pdf

Westerling, A.L., H.G. Hidalgo, , D.R. Cayan, , and T.W. Swetnam, 2006. Warming and earlier spring increase western US forest wildfire activity. *Science*, 313(5789):940-943.

Wickham, J.D., T.G. Wade, and K.H. Ritters. 2008. Detecting temporal change in watershed nutrient yields. *Environmental Management* 42:3223-231.

Wigington, P.J., J.L. Ebersole, M.E. Colvin, S.G. Leibowitz, B. Miller, B. Hansen, H. Lavigne, D. White, J.P. Baker, M.R. Church, J.R. Brooks, M.A. Cairns, and J.E. Compton. 2006. Coho salmon dependence on intermittent streams. *Frontiers in Ecology and the Environment* 4(10):514-519.

Wissmar, R.C. 1993. Long-term monitoring in stream ecosystems. *Environmental Monitoring and Assessment* 26: 219-234.

Wissmar, R.C. and R. Beschta. 1998. Restoration and the management of riparian ecosystems. *Freshwater Biology* 40(3): 571-585.

Wondzell, S.M. 2011. The role of the hyporheic zone across stream networks. *Hydrologic Processes* 25(22):3525-2532. DOI: 10.1002/hyp.8119

View publication stats

Furniss *et al. Fire Ecology* (2024) 20:105
https://doi.org/10.1186/s42408-024-00339-y

Fire Ecology

ORIGINAL RESEARCH

Open Access

Wildfire management decisions outweigh mechanical treatment as the keystone to forest landscape adaptation

Tucker J. Furniss[1*], Nicholas Povak[2,3], Paul F. Hessburg[2,4], R. Brion Salter[2], Zhuoran Duan[5] and Mark Wigmosta[5,6]

Abstract

Background Modern land management faces unprecedented uncertainty regarding future climates, novel disturbance regimes, and unanticipated ecological feedbacks. Mitigating this uncertainty requires a cohesive landscape management strategy that utilizes multiple methods to optimize benefits while hedging risks amidst uncertain futures. We used a process-based landscape simulation model (LANDIS-II) to forecast forest management, growth, climate effects, and future wildfire dynamics, and we distilled results using a decision support tool allowing us to examine tradeoffs between alternative management strategies. We developed plausible future management scenarios based on factorial combinations of restoration-oriented thinning prescriptions, prescribed fire, and wildland fire use. Results were assessed continuously for a 100-year simulation period, which provided a unique assessment of tradeoffs and benefits among seven primary topics representing *social*, *ecological*, and *economic* aspects of resilience.

Results Projected climatic changes had a substantial impact on modeled wildfire activity. In the *Wildfire Only* scenario (no treatments, but including active wildfire and climate change), we observed an upwards inflection point in area burned around mid-century (2060) that had detrimental impacts on total landscape carbon storage. While simulated mechanical treatments (~ 3% area per year) reduced the incidence of high-severity fire, it did not eliminate this inflection completely. Scenarios involving wildland fire use resulted in greater reductions in high-severity fire and a more linear trend in cumulative area burned. Mechanical treatments were beneficial for subtopics under the *economic* topic given their positive financial return on investment, while wildland fire use scenarios were better for *ecological* subtopics, primarily due to a greater reduction in high-severity fire. Benefits among the *social* subtopics were mixed, reflecting the inevitability of tradeoffs in landscapes that we rely on for diverse and countervailing ecosystem services.

Conclusions This study provides evidence that optimal future scenarios will involve a mix of active and passive management strategies, allowing different management tactics to coexist within and among ownerships classes. Our results also emphasize the importance of wildfire management decisions as central to building more robust and resilient future landscapes.

Keywords Carbon, Climate change, Decision support systems, Forest landscape models, LANDIS-II, Landscape ecology, Resilience, Temperate forests, Wildfire

*Correspondence:
Tucker J. Furniss
tucker.furniss@uwyo.edu
Full list of author information is available at the end of the article

© The Author(s) 2024. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

Resumen

Antecedentes El manejo moderno de tierras enfrenta incertidumbres sin precedentes relacionadas con el clima futuro, los nuevos cambios en los regímenes de fuegos, y retroalimentaciones ecológicas no anticipadas. El mitigar esta incertidumbre requiere de una aproximación al manejo de paisajes cohesivo, que utilice métodos simples para optimizar los beneficios, mientras se evaden riesgos sobre un futuro incierto. Usamos para ellos un modelo de simulación del paisaje basado en procesos (LANDIS-II), para pronosticar el manejo del bosque, su crecimiento, los efectos del clima, y dinámica de futuros fuegos, y filtramos los resultados usando una herramienta de soporte de decisiones, lo que nos permitió examinar las retroalimentaciones entre estrategias de manejo alternativas. Desarrollamos escenarios plausibles de manejo futuro basados en combinaciones factoriales de prescripciones de restauración mediante raleos, quemas prescriptas, y el aprovechamiento de incendios naturales. Los resultados fueron determinados de manera continua en un período simulado de 100 años, lo cual proveyó una valoración única de retroalimentaciones y beneficios entre siete tópicos primarios que representaron aspectos sociales, ecológicos y económicos de la resiliencia.

Resultados El cambio climático proyectado tuvo un impacto substancial en el modelado de la actividad de incendios. En el escenario de solamente incendios (sin tratamientos, pero incluyendo los efectos de incendios y el cambio climático), observamos un punto de inflexión ascendente en un área que se quemaría alrededor de mediados de este siglo (2060), que mostró impactos detrimentales en el almacenamiento de carbono a nivel de paisaje. Cuando simulamos los tratamientos mecánicos (~3% del área por año), si bien se redujo la incidencia de fuegos de alta severidad, esta inflexión no se eliminó completamente. Los escenarios que implicaron el uso de incendios naturales produjo una gran reducción en incendios severos y una tendencia más lineal en la acumulación del área quemada. Los tratamientos mecánicos fueron beneficiosos para los subtópicos que estaban bajo el tópico económico, dados sus retornos financieros relacionados con la inversión, mientras que el escenario de uso de los incendios naturales fue mejor para el subtópico ecológico, primariamente por una mayor reducción en los incendios de gran severidad. Los beneficios entre los subtópicos sociales fueron mixtos, reflejando la inevitabilidad de las retroalimentaciones en los paisajes de los que dependemos para los diversos y contrabalanceados servicios ecosistémicos.

Conclusiones Nuestros resultados proveen de evidencia de que el mejor escenario a futuro es el que implica una mezcla de estrategias pasivas y activas, lo que permitirá la coexistencia dentro y entre distintas clases de propiedad, y reconociendo la importancia de las decisiones de manejo del fuego como una actividad central en los esfuerzos para construir, a futuro, paisajes más robustos y resilientes.

Background

Land management in the modern era faces unprecedented uncertainty regarding future climatic changes, novel disturbance regimes, and unanticipated ecological feedbacks (Millar et al. 2007; Millar and Stephenson 2015; Hessburg et al. 2015, 2021; Schuurman et al. 2022). Wildfire poses both a challenge and a solution to these projected changes (Dombeck et al. 2004; North et al. 2015), and building climate-adapted forest landscapes will require restoring active wildfire regimes and reducing the fire deficit across much of the intermountain west (Moritz et al. 2014; Schoennagel et al. 2017; Hessburg et al. 2019). A challenge to this is that most landscapes of the intermountain west comprise a mosaic of public and private lands, large wildland areas, and extensive development in the wildland-urban interface (WUI). Employing a truly adaptive landscape management strategy requires participation across boundaries at scales large enough to restore a dynamic mosaic of forest and non-forest vegetation types that contribute to the resilience and self-regulation of active fire landscapes (Hessburg et al. 2015; Larson et al. 2022; Ager et al. 2022).

Recent investments in restorative forest treatments (e.g., US Forest Service Wildfire Crisis Strategy; USDA Forest Service 2022) are a necessary and long overdue part of the solution (Belavenutti et al. 2021), but fuel treatments alone are likely insufficient to alter fire regimes in the wildland-dominated landscapes of the west (North et al. 2015; Hessburg et al. 2015). Fuel treatments can reduce fire risk and improve resilience within the treated area (Stephens et al. 2012; Furniss et al. 2022a), but building resilient landscapes requires a multifaceted approach incorporating a combination of mechanical treatments, prescribed (Rx) fire, and wildland fire use (Miller 2003; van Wagtendonk 2007; North et al. 2012, 2015; Calkin et al. 2015; Stephens et al. 2016). Restoring natural wildfire regimes is a central part of the solution (Young and Ager 2024), as we are simply unable to duplicate the spatial scale and ecological complexity of wildfire effects (e.g., Furniss et al. 2020) with even our most sophisticated silvicultural tools.

Intact wildfire regimes function as a self-stabilizing ecological feedback process, contributing to landscape resilience by maintaining a shifting mosaic of forest

structure and age classes across the landscape (Hessburg et al. 2005, Berkey et al. 2021; Povak et al. 2023). Landscape-scale resilience is therefore an emergent property of complex and interconnected systems, and it is only evident at spatial scales greater than individual forest patches and temporal scales greater than individual fires (Falk et al. 2019; Hessburg et al. 2019). We cannot fully evaluate the resilience of a landscape without evaluating forest succession and disturbance dynamics at these grander scales (tens of thousands of hectares; tens or hundreds of years). This is where landscape simulation models excel, as they facilitate simulation of land management, forest growth, and disturbance dynamics at spatio-temporal scales that are not feasible with field-based studies (e.g., Ager et al. 2022; Young et al. 2022; Furniss et al. 2023; Povak et al. 2023).

Landscape simulation models can be used to simulate different management paradigms over long (10–100 year) timescales, enabling us to evaluate feedbacks and unanticipated dynamics that may emerge (Loehman et al. 2017; Scheller et al. 2019; Ager et al. 2020; Keane et al. 2022). Numerous studies have successfully used simulation modeling to compare the effects of different land management strategies, often in factorial arrangements, on future landscape resilience (Loudermilk et al. 2014; Keane et al. 2018; Krofcheck et al. 2019; Ager et al. 2022; Abelson et al. 2022; Young and Ager 2024). A common challenge that these studies face is in distilling the output of these complex models, as results may vary widely in both space and time. Decision support systems (DSSs) are often used here to synthesize the outputs, compare results across different simulated management strategies, and to make results more actionable for managers that are developing landscape adaptation strategies (Vogler et al. 2015; Abelson et al. 2022; Povak et al. 2020, 2022; Day et al. 2024).

In a recent study, Furniss et al. (2023) used a spatial decision support model to explore tradeoffs and synergies (sensu Maron and Cockfield 2008) in space, identifying areas in a large study domain in north-central Washington State that have the greatest potential for treatments to be effective. In this study, we use that same decision support model to explore tradeoffs in time over a 100-year simulation window, and we evaluate factorial combinations of treatment types to evaluate which alternative landscape management strategies optimize socio-ecological benefits. Specifically, we used a landscape simulation modeling approach to provide a time-series of landscape-level resource benefits provided by several alternative management strategies ranging in the frequency, intensity, and type of treatments applied to the landscape.

We used this simulation model and decision support system to investigate several questions related to management strategies designed to improve future landscape health and ecosystem functioning. These guiding questions included:

1) How do climate adaptation-oriented mechanical treatments, Rx fire, and wildland fire use compare in their potential to improve landscape resilience?
2) How do these different management tactics compare in their potential to produce benefits among a wide range of social, economic, and ecological values?
3) In landscapes dominated by wildlands (as in the present study), can thinning and Rx fire in a portion of the landscape stabilize future wildfire regimes across the landscape as a whole?

We hypothesized that future management scenarios involving thinning alone would perform best among *Economic* topic areas, while thinning plus Rx fire would perform well among *Social* and *Ecological* topic areas. We expected scenarios involving wildland fire use scenarios to perform best among *Ecological* topic areas. We also expected that thinning plus Rx fire would produce significantly better results than a "no treatment" scenario involving no management other than future wildfire activity calibrated to current levels of suppression effectiveness.

Methods

Study area

This study was conducted in a large landscape (4524 km^2) on the east side of the Cascade Range in Washington State (Fig. 1). The study domain was defined by the hydrological boundaries of the Wenatchee and Entiat River sub-basins. The model was run on a landscape that included a 5-km outer buffer (6078 km^2 total area) to simulate possible edge effects and immigration of wildfires, and this buffer was then trimmed prior to our analysis.

The study domain is characteristic of many mountainous landscapes of the interior Pacific Northwest, with steep terrain, high heterogeneity in forest communities, and historically active fire regimes (Hessburg et al. 2019). Climate in this region is humid continental with warm, dry summers and cold, wet winters. Further details about the study region may be found in Furniss et al. (2022b).

Simulation modeling

We simulated forest dynamics, tree growth, regeneration, and wildfire dynamics using LANDIS-II (Scheller et al. 2007) with the NECN (Scheller et al. 2011) and SCRPPLE extensions (Scheller et al. 2019). LANDIS-II

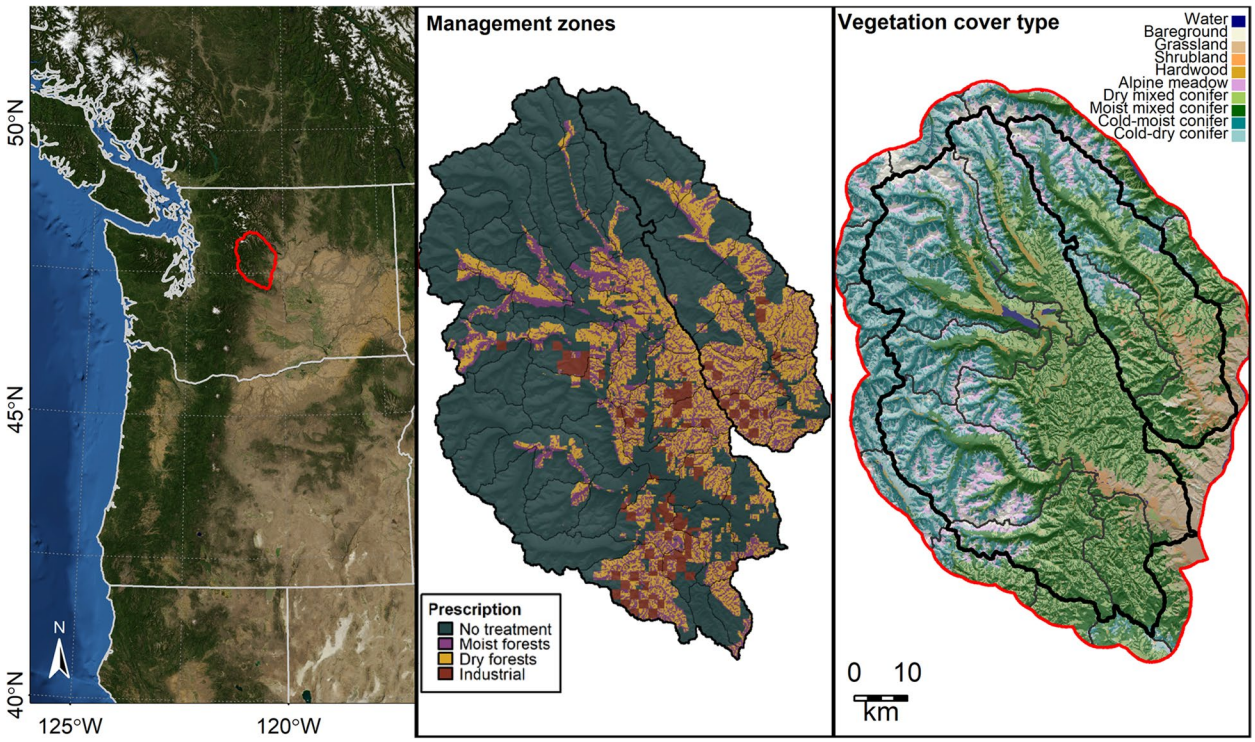


Fig. 1 Location of the study domain on the east slopes of the Washington Cascades (left). The study landscape is dominated by wilderness and roadless areas (54%), with the remainder comprising a mix of actively managed forests, private industrial timber lands, and wildland-urban interface (center). Vegetation in the study domain is heterogeneous, spanning from grass and shrub-dominated vegetation types in the lowlands to subalpine forests and alpine vegetation at the upper elevations (right). The dominant forest types on the landscape are dry and moist mixed-conifer, dominated by ponderosa pine and Douglas-fir, respectively, that occur on opposing aspects throughout most of the mid-elevations. The thick black lines in the right panel denote the boundaries of the Wenatchee and Entiat sub-basins, while the red perimeter represents a 5-km buffer that was included in the simulations to control for edge effects

is a spatially interactive forest landscape model that has been widely used to simulate climate effects on forest ecosystems and wildfire dynamics (Flatley and Fulé 2016; Loudermilk et al. 2017; Flanagan et al. 2019; Krofcheck et al. 2019). We coupled LANDIS-II with DHSVM (Wigmosta et al. 1994), a spatial distributed hydrology model for mountainous terrains that we then used to evaluate hydrologic functioning under various future management scenarios. Outputs from these models were analyzed in a decision support framework that leveraged fuzzy logic to integrate numerous ecological indicator metrics and evaluate positive and negative changes in overall ecosystem functioning (Reynolds et al. 2014; Povak et al. 2022, 2023; Furniss et al. 2023).

The initial vegetation layer for our LANDIS-II model was derived from TreeMap (Riley et al. 2021), a full-coverage raster of imputed Forest Inventory and Analysis (FIA) plot codes that could be used to develop tree lists for each 90-m pixel in the landscape. Edaphic characteristics were generated from the NRCS gSSURGO database (Soil Survey Staff 2020), and topographic layers were derived from the USGS 3D Elevation Program (Stoker and Miller 2022).

Wildfire ignitions were calibrated using the Fire Program Analysis Fire-Occurrence Database (FPA-FOD; Short 2017), and fire size and severity were calibrated to observed wildfire activity in the Monitoring Trends in Burn Severity (MTBS) database (Eidenshink et al. 2007). We used this combined empirical dataset (FPA-FOD and MTBS) to calibrate model behavior to observed patterns in wildfire frequency, area burned, and patch size distributions by severity class (Furniss et al. 2022a, b). We used the FPA-FOD alone to calibrate the frequency of small fires (< 400 ha) which are not present in the MTBS dataset. Simulated ignitions that did not spread produced fires that were 0.81 ha in size, an unavoidable consequence of the grain size of our 90-m raster grid.

We ran the wildfire and harvest extensions (SCRPPLE and Biomass Harvest, respectively) at an annual timestep, while the forest succession extension (NECN) had to be run at a 10-year timestep due to computational limitations. Each succession timestep took 3–5 h to run, so we used 10-year timesteps to keep each simulation within a

reasonable runtime (~48 h per simulation). Changing to 5- or 1-year timesteps would have vastly increased our processing time, reducing our ability to run the required number of scenarios and iterations of each scenario.

Regeneration was simulated using species-specific seed dispersal kernels and establishment probabilities which are based on available light, which is in turn determined by vegetation structure and composition at each site. Seed dispersal is determined by the presence of mature cohorts in adjacent cells, with maximum dispersal distance and probability given by species-specific parameters. Subsequent growth and mortality is determined by additional parameters that give the range of optimal climatic conditions for each species. This is the primary way that tree growth and mortality respond to different climate inputs. Further details about regeneration and vegetation succession may be found in published documentation for NECN (Scheller et al. 2011). A comprehensive description of our LANDIS-II model development and calibration work, including species parameters, can be found in Furniss et al. (2022b).

Management scenarios

To compare the tradeoffs between alternative management strategies, we designed six different management scenarios by using additive combinations of wildfire, mechanical harvest, Rx fire, and wildland fire use (hereafter, WFU). These eight scenarios were as follows: (1) *Wildfire Only*, (2) *Wildfire* + *WFU*, (3) *Wildfire* + *Rx*, (4) *Wildfire* + *Rx fire* + *WFU*, (5) *Wildfire* + *Harvest*, (6) *Wildfire* + *WFU* + *Harvest*, (7) *Wildfire* + *Rx* + *Harvest*, (8) *Wildfire* + *Rx fire* + *WFU* + *Harvest*. Additionally, we ran a *No Disturbance* scenario that simulated forest growth in the absence of wildfire and harvest, which we used to quantify the upper limit of biomass accumulation in the absence of all disturbances. All scenarios were run under a RCP8.5 climate change forecast (details under "Climate data," below). We refer to these scenarios without the RCP8.5 prefix for readability.

We ran five iterations of each management scenario to account for variability due to stochastic timing and spatial extent of treatment patches and wildfires. The number of simulations was chosen to provide a reliable estimate of uncertainty while remaining computationally feasible, a common tradeoff among simulation modeling studies. We generated simulation envelopes using the maximum and minimum values from the five iterations for each metric, and we used the average value to generate a mean trend line for each management scenario.

Vegetation pathway groups (PWGs)

The LANDFIRE biophysical settings (BpS, https://landfire.gov/bps.php) raster was used to allocate PWGs across the study area and to assign broad vegetation types (Povak et al. 2022). These data represent vegetation types that were likely present prior to Euro-American colonization, based on the biogeoclimatic conditions and characteristic disturbance regime (Rollins 2009). We used the BpS group level attribute to assign each 90-m cell into the following categories: water, snow/ice, rock, barren, grassland, shrubland, hardwood/riparian, alpine meadow, dry or moist mixed conifer forest, and dry or moist cold conifer forest conditions. The cold forest and mixed conifer forest BpS classes were further differentiated into dry-mixed (DMC), moist-mixed (MMC), cold-dry (CDC), or cold moist (CMC) conifer forest conditions based on topographic position, aspect, and elevation. Further details about the classification heuristic may be found in Furniss et al. (2023). The vegetation PWG map was not used to limit species composition or define successional trajectories. It was simply used as to create ecologically and biophysically similar areas (termed "ecoregions" in LANDIS-II) for downscaling the 4-km climate inputs. We defined these areas using a spatial intersection of vegetation PWG and HUC10-level watershed, resulting in 177 unique ecoregions that were used to extract area-weighted means from the 4-km future climate surfaces (details in "Climate data," below). Ecoregion assignment was static through time.

Management patches

We developed topographically entrained management patches using a 30-m digital elevation model (DEM) from the USGS National Elevation Data repository. Patches were primarily defined using a landscape topographic template as described by Hessburg et al. (2015) to spatially allocate forest restoration treatments across the study area. This template was further subdivided by hydrologic divides, land ownership, and land use allocation. Hydrologic divides were derived from nested Hydrologic Unit Codes (HUC) 10 (~20–80,000 ha) and 12 (~10–40,000 ha, Seaber et al. 1987).

All raster-based input layers were resampled to 90-m resolution, and a minimum mapping unit (MMU) of 4 ha (five contiguous cells) was applied to create management treatment patches. All raw and derived input spatial layers were clipped to the study area. The spatial patches and attributes were then processed through a series of spatial intersections where the MMU was enforced at each step to best maintain the integrity of the input data.

Treatments

For scenarios involving mechanical harvest, we simulated low and variable density thinning-based restoration treatments (Graham et al. 1999) using the Biomass Harvest extension (Gustafson et al. 2000). We partitioned the

landscape into wildlands, actively managed public lands, and industrial timber lands (Fig. S1, Table S1). We further sub-divided actively managed public lands into dry forests and moist forests. This produced four management zones within which we applied a single treatment prescription. Treatments occurred at the patch-level, where patches were selected at random and evaluated for their eligibility for treatment. If eligible, treatments were applied, and additional patches were selected until the target treatment rate (% area per year) was reached. Ineligible patches included patches in wildland areas and patches that had been recently treated (10 years for dry forests, 30 years for moist forests). We used random patch selection because there was not a way to optimize patch selection using an ecological basis in this version of the Biomass Harvest extension. Patches were developed by grouping pixels that shared similar ownership, topographic setting, and PWG.

In dry forests, treatments were designed to reduce surface fuels, retain medium and large sized trees, and to shift composition toward climate- and fire-adapted species (Hessburg et al. 2015; Stephens et al. 2013). This was achieved by thinning from below, removing young stems of all species and mature stems of shade-tolerant species. Slash and non-live surface fuels were reduced by 90% to simulate post-harvest pile and broadcast burning, but these simulated pile-burns were not counted when summarizing annual area burned. Treatments were applied to adjacent patches until treatment areas were between 20 and 100 ha to reduce wildfire risk at scales larger than individual patches. Target treatment area was $3\% \cdot \text{year}^{-1}$ to achieve fuel reduction efforts as quickly as possible.

The moist forest treatment was designed to increase heterogeneity and diversify habitat by creating small gaps and openings. This involved variable density thinning (75% reduction) among all size classes, for immature trees < 120 years old, across all species present in small patches (< 3 ha). Harvest gap size was set at 30% of each forest patch. Surface fuels were reduced by 50% to simulate slash piling and burning. The target treatment area was set at $1\% \cdot \text{year}^{-1}$ of available patches to maintain a sustainable level of biomass extraction throughout the simulation period.

Industrial forest lands were treated with clearcutting on a 35–50-year rotation to simulate the trend of moving toward short rotation industrial forestry in the twenty-first century. The treatment rate was set at $4\% \cdot \text{year}^{-1}$, and surface fuels were reduced by 50% to represent slash piling and burning.

Wildfire suppression and wildland fire use scenarios

We tuned the suppression levels in our *Wildfire Only* scenario to match the fire event size and severity patch size distributions based on empirical fire activity from 1984 to 2019 found in the monitoring trends in burn severity (MTBS, Eidenshink et al. 2007) dataset. To calibrate frequency of fires smaller than 400 ha, we used the spatial wildfire occurrence (FPA-FOD; Short 2017) dataset. During this period, suppression was the default response to wildfire, and suppression efforts were applied to most fire events. As such, we applied an intermediate amount of suppression effort using the SCRPPLE extension to create a "suppression-as-usual" fire suppression scenario. Under this scenario, suppression was most effective under mild and moderate fire weather conditions, natural ignitions were suppressed with the same vigor as accidental ignitions, and suppression efforts were strongest in developed areas and in the WUI. The level of suppression in the model was calibrated in conjunction with the other fire spread parameters to produce a simulated fire regime consistent with observed fire activity in terms of fire frequency, severity, and patch size distributions (Furniss et al. 2022b). This scenario should therefore be thought of as a "suppression-as-usual" suppression strategy, which is notably different from a "no action" strategy. Instead, it may be thought of as an intensive suppression scenario, with its own set of merits and consequences.

We simulated alternative future wildfire management scenarios by redistributing how suppression was applied, both geographically and temporally. We first defined four suppression zones on the landscape, and we applied variable levels of suppression depending on ignition type, fire weather index (FWI), and location on the landscape (Table S2). For management scenarios involving wildland fire use (*WFU*), we reduced suppression effort by 95% under mild weather conditions and 25% under moderate weather conditions to allow more natural wildfire ignitions to burn when weather conditions were not severe. Under extreme weather conditions, slightly more suppression effort was applied (average of 10%), representing the increased availability of resources that could be saved by letting most wildfires burn with minimal intervention. The net effect of this redistribution was that less suppression was applied overall in the WFU scenarios, while slightly more suppression was applied to ignitions occurring under extreme weather conditions. This approach is consistent with other recent studies that have used the suppression parameters in SCRPPLE to simulate alternative future wildfire management scenarios (e.g., Abelson et al. 2022).

Our implementation of WFU is not necessarily representative of wildland fire use as implemented in real-world landscapes. Instead, it was intended to be an idealized form of WFU that could be possible in a future "post-suppression" wildfire management paradigm. The assumption that WFU could make suppression more

effective under extreme weather conditions is contingent upon the idea that suppression resources stay the same (or increase) and are deployed with lower frequency but greater intensity by having increased availability of suppression resources that would be diverted from other areas throughout the region where fires were allowed to burn under moderate weather conditions. This assumption requires wildland fire use to be the default response across the region. Wildland fire use has never been tested at such a broad scale (van Wagtendonk 2007) and doing so would require a paradigm shift in wildfire management policy, culture, and legal liability (North et al. 2015).

Climate data

We generated future climate inputs using the MACAv2-METDATA CCSM4 dataset (Abatzoglou and Brown 2012), a spatially downscaled dataset containing daily climate forecasts at a 4-km resolution for the contiguous United States. We developed a baseline climate scenario by resampling historical climate from 1980 to 2010, with 3-year temporal autocorrelation (future years were drawn in sets of 3 re-ordered historical years) to create a synthetic forecast representing contemporary climate normals. This baseline climate forecast was not intended to predict plausible future weather streams, rather it provided a baseline with which we could compare the RCP8.5 climate forecast that we used to simulate the effects of climate change. We chose to use the RCP8.5 emissions scenario to simulate climate change as evidence suggests that this scenario will continue to be a good fit for anticipated climate changes for at least the next several decades (Schwalm et al. 2020).

Hydrology modeling

We used the Distributed Hydrology Soil Vegetation Model (DHSVM; Wigmosta et al. 1994) to simulate streamflow and snowpack dynamics at a daily resolution for the full 100-year simulation period. By updating the vegetation layers in DHSVM annually, we were able to create dynamic vegetation inputs that responded to forest growth, treatments, and wildfire events in LANDIS-II. We updated four vegetation parameters in DHSVM at annual intervals: canopy height, canopy fractional coverage, leaf area index (LAI), and vegetation type. LANDIS-II outputs are only available every 10 years (LAI, biomass, and age). Thus, we used linear interpolation of the decadal outputs to estimate intermediate values for each year. We ran DHVSM with a 90-m cell size to match the spatial resolution of the LANDIS-II model.

We modeled height and fractional coverage (which are not directly available from LANDIS-II) using generalized linear mixed effects models using the lme4 package in R (Bates et al 2015). We used FIA plot data to fit these models, and we applied the models to LANDIS-II outputs to estimate canopy height and cover for DHSVM (Fig. S1). The canopy height model used ln(age) and ln(biomass) to predict individual tree height, with random intercepts and slopes for age by species and PWG ($R^2 = 0.78$). Cover height for each cell was calculated as the 90th percentile of individual tree height. The fractional cover model used a third-order polynomial of stand biomass, stand age, and elevation to predict fractional coverage, with random slope and intercepts for biomass by PWG ($R^2 = 0.67$).

The DHSVM model was calibrated using annual meteorology data derived from the 1/16 degree (~6×6 km grid cells) Livneh dataset (Livneh et. al. 2015). Initial snow parameters were calibrated using empirical data from nearby SNOTEL stations (Trinity Snow Telemetry site). The model was then further calibrated using streamflow records (USGS gauges 12,456,500, 1,245,800) for the Wenatchee and Entiat sub-basins from the water years 1997–2003 and 1966–1971, respectively. Future climate forecasts were derived from the MACA Livneh climate dataset (Abatzoglou and Brown 2012).

Decision support system

We evaluated the performance of each management scenario using a custom decision support tool (DST) designed to assess ecological functioning and ecosystem services among seven primary topic areas: Sustainable Biomass, Economics, Carbon Storage, Water, Wildfire, Forest Health, and Landscape Integrity. We selected these topics to represent a broad range of important ecosystem services that are of central importance to managers and local stakeholders throughout the western US (Povak et al. 2023). For each topic area, we developed a set of 3 to 7 indicator metrics (e.g., C storage and fluxes for Carbon, peak snow water equivalent and late season flow volume for Water, etc.) that were used to assess the quality of ecosystem health and functioning (Table S3, also see Furniss et al. 2023). For each indicator metric, we assigned a logical premise that was evaluated using fuzzy logic to translate metric values into "strength-of-evidence" (SOE) scores, which use a −1 to +1 scale to represent the degree to which each metric satisfies a proposition. Fuzzy logic may be thought of as simply a way to standardize disparate unit scales onto a −1 to 1 scale, in contrast to Boolean logic which only allows values of 0 and 1. With fuzzy logic, scores can range from −1 to 1 with a SOE score of +1 indicates strong support for a proposition (e.g., carbon sequestration is maximized), a score of 0.75 indicating strong support (e.g., carbon sequestration is high), and a SOE score of −1 indicates poor support for the same proposition (e.g., carbon sequestration is minimized). Importantly, we centered all SOE scores relative to the *Wildfire Only* scenario so that positive values indicated that

a given scenario performed better than the *Wildfire Only* scenario, while a negative score indicated that the *Wildfire Only* scenario outperformed the treatment scenario.

We grouped the primary topics into three partially overlapping groups (also see Table S3) representing key facets of resilience: *Economic* (Economics and Sustainable Biomass), *Social* (Sustainable Biomass, Carbon, Water, and Wildfire), and *Ecological* (Water, Wildfire, Forest Health, and Landscape Integrity). When all primary topics were grouped together, we referred to the SOE scores as *Overall* benefits.

All metrics were initially evaluated spatially using raster outputs from LANDIS-II and DHSVM. We then used these spatial maps to build a *spatial* DST that allowed us to evaluate what parts of the study landscape had the greatest potential for treatment synergy (Furniss et al. 2023). To evaluate trends in ecosystem function over time, and to compare the effects of various alternative management scenarios, we built an *aspatial* DST by aggregating the spatial SOE scores at the patch, HUC12, and PWG level. We summarized these scores using area-weighted averages of HUC12 scores to generate landscape-level scores, for each scenario, in each year. In contrast to the spatial DST that quantified potential benefits at the end of the simulation, these aspatial SOE scores allowed us to evaluate how potential benefits changed throughout the simulation period, at the landscape scale.

We further evaluated SOE scores for each topic at simulation year 10, 50, and 100 to distill general patterns over time. We plotted these scores using heatmaps, with scenarios assigned to rows and topics assigned to columns. We built dendrograms for the scenarios to generate groupings of similar scenarios. We used the *heatmap.2* (v3.1.3) function in R with the default clustering parameters (Warnes et al. 2022).

Software versions

Landscape simulations were generated with LANDIS-II v7.0 (Scheller et al. 2007) using the NECN v6.8 (Scheller et al. 2011), SCRPPLE v3.2.1 (Scheller et al. 2019), and Biomass Harvest v4.4 (Gustafson et al. 2000) extensions. All data pre-processing, post-processing, and subsequent analyses were performed in R v4.1.3 (R Core Team 2020) using *terra*, *whitebox*, *vegan*, and *tidyr* packages.

Results

Effects of climate change on wildfire and biomass dynamics

In the absence of wildfire and mechanical harvesting, biomass accumulated over the full 100-year simulation period, and climate effects on projected biomass accretion were negligible (Fig. 2). When we added wildfire disturbance, stark differences between future climate scenarios became evident. While area burned per year under the baseline climate scenario was relatively steady (i.e., average annual area burned was similar at the beginning and the end of the simulation), there was a notable increase in area burned between under the RCP8.5 climate scenario, particularly for moderate- and high-severity classes (Fig. 3). Cumulative area burned diverged around years 2060–2070 where annual area burned under the RCP8.5 scenario began to increase more rapidly compared to area burned under the baseline climate. Average area burned (*Wildfire Only* scenario, RCP8.5 climate) before the inflection point (2020–2060) was 1687 ha · year^{-1}, while after the inflection (2080–2120) it grew to 11,237 ha · year^{-1}. Consequently, the vast majority of area burned (and area burned at high severity) occurring during the latter half of the simulation (21% from 2020 to 2070 versus 79% from 2070 to 2120). This inflection point was evident even when the climate forecast was shuffled (i.e., random ordering of years from the RCP8.5 climate projection; Fig. S2), indicating that the inflection was not caused by an underlying trend in the RCP8.5 climate forecast (dotted line in Fig. S2).

These increases in wildfire activity had a significant impact on aboveground biomass in all vegetation types (Fig. S3). Under the baseline climate scenario, potential biomass losses from wildfire did not offset forest growth, allowing biomass to accumulate throughout the simulation period (albeit at a lower rate compared to the *No Disturbance* scenario; Fig. 2). Under the RCP8.5 scenarios, however, biomass levels in all tree-dominated vegetation types peaked around 2060, then declined for the rest of the simulation (Fig. S3). The timing of this biomass decline aligns with the inflection point observed in moderate- and high-severity area burned (Fig. 3), suggesting that direct climate effects on biomass (hence carbon storage) were negligible and were instead primarily mediated by future wildfire dynamics. The reduced biomass may also be an indication of wildfire-driven type conversion, which would result in a persistent reduction in carbon storage potential even if future wildfire activity were to stabilize, but we were not able to test that directly.

Management impacts on ecosystem functions and services

We generated landscape-level mean SOE scores to evaluate potential benefits under each treatment scenario over the entire 100-year simulation period. Recall that positive values indicated that a given treatment scenario performed better than the *Wildfire Only* scenario (with RCP8.5), while negative values indicated a poorer than *Wildfire Only*.

Primary topic results revealed intuitive short-term and long-term tradeoffs between management scenarios

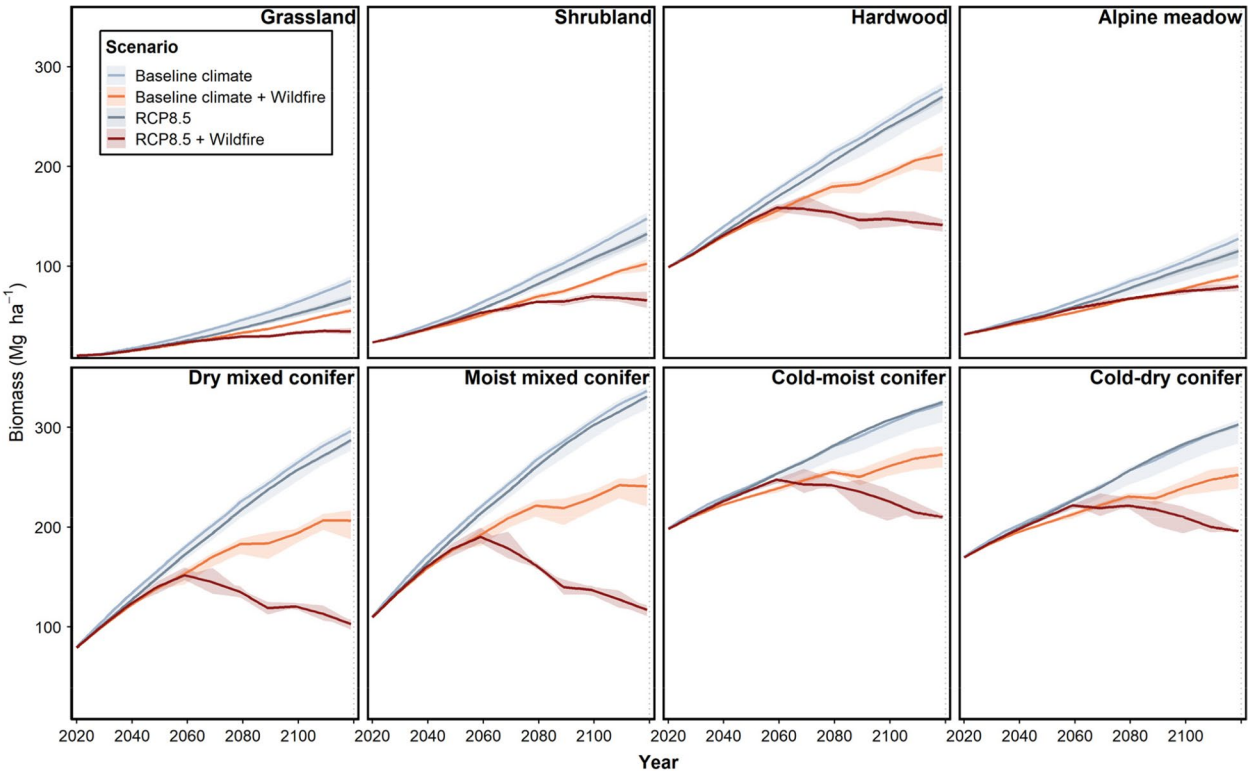


Fig. 2 Biomass accumulation per vegetation type under a *No Disturbance* scenario (cool colors) and the *Wildfire Only* scenario (warm colors). Each scenario was run under two climate forecasts: a baseline forecast representing late twentieth century climate ("Baseline climate") and a more realistic forecast based on a RCP8.5 emission scenario ("RCP8.5"). Direct effects of climate change on biomass accumulation were minimal. Wildfire had a substantial impact on biomass under the baseline climate scenario (orange lines), and an even greater impact under the RCP8.5 scenario (red lines)

(Fig. 4). In the short term (2020–2040), scenarios involving forest thinning (green lines in Fig. 4) generally performed best among Economic, Sustainable Biomass, and Water topics, with reduced benefits among the ecological categories including Forest Health, Carbon Storage, and Landscape Integrity. Existing timber stocks were depleted relatively quickly in the context of ongoing wildfires and small available treatable area, which reduced the size of potential benefits for the latter part of the simulations (Fig. 4).

Longer term benefits among all primary topics were strongly influenced by the inflection point in wildfire activity under the *Wildfire Only* scenario (under the RCP8.5 climate scenario). The rapid increase in area burned under *Wildfire Only* around 2060 (Fig. 3) led to an overall decline in benefits among most topics, and this decline contrasted with relative increases in the benefits among the other management scenarios (Fig. 4).

High interannual variability in area burned statistics, and a limited number of iterations of each scenario, precluded identifying significant differences among management scenarios at an annual resolution (Fig. 4). However, main treatment effects were observed for cumulative area burned by severity class (Fig. 3). Harvest treatments resulted in a slight reduction in cumulative area burned at high severity, while WFU produced a much more significant decrease in cumulative area burned at both moderate and high severity (Fig. 3).

When *Overall* benefits were assessed, all treatment scenarios except *Wildfire + Rx fire* performed better than the *Wildfire Only* by the end of the simulation (Fig. 5). *Economic* benefits were greatest in the scenarios involving harvest, but these benefits declined after available biomass for harvest was depleted in the context of ongoing wildfires and small treatable area (~ 2050; Fig. 5). *Social* benefits were greatest for scenarios that involved Harvest and/or WFU, which was surprising given that these scenarios tended to have the lowest benefits around mid-century. This dip was primarily driven by the depletion of carbon stocks associated with harvesting and elevated wildfire activity (Figs. 3, S2, S3). Yet as carbon and biomass stores recovered and area burned under the *Wildfire Only* scenario began to rise (Fig. 3), benefits associated with the treatment scenarios began to increase rapidly.

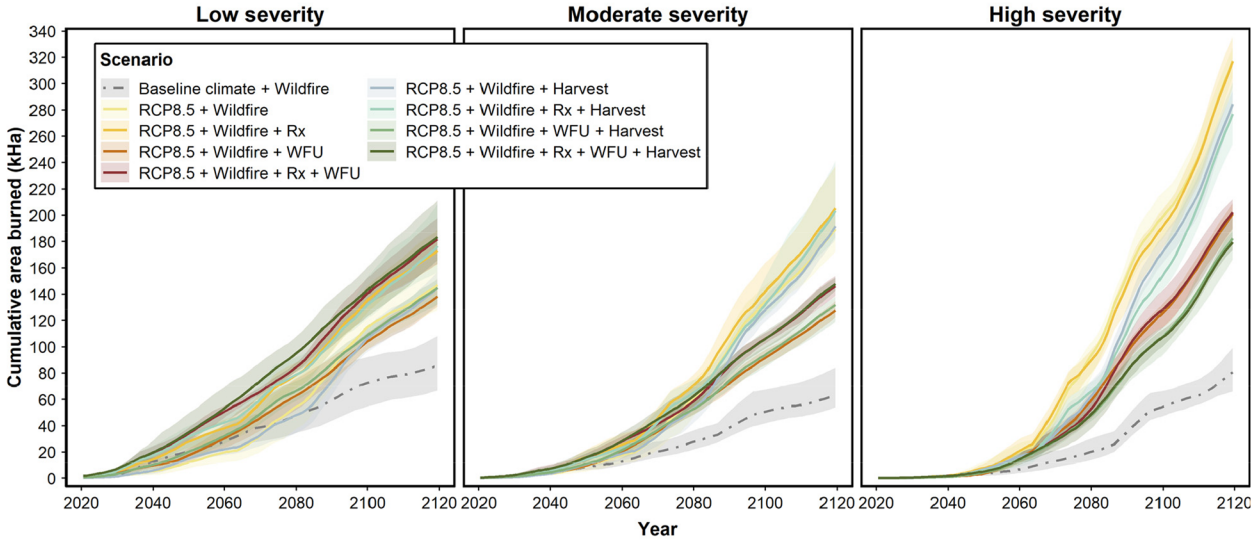


Fig. 3 Simulated area burned by severity class under historical conditions ("Baseline climate"), future ("RCP8.5") climate, and alternative management scenario (*Wildfire Only* = "RCP8.5 + Wildfire"). Model uncertainty is represented by the simulation envelopes (shaded regions) which were generated by running five iterations of each scenario. The shaded regions represent the highest and lowest values, while the solid lines represent mean values from the five simulation runs. Cool colors indicate scenarios with mechanical harvest treatments, while warm colors indicate scenarios without harvest. Darker colors indicate scenarios with wildland fire use (WFU). Differences in area burned at moderate and high severity were pronounced for the WFU scenarios, while harvest scenarios conferred a slight reduction in area burned at high severity

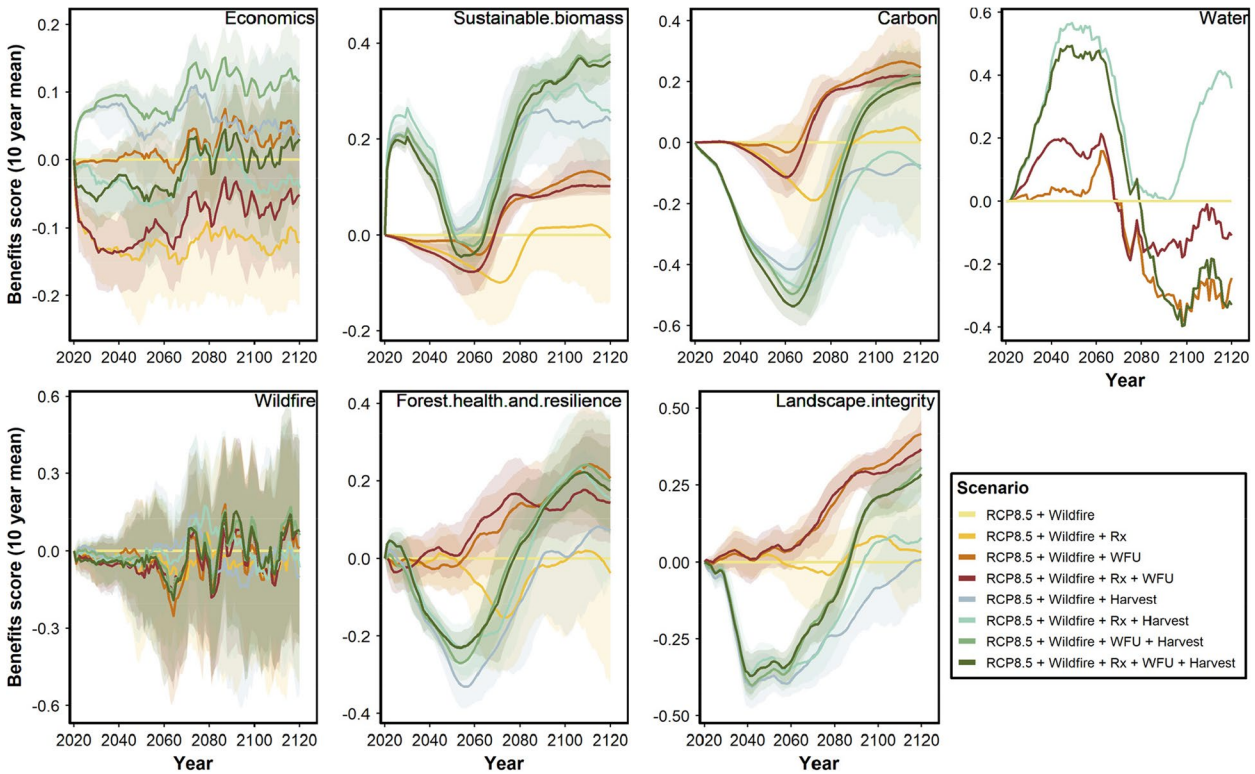


Fig. 4 Potential treatment benefits among seven primary topics for eight alternative future management scenarios. Benefits were assessed relative to the "no treatment" (*Wildfire Only*) scenario. Model uncertainty is represented by the simulation envelopes (shaded regions) which were generated by running five iterations of each scenario. The shaded regions represent the highest and lowest values, while the solid lines represent mean values from the five simulation runs

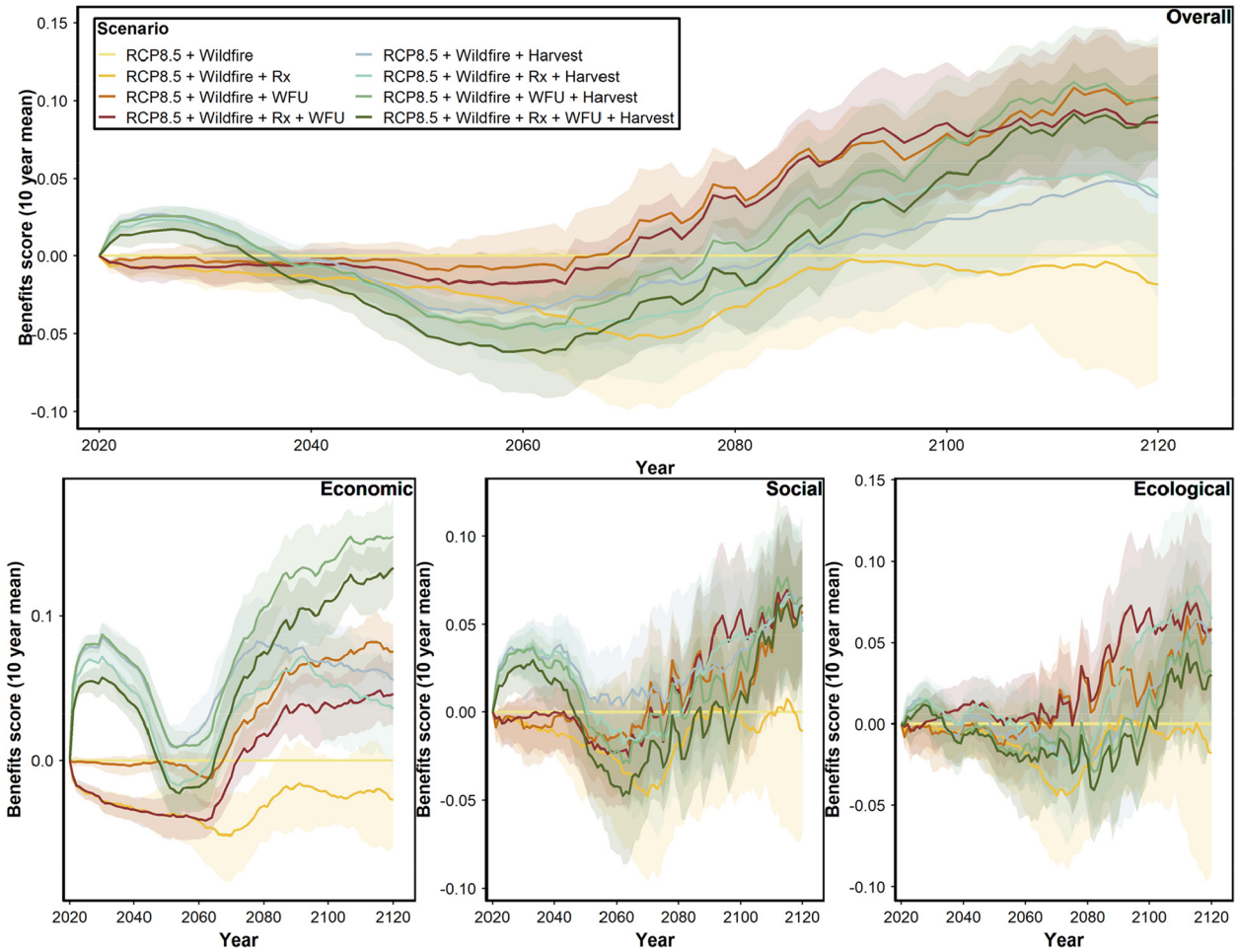


Fig. 5 Potential treatment benefits for eight alternative future management scenarios. Benefits were assessed relative to the "no treatment" scenario (*Wildfire Only*). Model uncertainty is represented by the simulation envelopes (shaded regions) which were generated by running five iterations of each scenario. The shaded regions represent the highest and lowest values, while the solid lines represent mean values from the five simulation runs

Ecological benefits showed a similar trend, although the mid-century dip was not as evident (Fig. 5).

To investigate the relative influence of Harvest versus WFU treatments, we examined the reduction in area burned due to harvest (i.e., *Wildfire Only* minus *Wildfire + Harvest*; *Wildfire + WFU* minus *Wildfire + WFU + Harvest*). Interestingly, mechanical treatments (*Harvest*) reduced area burned relative to the *Wildfire Only* scenario, but only if WFU was not applied. In the WFU scenarios, the addition of mechanical harvest did not have a discernable effect on area burned (Figs. S4 and 3).

Discussion

Scenarios involving harvest did perform best among the *Economic* categories as we expected, but the addition of Rx fire did not improve benefits to *Social* and *Ecological* topics. Wildland fire use emerged as the single most influential management tactic, and scenarios involving WFU performed well among all categories because it was most effective at curbing the amount of future high-severity fire. This was a surprising result, and it highlights the importance of wildfire as a foundational process governing the functioning and health of forest landscapes. We were also surprised by the variability in benefits across the 100-year simulation period. Even though our simulations applied the same management strategies throughout the entire simulations, future landscapes and the benefits they conferred were vastly different at year 50 versus year 100. These extended timeframes carry a great deal of uncertainty, of course, but the point remains that management actions with short-term benefits can be inconsequential or even detrimental in the long term (Young and Ager 2024). This is an important perspective for land managers and policymakers to consider. Estimating the consequences of current actions over decadal and

century timescales is not easy, but it is necessary when managing large landscapes with the potential for feedbacks and complex disturbance dynamics.

Future wildfire dynamics

Future wildfire dynamics and low available treatment area were central to the interpretation of all results of this simulation modeling study. The *Wildfire Only* management scenario under the RCP8.5 climate change demonstrated a positive feedback cycle that began mid-century (~2060), driving a marked increase in high-severity wildfire (Figs. 3, S2). Importantly, this feedback was not evident among all management scenarios, indicating that it was caused by something that differed between scenarios rather than something intrinsic to the model itself. The inflection point was present in the *Wildfire Only* scenario and given that our DST results were assessed in contrast to the *Wildfire Only* scenario, the impacts of these emergent wildfire dynamics were pervasive.

The inflection point in future area burned was a striking result of this study. For context, average area burned under RCP8.5 climate before the inflection (2020–2060) was 1687 ha·year^{-1}, corresponding to represent the 60th percentile of area burned under the baseline climate scenario, which was calibrated to empirical fire activity. Average area burned per year after the inflection point, however, was 11,237 ha · year^{-1}, corresponding to the 98th percentile of area burned under a historical climate. In other words, an average fire year during the later half of the century would represent the most severe fire year from the first half of the century. This demonstrates the potential for wildfire to create positive feedbacks that can have profound and lasting impacts on the structure, function, and resilience of large landscapes.

There are two plausible reasons for this inflection point. First, the climate forecast could have an inflection in temperature around this period, and the inflection in fire activity may simply be responding to that increase in temperature (i.e., first order effects of climate on fire spread rates). Second, the inflection could be due to a positive feedback cycle between area burned and resultant patterns of landscape contagion and susceptibility to large fire spread. Both of these explanations have support from empirical studies (Halofsky et al. 2011; Abatzoglou et al. 2021; Povak et al. 2024), providing some reassurance that this trend was not an anomaly of our model.

We distinguished between these two explanations using the randomly shuffled RCP8.5 scenario. If the inflection point was climate driven, cumulative area burned for that scenario would have been linear (because we removed any underlying structure in the climate data by shuffling the years). Instead, we saw that both shuffled and non-shuffled RCP8.5 scenarios exhibited an inflection point (Fig. S2), indicating a tipping point where positive feedbacks between wildfire and surface fuels began to rapidly accelerate reburn frequency. This finding is consistent with recent empirical work that has documented increasing wildfire activity due to both climate and fuels (Coop et al. 2020; Hagmann et al. 2021; Abatzoglou et al. 2021; Povak et al. 2023; Prichard et al. 2023), and it is further evidence for the importance of pattern and structure in determining the contagious potential of wildfire (Povak et al. 2023). The exogenous influence of climate was clearly important as well, but these results indicate that climate alone did not account for the wildfire regime change that can emerge when high-severity fire initiates a positive feedback cycle with endogenous controls on fire behavior.

These dynamics are a feature, not a fault, of simulation modeling approaches with dynamic fire models (e.g., Ager et al. 2022; Young et al. 2022; Prichard et al. 2023). As wildfire activity is determined by process-oriented algorithms within a given model, fire regimes are allowed to evolve over the simulation period rather than being constrained by a pre-defined fire size distribution. Dynamic fire modeling allows simulated fire activity to respond to changes in fuels, climate, and landscape patterns, capturing dynamics that are foundational to the emergence of wildfire regimes in real landscapes (Agee 1998; Scholl and Taylor 2010; Hessburg et al. 2019).

Alternative management scenarios

Our *Harvest* treatments produced benefits in the form of economic returns and biomass production, but even these restoration-oriented thinning treatments did little to alter projected trends in wildfire activity. Treatments were primarily effective over the next several decades before existing biomass stores were depleted (around 2050), after which point treatments continued but were less economically viable. Around this time, simulated wildfire activity began to increase rapidly. Despite the *Harvest* treatments reducing surface fuels, total area burned under the *Wildfire + Harvest* scenario was not substantially lower than the *Wildfire Only* scenario (Fig. 3).

The near-term impacts of harvest were overwhelmed by the self-regulation of wildfire that eventually emerged in the WFU scenarios (Fig. 3). Interestingly, this led to more similarity between the WFU scenarios compared to the Harvest scenarios by the end of the simulation period (Fig. 6). In other words, the *Wildfire + Harvest* scenario was more similar to the *Wildfire Only* scenario than it was to the *Wildfire + Harvest + WFU* scenario. Similarly, *Wildfire + WFU* was more similar to the *Wildfire + WFU + Harvest* than to *Wildfire Only* scenario (Fig. 6). Harvest effects were prominent early in the

simulation, but the effects of wildfire use eventually grew to dominate the scenario differences by the end of the century.

Wildland fire use

Wildland fire use (*WFU*) scenarios had profound impacts on wildfire activity that permeated to all other landscape metrics. Allowing more wildfire to burn in the wildlands produced benefits among the Water topic, at least for the first half of the century (Fig. 4). Benefits to other topic areas were slow to emerge, but the reduced amount of high-severity wildfire in the *WFU* scenarios (Fig. 3) eventually translated into greater carbon storage (Fig. S3), Landscape integrity (Fig. 4), and Ecological benefits (Fig. 5). This finding is particularly notable because most of the carbon is stored in the upper elevation wilderness areas (~200 Mg ha^{-1} in "Cold Moist Conifer" vs. ~100 Mg ha^{-1} in "Moist Mixed Conifer") where the *WFU* scenarios involved less suppression effort under *all* circumstances, even during extreme fire weather conditions. These results underscore the importance of wildfire management as a primary tool in the management toolbox (North et al. 2015; Barros et al. 2018; Young et al. 2022; Ager et al. 2022), highlighting the potential for managed wildfire use to alter fire regimes and mitigate high-severity area of future fires (e.g., Barros et al. 2018; Young and Ager 2024). Choosing how and when to suppress wildfire is the primary tactic available in large landscapes with substantial proportions of wilderness and roadless areas (Miller 2003; van Wagtendonk 2007; North et al. 2012; Stephens et al. 2016), and this study demonstrates that those wildfire management decisions can match or even exceed the impact of more active management tactics such as thinning and Rx fire.

Mechanical treatments

Interestingly, mechanical adaptation treatments (*Harvest*) only reduced area burned in the absence of a *WFU* suppression paradigm (Fig. S4). In the *WFU* scenarios, mechanical harvest resulted in a slight reduction in area burned (mean value was below 0), but this trend was not significantly different (simulation envelope overlapped 0). These results suggest that while active management can mediate future wildfire behavior, the effects of different management tactics are not necessarily cumulative, indicating diminishing returns in benefits. The same level of benefits was achieved through restoration via either mechanical methods (*Harvest* scenarios) or through alternative wildfire management paradigm (*WFU* scenarios), but applying harvest *and* WFU as well did not produce additional benefits (Fig. 5). The *Wildfire + WFU* scenario was equivalent in overall benefits to the *Wildfire + WFU + Harvest* scenario, as applying harvest increased benefits among Economic and Sustainable biomass topics while reducing benefits to Carbon and Landscape integrity (Fig. 4). Results indicate that tradeoffs among management strategies are inevitable. Therefore, managers and policy makers must decide how

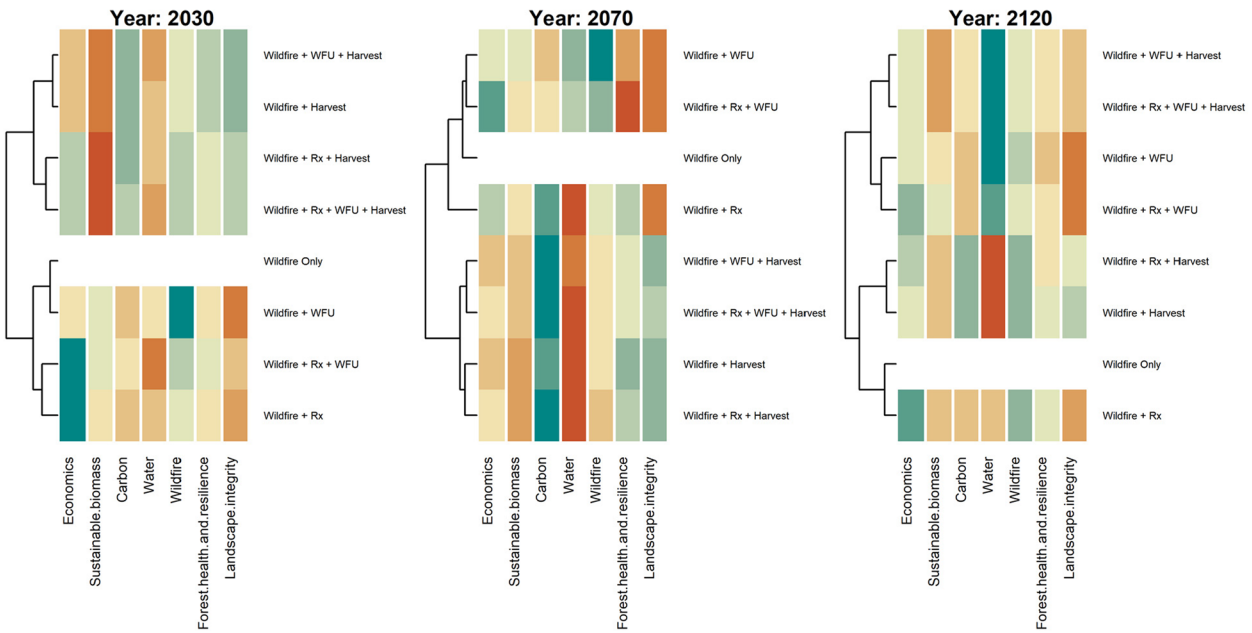


Fig. 6 Heatmap and dendrogram showing benefits among the seven primary topics (red = strong support, blue = weak support) and clustering of scenarios based on dissimilarity at three timesteps (simulation year 10, 50, and 100)

to distribute benefits, identify opportunities to manage for multiple resources at once, and determine when and where to prioritize benefits among certain topics (e.g., Ager et al. 2016; Povak et al. 2022; Furniss et al. 2023).

Prescribed fire

The Rx fire scenarios showed very little distinction from their comparison scenarios without Rx fire. This result was surprising, given that the rate of Rx fire was equal to the rate of harvest being applied (~5000 ha·year^{-1}). One explanation is that Rx fire was applied to the wildlands as well as the actively managed parts of the landscape, so the Rx fire treatments were more diffuse and therefore perhaps less impactful to overall landscape functioning. We scaled this annual rate to approximate the actual amount of Rx fire being applied in this landscape today. Our findings suggest that this level of Rx fire is wholly insufficient to alter wildfire behavior in such a large landscape. Rx fire is an effective management tool to reduce fuels at the patch-scale but generating benefits for landscape resilience will likely require far more Rx fire application and/or more wildland fire use.

Wildfire, fuel reduction, and carbon storage

Mechanical fuel reduction efforts mediated wildfire severity (Fig. 3), but these deferred losses to wildfire were offset by C losses due to harvest. This resulted in similar levels of residual biomass between the *Wildfire Only* and *Wildfire + Harvest* scenarios at the end of the simulation period (Fig. S3). This provides an interesting complement to prior studies that have shown restoration treatments (e.g., thinning + Rx fire) to be an effective way to increase forest C storage by mitigating future wildfire severity (Loudermilk et al. 2017; Young and Ager 2024). This potential for long-term benefits to forest C storage is well-established in the literature, but achieving net C gains requires carbon losses due to treatments to be effectively offset by reduced fire-related C emissions and increased productivity of residual trees. The efficacy with which restoration treatments reduce fire severity is contingent upon many factors including the timing and location of treatments (Loudermilk et al. 2014; Krofcheck et al. 2019), landscape configuration and forest conditions, and dominant fire regimes. Achieving net C gains through restoration treatments is therefore most likely in areas that are vulnerable to high-severity fire (Krofcheck et al. 2019), forests with high densities of small trees, and in places that will strategically impede fire flow.

In this study, simulated thinning treatments did not reduce fire severity enough to offset the C losses due to the thinning treatments themselves (Figs. 3, 4). In other words, scenarios without mechanical harvest resulted in higher C storage potential, with the *Wildfire + WFU* scenario showing the greatest C storage at the end of the simulation (Fig. S3). We may have achieved net C gains if simulated thinning treatments had a greater impact on fire severity and area burned, as was evident in the WFU scenarios (Fig. 3). It is also possible that post-treatment growth responses were not well represented in the model, which would have also influenced simulated carbon storage. Nonetheless, this result from our simulations reflects a real-world challenge in mitigating wildfire activity using thinning treatments: wildfire is not a deterministic process. Many treated areas never see fire, and other treated areas may burn at high severity due to top-down influences. Treatments can effectively mitigate fire severity, but it is difficult to know exactly when and where treatments may be most likely to maximize their intended benefits.

Interannual variability

For both Wildfire and Water topics, interannual variability between years was far greater than variability between management scenarios (Fig. S5). Differences between scenarios were evident when we used the *Wildfire Only* scenario as a reference, but examining the raw SOE scores revealed a great deal of noise from year to year. This noise may be largely attributed to annual climate fluctuations, as both Wildfire and Water topics were very sensitive to the timing of precipitation and within-year temperatures (via increased wildfire activity and decreased snowpack retention, respectively). Additionally, we were not able to generate simulation envelopes for the Water topic because we only performed a single DHSVM run per scenario due to computational limitations. Since DHSVM is a deterministic model and the climate stream fed into DHSVM was the same for all scenarios, all the scenarios tracked each other very closely (Fig. S5). The Wildfire topic, in contrast, was driven by wildfire activity in LANDIS-II which is stochastic and therefore produced noticeable differences between different runs of the same scenario (hence the wide simulation envelopes). For example, one iteration of *Wildfire Only* may have had a big fire year in year 10 while another iteration had a big fire year in year 11, leading to wide simulation envelopes and making differences between scenarios on a year-to-year basis difficult to detect (Fig. 4). We were able to tease out differences between management scenarios by evaluating cumulative area burned by severity which allowed differences in wildfire behavior to accumulate through time, highlighting the differences between scenarios that were evident over long enough time scales (Fig. 3).

Tradeoffs in space and time

Our simulation modeling revealed that ecosystem responses to future management scenarios are highly

dynamic, and potential benefits are unstable over time. Fluctuations in ecosystem functioning point to the importance of underlying feedbacks and destabilizing processes in shaping future landscapes. These second-order landscape dynamics were evident in the inflection point in area burned under *Wildfire Only*, the rise and fall of available biomass under the *Harvest* scenarios, and the high Carbon scores for the *WFU* scenarios. These results emphasize the importance of adaptive land management strategies that periodically re-assess management tactics in response to ever-changing ecological challenges. They also provide a way to visualize the uncertainty that managers and policy makers must reconcile (e.g., Miller 2007; Lynch et al. 2022), demonstrating how scenarios that appear best in the short term can yield less-desirable outcomes over longer time spans (e.g., Young and Ager 2024).

Limitations and future research

Caution must be exercised when interpreting the results of decision support systems. The relative ranking of various scenarios is highly sensitive to the selection of evaluation metrics and the structure of the DST logic model. Results of the DST modeling are sensitive to the number of topics and the weight given to each of the topics in the final assessment. This is a strength of fuzzy logic models: they can be adapted to reflect stakeholder values and the relative importance of different topics of interest. It is likely that these seven topics would not carry equal weight if this model were to be applied in a management context. Equal weight was applied by using union operators in the logic model (Reynolds et al. 2014). Accordingly, the overall benefits scores associated with each management scenario would change to reflect the concerns and values of managers and the local community. We used the *Social*, *Economic*, and *Ecological* groupings to get at this, as these topic groupings reflect what the decision support model results would look like if it were to include only a subset of topics.

Another difficulty in interpreting our results is that the fuzzy logic model translated absolute values into a relativized scale, which is necessary to be able to aggregate diverse units of measurement into the primary topic areas. However, this translation may obscure the magnitude of treatment effects because we set the fuzzy logic breakpoints to the 10th and 90th percentiles of observed delta values to represent the middle 80th percentile range of values. For the mean annual flow metric, for example, differences in mean annual flow between scenarios each year were very small, yet these small differences still received scores ranging from − 1 to 1. This allowed us to evaluate differences between scenarios, but it obscured the fact that year-to-year variability in mean annual flow was far greater than the within-year variability due to scenario differences (Fig. S5).

This study builds upon a growing body of research leveraging decision support systems to evaluate tradeoffs and synergies among important ecological and social values, both in space and over time, to project future landscape dynamics and management effects (Reynolds et al. 2014; Abelson et al. 2022; Maxwell et al. 2022; Povak et al. 2022; Furniss et al. 2023). A significant advancement made here is the integration of LANDIS-II with a distributed hydrology model (DHSVM), enabling us to quantify impacts of forest treatments on snowpack and streamflow dynamics. An important next step will be to make this integration more accessible, perhaps through the development of a new model extension, and to consider ways to couple the models to improve hydrology dynamics (hence water availability) within LANDIS-II.

Conclusions

We found that most alternative future management scenarios produced discernable benefits among *Economic*, *Social*, and *Ecological* primary topic areas. These gains were both robust and fragile, with the *Wildfire Only* scenario having the greatest overall performance part way through the simulation (2040–2070), then declining as positive feedbacks in wildfire activity under this scenario caused a steep increase in high-severity fire. Simulated management actions were able to mitigate this high-severity fire feedback, with both mechanical forest treatments and wildland fire use tactics reducing high-severity area burned and resulting in better overall landscape health. Unsurprisingly, mechanical treatments were more beneficial for *Economic* categories while wildland fire use alone was better for some of the *Ecological* topics. Benefits for the *Social* topics were somewhere in between, reflecting the inevitability of tradeoffs among countervailing needs such as carbon storage and streamflow enhancement. These tradeoffs highlight the need for diverse and cohesive landscape management strategies, as no single management scenario will produce optimal results across the board.

Tradeoffs are at the very core of wicked problems; positive outcomes in some areas yield negative cascades in others. Disentangling these problems requires managers and stakeholders to identify shared values, priorities, and tolerable tradeoffs, and to apply a mix of methods that reflect the diversity of desired benefits associated with various management strategies. This study demonstrates what these future scenarios can look like, underscoring the importance of both active and passive management strategies—and wildfire management decisions in particular—in building more robust and resilient future landscapes.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00339-y.

Supplementary Material 1.

Acknowledgements
We thank three anonymous reviewers for constructive comments and suggestions on a prior draft of this manuscript. This work was partially funded the US Department of Energy (USDOE) Bioenergy Technologies Office (DE-SC0017519/0005) and was supported through an appointment of the senior author to the Research Participation Program at the PNWRS, administered by the Oak Ridge Institute for Science and Education (ORISE) through an interagency agreement between the USDOE and the PNWRS. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. The views of the authors expressed herein do not represent the official views of the USDOE, ORISE, or the USDA-FS.

Authors' contributions
TJF, PFH, and NAP conceived of the study. TJF performed the majority of analysis and prepared the first draft. MW and ZD performed the hydrology modeling, and RBS helped collect and prepare foundational data layers. PFH and MW provided funding. All authors contributed to writing and editing of the final manuscript.

Funding
This work was partially funded the US Department of Energy (USDOE) Bioenergy Technologies Office (DE-SC0017519/0005) and the USDA-FS, PNW Research Station (PNWRS).

Data availability
This study leveraged existing datasets, all of which have been cited appropriately in the "Methods" section. No new data was collected for this study.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY, USA. [2]USDA Forest Service, Pacific Northwest Research Station, Wenatchee, WA, USA. [3]USDA Forest Service, Pacific Southwest Research Station, Placerville, CA, USA. [4]School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA. [5]Pacific Northwest National Laboratory, Richland, WA, USA. [6]School of Civil and Environmental Engineering, University of Washington, Seattle, WA, USA.

Received: 13 December 2023 Accepted: 8 November 2024
Published online: 18 December 2024

References

Abatzoglou, J.T., and T.J. Brown. 2012. A comparison of statistical downscaling methods suited for wildfire applications. *International Journal of Climatology* 32 (5): 772–780. https://doi.org/10.1002/joc.2312.

Abatzoglou, J.T., D.S. Battisti, A.P. Williams, W.D. Hansen, B.J. Harvey, and C.A. Kolden. 2021. Projected increases in western US forest fire despite growing fuel constraints. *Communications Earth & Environment* 2 (1): 227. https://doi.org/10.1038/s43247-021-00299-0.

Abelson, E., K. Reynolds, A. White, J. Long, C. Maxwell, and P. Manley. 2022. Evaluating pathways to social and ecological landscape resilience. Ecology and Society 27(4):art8. https://doi.org/10.5751/ES-13243-270408

Agee, J.K. 1998. The landscape ecology of western forest fire regimes. *Northwest Science* 72 (24): 12.

Ager, A.A., M.A. Day, and K. Vogler. 2016. Production possibility frontiers and socioecological tradeoffs for restoration of fire adapted forests. *Journal of Environmental Management* 176: 157–168. https://doi.org/10.1016/j.jenvman.2016.01.033.

Ager, A.A., A.M.G. Barros, R. Houtman, R. Seli, and M.A. Day. 2020. Modelling the effect of accelerated forest management on long-term wildfire activity. *Ecological Modelling* 421: 108962. https://doi.org/10.1016/j.ecolmodel.2020.108962.

Ager, A.A., A.M.G. Barros, and M.A. Day. 2022. Contrasting effects of future wildfire and forest management scenarios on a fire excluded western US landscape. *Landscape Ecology* 37 (4): 1091–1112. https://doi.org/10.1007/s10980-022-01414-y.

Barros, A.M.G., A.A. Ager, M.A. Day, M.A. Krawchuk, and T.A. Spies. 2018. Wildfires managed for restoration enhance ecological resilience. *Ecosphere* 9 (3): e02161. https://doi.org/10.1002/ecs2.2161.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1). https://doi.org/10.18637/jss.v067.i01.

Belavenutti, P., W. Chung, and A.A. Ager. 2021. The economic reality of the forest and fuel management deficit on a fire prone western US national forest. *Journal of Environmental Management* 293: 112825.

Berkey, J.K., R.T. Belote, C.T. Maher, and A.J. Larson. 2021. Structural diversity and development in active fire regime mixed-conifer forests. *Forest Ecology and Management* 479: 118548. https://doi.org/10.1016/j.foreco.2020.118548.

Calkin, D.E., M.P. Thompson, and M.A. Finney. 2015. Negative consequences of positive feedbacks in US wildfire management. *Forest Ecosystems* 2 (1): 9. https://doi.org/10.1186/s40663-015-0033-8.

Coop, J.D., S.A. Parks, C.S. Stevens-Rumann, S.D. Crausbay, P.E. Higuera, M.D. Hurteau, A. Tepley, E. Whitman, T. Assal, B.M. Collins, K.T. Davis, S. Dobrowski, D.A. Falk, P.J. Fornwalt, P.Z. Fulé, B.J. Harvey, V.R. Kane, C.E. Littlefield, E.Q. Margolis, M. North, M.-A. Parisien, S. Prichard, and K.C. Rodman. 2020. Wildfire-driven forest conversion in Western North American landscapes. *BioScience* 70 (8): 659–673. https://doi.org/10.1093/biosci/biaa061.

Day, M. A., A. A. Ager, R. M. Houtman, and C. R. Evers. 2024. Prioritizing restoration and risk reduction landscape projects with the ForSys planning system. Page RMRS-GTR-437. No. RMRS-GTR-437, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Dombeck, M.P., J.E. Williams, and C.A. Wood. 2004. Wildfire policy and public lands: Integrating scientific understanding with social concerns across landscapes. *Conservation Biology* 18 (4): 883–889. https://doi.org/10.1111/j.1523-1739.2004.00491.x.

Eidenshink, J., B. Schwind, K. Brewer, Z.-L. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. *Fire Ecology* 3 (1): 3–21. https://doi.org/10.4996/fireecology.0301003.

Falk, D. A., A. C. Watts, and A. E. Thode. 2019. Scaling ecological resilience. Frontiers in Ecology and Evolution 7:Article 275. https://doi.org/10.3389/fevo.2019.00275.

Flanagan, S. A., S. Bhotika, C. Hawley, G. Starr, S. Wiesner, J. K. Hiers, J. J. O'Brien, S. Goodrick, M. A. Callaham, R. M. Scheller, K. D. Klepzig, R. S. Taylor, and E. L. Loudermilk. 2019. Quantifying carbon and species dynamics under different fire regimes in a southeastern U.S. pineland. Ecosphere 10(6):e02772. https://doi.org/10.1002/ecs2.2772.

Flatley, W.T., and P.Z. Fulé. 2016. Are historical fire regimes compatible with future climate? *Implications for Forest Restoration. Ecosphere* 7 (10): e01471. https://doi.org/10.1002/ecs2.1471.

Furniss, T.J., A.J. Larson, V.R. Kane, and J.A. Lutz. 2020. Wildfire and drought moderate the spatial elements of tree mortality. *Ecosphere* 11 (8): e03214. https://doi.org/10.1002/ecs2.3214.

Furniss, T. J., A. J. Das, P. J. Mantgem, N. L. Stephenson, and J. A. Lutz. 2022a. Crowding, climate, and the case for social distancing among trees. Ecological Applications:e2507. https://doi.org/10.1002/eap.2507.

Furniss, T.J., P.F. Hessburg, N.A. Povak, R.B. Salter, and M.S. Wigmosta. 2022b. Predicting future patterns, processes, and their interactions: Benchmark

calibration and validation procedures for forest landscape models. *Ecological Modelling* 473: 110099.
Furniss, T.J., N.A. Povak, P.F. Hessburg, R.B. Salter, Z. Duan, and M.S. Wigmosta. 2023. Informing climate adaptation strategies using ecological simulation models and spatial decision support tools. *Frontiers in Forests and Global Change* 6: 1269081. https://doi.org/10.3389/ffgc.2023.1269081.
Graham, R. T., A. E. Harvey, T. B. Jain, J. R. Tonn. 1999. The effects of thinning and similar stand treatments on fire behavior in western forests. Gen. Tech. Rep. PNW-GTR-463. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 27 p.
Gustafson, E.J., S.R. Shifley, D.J. Mladenoff, K.K. Nimerfro, and H.S. He. 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. *Canadian Journal of Forest Research* 30: 32–43.
Hagmann, R.K., P.F. Hessburg, S.J. Prichard, N.A. Povak, P.M. Brown, P.Z. Fulé, R.E. Keane, E.E. Knapp, J.M. Lydersen, K.L. Metlen, M.J. Reilly, A.J. Sánchez Meador, S.L. Stephens, J.T. Stevens, A.H. Taylor, L.L. Yocom, M.A. Battaglia, D.J. Churchill, L.D. Daniels, D.A. Falk, P. Henson, J.D. Johnston, M.A. Krawchuk, C.R. Levine, G.W. Meigs, A.G. Merschel, M.P. North, H.D. Safford, T.W. Swetnam, and A.E.M. Waltz. 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecological Applications* 31 (8): e02431. https://doi.org/10.1002/eap.2431.
Halofsky, J., D. Donato, D. Hibbs, J. Campbell, M.D. Cannon, J.B. Fontaine, J.R. Thompson, R. Anthony, B. Bormann, L. Kayes, et al. 2011. Mixed-severity fire regimes: Lessons and hypotheses from the Klamath-Siskiyou Ecoregion. *Ecosphere* 2 (4): 1–19.
Hessburg, P.F., D.J. Churchill, A.J. Larson, R.D. Haugo, C. Miller, T.A. Spies, M.P. North, N.A. Povak, R.T. Belote, P.H. Singleton, W.L. Gaines, R.E. Keane, G.H. Aplet, S.L. Stephens, P. Morgan, P.A. Bisson, B.E. Rieman, R.B. Salter, and G.H. Reeves. 2015. Restoring fire-prone Inland Pacific landscapes: Seven core principles. *Landscape Ecology* 30 (10): 1805–1835. https://doi.org/10.1007/s10980-015-0218-0.
Hessburg, P.F., C.L. Miller, S.A. Parks, N.A. Povak, A.H. Taylor, P.E. Higuera, S.J. Prichard, M.P. North, B.M. Collins, M.D. Hurteau, A.J. Larson, C.D. Allen, S.L. Stephens, H. Rivera-Huerta, C.S. Stevens-Rumann, L.D. Daniels, Z. Gedalof, R.W. Gray, V.R. Kane, D.J. Churchill, R.K. Hagmann, T.A. Spies, C.A. Cansler, R.T. Belote, T.T. Veblen, M.A. Battaglia, C. Hoffman, C.N. Skinner, H.D. Safford, and R.B. Salter. 2019. Climate, environment, and disturbance history govern resilience of western North American forests. *Frontiers in Ecology and Evolution* 7: 239. https://doi.org/10.3389/fevo.2019.00239.
Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. *Forest Ecology and Management* 211:117–139. https://doi.org/10.1016/j.foreco.2005.02.016.
Hessburg, P. F., S. Charnley, A. N. Gray, T. A. Spies, D. W. Peterson, R. L. Flitcroft, K. L. Wendel, J. E. Halofsky, E. M. White, and J. Marshall. 2021. Climate and wildfire adaptation of inland Northwest US forests. Frontiers in Ecology and the Environment:fee.2408. https://doi.org/10.1002/fee.2408.
Keane, R.E., R.A. Loehman, L.M. Holsinger, D.A. Falk, P. Higuera, S.M. Hood, and P.F. Hessburg. 2018. Use of landscape simulation modeling to quantify resilience for ecological applications. *Ecosphere* 9 (9): e02414. https://doi.org/10.1002/ecs2.2414.
Keane, R.E., B. Bentz, L.M. Holsinger, V.A. Saab, and R. Loehman. 2022. Modeled interactions of mountain pine beetle and wildland fire under future climate and management scenarios for three western US landscapes. *Fire Ecology* 18 (1): 12. https://doi.org/10.1186/s42408-022-00137-4.
Krofcheck, D. J., E. L. Loudermilk, J. K. Hiers, R. M. Scheller, and M. D. Hurteau. 2019. The effects of management on long-term carbon stability in a southeastern U.S. forest matrix under extreme fire weather. Ecosphere 10(3):e02631. https://doi.org/10.1002/ecs2.2631.
Larson, A.J., S.M.A. Jeronimo, P.F. Hessburg, J.A. Lutz, N.A. Povak, C.A. Cansler, V.R. Kane, and D.J. Churchill. 2022. Tamm review: Ecological principles to guide post-fire forest landscape management in the Inland Pacific and Northern Rocky Mountain regions. *Forest Ecology and Management* 504: 119680. https://doi.org/10.1016/j.foreco.2021.119680.
Livneh, B., T. J. Bohn, D. W. Pierce, F. Munoz-Arriola, B. Nijssen, R. Vose, D. R. Cayan, and L. Brekke. 2015. A spatially comprehensive, hydrometeorological data set for Mexico, the US, and Southern Canada 1950–2013. *Scientific Data* 2 (1): 1–12.
Loehman, R.A., R.E. Keane, L.M. Holsinger, and Z. Wu. 2017. Interactions of landscape disturbances and climate change dictate ecological pattern and process: Spatial modeling of wildfire, insect, and disease dynamics under future climates. *Landscape Ecology* 32 (7): 1447–1459. https://doi.org/10.1007/s10980-016-0414-6.
Loudermilk, E.L., A. Stanton, R.M. Scheller, T.E. Dilts, P.J. Weisberg, C. Skinner, and J. Yang. 2014. Effectiveness of fuel treatments for mitigating wildfire risk and sequestering forest carbon: A case study in the Lake Tahoe Basin. *Forest Ecology and Management* 323: 114–125. https://doi.org/10.1016/j.foreco.2014.03.011.
Loudermilk, E.L., R.M. Scheller, P.J. Weisberg, and A. Kretchun. 2017. Bending the carbon curve: Fire management for carbon resilience under climate change. *Landscape Ecology* 32 (7): 1461–1472. https://doi.org/10.1007/s10980-016-0447-x.
Lynch, A.J., L.M. Thompson, J.M. Morton, E.A. Beever, M. Clifford, D. Limpinsel, R.T. Magill, D.R. Magness, T.A. Melvin, R.A. Newman, M.T. Porath, F.J. Rahel, J.H. Reynolds, G.W. Schuurman, S.A. Sethi, and J.L. Wilkening. 2022. RAD adaptive management for transforming ecosystems. *BioScience* 72 (1): 45–56. https://doi.org/10.1093/biosci/biab091.
Maron, M., and G. Cockfield. 2008. Managing trade-offs in landscape restoration and revegetation projects. *Ecological Applications* 18 (8): 2041–2049.
Maxwell, C., R. M. Scheller, J. W. Long, and P. Manley. 2022. Frequency of disturbance mitigates high-severity fire in the Lake Tahoe Basin, California and Nevada. Ecology and Society 27(1):art21. https://doi.org/10.5751/ES-12954-270121.
Millar, C.I., and N.L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349 (6250): 823–826. https://doi.org/10.1126/science.aaa9933.
Millar, C.I., N.L. Stephenson, and S.L. Stephens. 2007. Climate change and forests of the future: Managing in the face of uncertainty. *Ecological Applications* 17 (8): 2145–2151.
Miller, C. 2003. Wildland fire use: a wilderness perspective on fuel management. Page USDA Forest Service Proceedings RMRS-P-29. USDA Forest Service Rocky Mountain Research Station, 2150 Centre Avenue Fort Collins CO 80526 USA.
Miller, C. 2007. Simulation of the consequences of different fire regimes to support wildland fire use decisions. *Fire Ecology* 3 (2): 83–102. https://doi.org/10.4996/fireecology.0302083.
Moritz, M.A., E. Batllori, R.A. Bradstock, A.M. Gill, J. Handmer, P.F. Hessburg, J. Leonard, S. McCaffrey, D.C. Odion, T. Schoennagel, and A.D. Syphard. 2014. Learning to coexist with wildfire. *Nature* 515 (7525): 58–66. https://doi.org/10.1038/nature13946.
North, M., B.M. Collins, and S. Stephens. 2012. Using fire to increase the scale, benefits, and future maintenance of fuels treatments. *Journal of Forestry* 110 (7): 392–401. https://doi.org/10.5849/jof.12-021.
North, M.P., S.L. Stephens, B.M. Collins, J.K. Agee, G. Aplet, J.F. Franklin, and P.Z. Fulé. 2015. Reform forest fire management. *Science* 349 (6254): 1280–1281. https://doi.org/10.1126/science.aab2356.
Povak, N.A., C.P. Giardina, P.F. Hessburg, K.M. Reynolds, R.B. Salter, C. Heider, E. Salminen, and R. MacKenzie. 2020. A decision support tool for the conservation of tropical forest and nearshore environments on Babeldaob Island. *Palau. Forest Ecology and Management* 476: 118480. https://doi.org/10.1016/j.foreco.2020.118480.
Povak, N.A., T.J. Furniss, P.F. Hessburg, R.B. Salter, M. Wigmosta, Z. Duan, and M. LeFevre. 2022. Evaluating basin-scale forest adaptation scenarios: Wildfire, streamflow, biomass, and economic recovery synergies and trade-offs. *Frontiers in Forests and Global Change* 5: 805179.
Povak, N.A., P.F. Hessburg, R.B. Salter, S.J. Prichard, and R.W. Gray. 2023. System-level feedbacks of active fire regimes in large landscapes. *Fire Ecology.* 19 (1): 45. https://doi.org/10.1186/s42408-023-00197-0.
Povak, N. A., P. N. Manley, and K. N. Wilson. 2024. Quantitative methods for integrating climate adaptation strategies into spatial decision support models. Frontiers in Forests and Global Change 7. https://doi.org/10.3389/ffgc.2024.1286937.
Prichard, S.J., R.B. Salter, P.F. Hessburg, N.A. Povak, and R.W. Gray. 2023. The REBURN model: Simulating system-level forest succession and wildfire dynamics. *Fire Ecology* 19 (1): 1–32.
R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Reynolds, K.M., P.F. Hessburg, and P. Bourgeron. 2014. *Making transparent environmental management decisions applications of the ecosystem management decision support system.* Springer.

Riley, K.L., I.C. Grenfell, M.A. Finney, and J.M. Wiener. 2021. TreeMap, a tree-level model of conterminous US forests circa 2014 produced by imputation of FIA plot data. *Scientific Data* 8 (1): 11. https://doi.org/10.1038/s41597-020-00782-x.

Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. *International Journal of Wildland Fire* 18 (3): 235. https://doi.org/10.1071/WF08088.

Scheller, R.M., J.B. Domingo, B.R. Sturtevant, J.S. Williams, A. Rudy, E.J. Gustafson, and D.J. Mladenoff. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling* 201 (3–4): 409–419. https://doi.org/10.1016/j.ecolmodel.2006.10.009.

Scheller, R.M., D. Hua, P.V. Bolstad, R.A. Birdsey, and D.J. Mladenoff. 2011. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. *Ecological Modelling* 222 (1): 144–153. https://doi.org/10.1016/j.ecolmodel.2010.09.009.

Scheller, R., A. Kretchun, T.J. Hawbaker, and P.D. Henne. 2019. A landscape model of variable social-ecological fire regimes. *Ecological Modelling* 401: 85–93. https://doi.org/10.1016/j.ecolmodel.2019.03.022.

Schoennagel, T., J.K. Balch, H. Brenkert-Smith, P.E. Dennison, B.J. Harvey, M.A. Krawchuk, N. Mietkiewicz, P. Morgan, M.A. Moritz, R. Rasker, M.G. Turner, and C. Whitlock. 2017. Adapt to more wildfire in western North American forests as climate changes. *Proceedings of the National Academy of Sciences* 114 (18): 4582–4590. https://doi.org/10.1073/pnas.1617464114.

Scholl, A.E., and A.H. Taylor. 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. *Ecological Applications* 20 (2): 362–380.

Schuurman, G.W., D.N. Cole, A.E. Cravens, S. Covington, S.D. Crausbay, C.H. Hoffman, D.J. Lawrence, D.R. Magness, J.M. Morton, E.A. Nelson, and R. O'Malley. 2022. Navigating ecological transformation: Resist–accept–direct as a path to a new resource management paradigm. *BioScience* 72 (1): 16–29. https://doi.org/10.1093/biosci/biab067.

Schwalm, C. R., S. Glendon, and P. B. Duffy. 2020. RCP8.5 tracks cumulative CO2 emissions. Proceedings of the National Academy of Sciences 117(33):19656–19657.

Seaber, P.R., Kapinos, F.P. and Knapp, G.L., 1987. Hydrologic unit maps (Vol. 2294, p. 1987). Washington, DC, USA: US Government Printing Office.

Short, K. C. 2017. Spatial wildfire occurrence data for the United States, 1992–2015 [FPA_FOD_20170508].

Soil Survey Staff. 2020. Gridded National Soil Survey Geographic (gNATSGO) Database for Washington State. United States Department of Agriculture, Natural Resources Conservation Service. Available online at https://nrcs.app.box.com/v/soils. November 1, 2020 (FY2020 official release).

Stephens, S.L., J.D. McIver, R.E.J. Boerner, C.J. Fettig, J.B. Fontaine, B.R. Hartsough, P.L. Kennedy, and D.W. Schwilk. 2012. The effects of forest fuel-reduction treatments in the United States. *BioScience* 62 (6): 549–560. https://doi.org/10.1525/bio.2012.62.6.6.

Stephens, S.L., J.K. Agee, P.Z. Fule, M.P. North, W.H. Romme, T.W. Swetnam, and M.G. Turner. 2013. Managing forests and fire in changing climates. *Science* 342 (6154): 41–42.

Stephens, S. L., B. M. Collins, E. Biber, and P. Z. Fulé. 2016. U.S. federal fire and forest policy: emphasizing resilience in dry forests. Ecosphere 7(11). https://doi.org/10.1002/ecs2.1584.

Stoker, J., and B. Miller. 2022. The accuracy and consistency of 3D elevation program data: A systematic analysis. *Remote Sens.* 14: 940. https://doi.org/10.3390/rs14040940.

USDA Forest Service. 2022. Confronting the wildfire crisis: a strategy for protecting communities and improving resilience in America's forests. Page 25. No. FS-1187a, USDA Forest Service.

van Wagtendonk, J.W. 2007. The history and evolution of wildland fire use. *Fire Ecology* 3 (2): 3–17. https://doi.org/10.4996/fireecology.0302003.

Vogler, K.C., A.A. Ager, M.A. Day, M. Jennings, and J.D. Bailey. 2015. Prioritization of forest restoration projects: Tradeoffs between wildfire protection, ecological restoration and economic objectives. *Forests* 6 (12): 4403–4420.

Warnes, G. R., B. Bolker, L. Bonebakker, R. Gentleman, W. Huber, A. Liaw, T. Lumley, M. Maechler, A. Magnusson, S. Moeller, M. Schwartz, and B. Venables. 2022. gplots: various R programming tools for plotting data.

Wigmosta, M.S., L.W. Vail, and D.P. Lettenmaier. 1994. A distributed hydrology-vegetation model for complex terrain. *Water Resources Research* 30 (6): 1665–1679. https://doi.org/10.1029/94WR00436.

Young, J.D., and A.A. Ager. 2024. Resource objective wildfire leveraged to restore old growth forest structure while stabilizing carbon stocks in the southwestern United States. *Ecological Modelling* 488: 110573. https://doi.org/10.1016/j.ecolmodel.2023.110573.

Young, J.D., A.A. Ager, and A.E. Thode. 2022. Using wildfire as a management strategy to restore resiliency to ponderosa pine forests in the southwestern United States. *Ecosphere* 13 (5): e4040. https://doi.org/10.1002/ecs2.4040.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Forest Ecology and Management 335 (2015) 37–50

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

A new approach to evaluate forest structure restoration needs across Oregon and Washington, USA

Ryan Haugo [a,*], Chris Zanger [b], Tom DeMeo [c], Chris Ringo [d], Ayn Shlisky [e], Kori Blankenship [b], Mike Simpson [f], Kim Mellen-McLean [c], Jane Kertis [g], Mark Stern [h]

[a] The Nature Conservancy, 32 N 3rd St, Ste. 412, Yakima, WA 98901, United States
[b] The Nature Conservancy, 999 Disk Drive, Ste. 104, Bend, OR 97702, United States
[c] US Forest Service, 1220 SW 3rd Ave, Portland, OR 97024, United States
[d] Department of Crop and Soil Science, Oregon State University, Corvallis, OR 97331, United States
[e] US Forest Service, 72510 Coyote Rd., Pendleton, OR 97801, United States
[f] US Forest Service, 63095 Deschutes Market Rd., Bend, OR 97701, United States
[g] US Forest Service, 3200 SW Jefferson Way, Corvallis, OR 97331, United States
[h] The Nature Conservancy, 821 SE 14th Ave, Portland, OR 97214, United States

ARTICLE INFO

Article history:
Received 30 June 2014
Received in revised form 12 September 2014
Accepted 15 September 2014
Available online 10 October 2014

Keywords:
Pacific Northwest
Ecological restoration
Landfire
Fire Regime Condition Class
Gradient nearest neighbor
Natural range of variation

ABSTRACT

Widespread habitat degradation and uncharacteristic fire, insect, and disease outbreaks in forests across the western United States have led to highly publicized calls to increase the pace and scale of forest restoration. Despite these calls, we frequently lack a comprehensive understanding of forest restoration needs. In this study we demonstrate a new approach for evaluating where, how much, and what types of restoration are needed to move present day landscape scale forest structure towards a Natural Range of Variability (NRV) across eastern Washington, eastern Oregon, and southwestern Oregon. Our approach builds on the conceptual framework of the LANDFIRE and Fire Regime Condition Class programs. Washington–Oregon specific datasets are used to assess the need for changes to current forest structure resulting from disturbance and/or succession at watershed and regional scales.

Across our analysis region we found that changes in current structure would be needed on an estimated 4.7 million+ ha (40% of all coniferous forests) in order to restore forest structure approximating NRV at the landscape scale. Both the overall level and the type of restoration need varied greatly between forested biophysical settings. Regional restoration needs were dominated by the estimated 3.8+ million ha in need of thinning and/or low severity fire in forests that were historically maintained by frequent low or mixed severity fire (historical Fire Regime Group I and III biophysical settings). However, disturbance alone cannot restore NRV forest structure. We found that time to transition into later development structural classes through successional processes was required on approximately 3.2 million ha (over 25% of all coniferous forests). On an estimated 2.3 million ha we identified that disturbance followed by succession was required to restore NRV forest structure.

The results of this study are intended to facilitate the ability of local land managers to incorporate regional scale, multi-ownership context into local forest management and restoration. Meeting the region-wide restoration needs identified in this study will require a substantial increase in the pace and scale of restoration treatments and coordination amongst governments, agencies, and landowners.
© 2014 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-SA license (http://creativecommons.org/licenses/by-nc-sa/3.0/).

1. Introduction

Ecological restoration has become a dominant paradigm for the management of many public forests across the United States (USDA Forest Service, 2012a,b). Ecological restoration is "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER, 2004). Within western states, this present focus on restoration is largely in response to the widespread degradation of terrestrial and aquatic habitats and uncharacteristic fire, insect, and disease outbreaks resulting from a century or more of wildfire suppression, intensive harvesting, grazing, and mining (Brown et al., 2004; Franklin et al., 2008; Hessburg and Agee, 2003; Hessburg et al., 2005; North et al., 2009; Peterson et al., 2005; Schoennagel et al., 2004). Since 2010 $20 to

* Corresponding author. Tel.: +1 509 248 6672.
E-mail address: rhaugo@tnc.org (R. Haugo).

http://dx.doi.org/10.1016/j.foreco.2014.09.014
0378-1127/© 2014 The Authors. Published by Elsevier B.V.
This is an open access article under the CC BY-NC-SA license (http://creativecommons.org/licenses/by-nc-sa/3.0/).

$40 million has been appropriated annually for the ecological restoration of federal forests through the Collaborative Landscape Restoration Program (CFLRP; H.R. 5263, fs.fed.us/restoration/CFLRP). In addition to CFLRP, the USDA Forest Service has undertaken a number of initiatives in recent years to increase the pace and scale of forest restoration including but not limited to implementing a new forest planning rule (USDA Forest Service, 2012a), the Watershed Condition Framework (USDA Forest Service, 2011a), and a bark beetle strategy (USDA Forest Service, 2011b). Similarly, state governments in Oregon, Washington and elsewhere are promoting both the ecological and economic benefits of forest restoration. For example, the Oregon Federal Forest Health Package (SB 5521 passed by the Oregon Legislature in 2013) is providing nearly $2.9 million for technical assistance and scientific support needed to increase the pace and scale of collaboratively developed management efforts and to pilot a new business model that contributes funding directly to help increase the pace and scale of implementing restoration work on national forests.

Despite highly publicized calls to increase the pace and scale of forest restoration (Rasmussen et al., 2012; USDA Forest Service, 2012b) we lack a comprehensive understanding of forest restoration needs. In many, but not all, of the interior Pacific Northwest forest ecosystems previous studies have documented patterns of departure from historical conditions (e.g., Everett et al., 2000; Hagmann et al., 2013; Haugo et al., 2010; Hessburg et al., 2005, 2000b; Heyerdahl et al., 2014; Perry et al., 2011; Wright and Agee, 2004). However these studies are not able to provide a systematic evaluation of where, how much, and what types of treatments are needed to restore forest structure at regional scales (100,000s–1,000,000s of ha). Until recently most restoration planning and implementation has occurred at scales of watersheds or smaller ($\leqslant$5000 ha). Although there has been a gradual increase in the size of proposed projects, small project areas are still often used. Because the overarching objectives of forest restoration are frequently to influence ecological processes such as disturbance regimes and habitat connectivity operating at very large spatial scales (10,000's–100,000's of ha), a broader spatial perspective is required to evaluate the overall magnitude of ecological and planning needs. Without an understanding of regional scale restoration needs it is difficult to accurately quantify the magnitude of restoration funding needs for state and national entities or to set the context for prioritization of limited land management resources. It is also difficult to determine the cumulative, regional scale impact of current restoration efforts and evaluate whether these efforts are "making a difference". Consequently, evaluation of restoration needs requires a perspective larger than individual watersheds or even individual national forests, and that considers forested lands across all ownerships within a region.

In this study we demonstrate a new approach for evaluating where, how much, and what types of treatments are currently needed to restore a Natural Range of Variability (NRV) in forest structure across eastern Washington, eastern Oregon, and southwestern Oregon. NRV is defined as a frequency distribution of ecosystem characteristics, including the appropriate spatial and temporal scales for those distributions and a reference period, typically prior to European settlement. These ecosystem characteristics may encompass a wide suite of terrestrial and aquatic considerations (Keane et al., 2009; Landres et al., 1999; Morgan et al., 1994; USDA Forest Service, 2012a); here we focus on forest structure.

We acknowledge the limitations of focusing on forest structure as an indicator of ecosystem health, and the NRV as the reference condition. Many biotic and abiotic components must be considered for comprehensive restoration of forest ecosystems, including forest structure. Nevertheless, forest structure presents a tractable coarse filter to which many other aspects of biodiversity (e.g., terrestrial wildlife habitat, riparian and aquatic habitat, herbaceous diversity and productivity, and fire, insect, and disease frequency and severity) respond (Agee, 1993; Hessburg et al., 1999; Johnson and O'Neil, 2001; Peterson et al., 2005). Ideally, we would also evaluate future range of variability (FRV) reference conditions that describe the expected response of forest ecosystems to climate change (Gartner et al., 2008; Keane et al., 2009). FRV is an emerging concept, but FRV reference models are not yet consistently available at a regional scale. While the specific impacts of climate change are uncertain, restoring to a NRV is assumed to increase forests' resilience and adaptive capacity (Agee, 2003; Hessburg et al., 1999; Keane et al., 2009; Millar et al., 2007; Stephens et al., 2013; Stine et al., in press). Finally, NRV does not necessarily represent desired conditions for federal forests, which reflect social and economic concerns as well as ecological ones. Nevertheless, NRV represents a strong foundation for developing desired conditions because it represents the ecological capability of the landscape (USDA Forest Service, 2012a).

2. Methods

2.1. Study area

We assessed forest vegetation restoration needs for the approximately 11,619,000 ha of forest across eastern Washington and eastern and southwestern Oregon, USA (Fig. 1). This geography generally includes the extent of historically frequent fire forests within the USDA Forest Service's Pacific Northwest Region. These forests cover very broad climatic, edaphic, and topographic gradients with widely varying natural disturbance regimes. They range from *Tsuga mertensiana forests* and parklands along the crest of the Cascade Range with a mean annual precipitation of 1600–2800 mm per year and historical fire return intervals of several centuries to dry *Pinus ponderosa* forests in southeast Oregon with mean annual precipitation of 355–760 mm per year and historical fire return intervals of less than 10 years (Agee, 1993; Franklin and Dyrness, 1973). Our challenge was to develop an approach that can be applied across this vast extent encompassing large environmental gradients with data that are consistent and meaningful.

2.2. Core concepts and data sources

We built upon the conceptual framework of the LANDFIRE and Fire Regime Condition Class (FRCC) programs (Barrett et al., 2010; Rollins, 2009) and incorporated Washington–Oregon specific datasets. Our assessment of forest vegetation restoration need is based on four primary data inputs: (1) a classification and map of forested biophysical settings, (2) NRV reference conditions for each biophysical setting, (3) a delineation of "landscape units" for each biophysical setting, and (4) a map of present day forest vegetation structure.

2.2.1. Mapping forested biophysical settings

Biophysical settings are potential vegetation units associated with characteristic land capabilities and disturbance regimes (Barrett et al., 2010). Many different forested biophysical settings are found across Washington and Oregon based on vegetation, soils, climate, topography, and historic disturbance regimes (Keane et al., 2007; Pratt et al., 2006; Rollins, 2009). They provide the framework for describing fire regimes. We mapped biophysical settings across Washington and Oregon using the 30 m pixel Integrated Landscape Assessment Projects' Potential Vegetation Type (PVT) dataset (Halofsky et al., in press), which compiled previous potential forest vegetation classification and mapping efforts including Simpson (2007) and Henderson et al. (2011). We also incorporated subsequent refinements to PVT mapping in

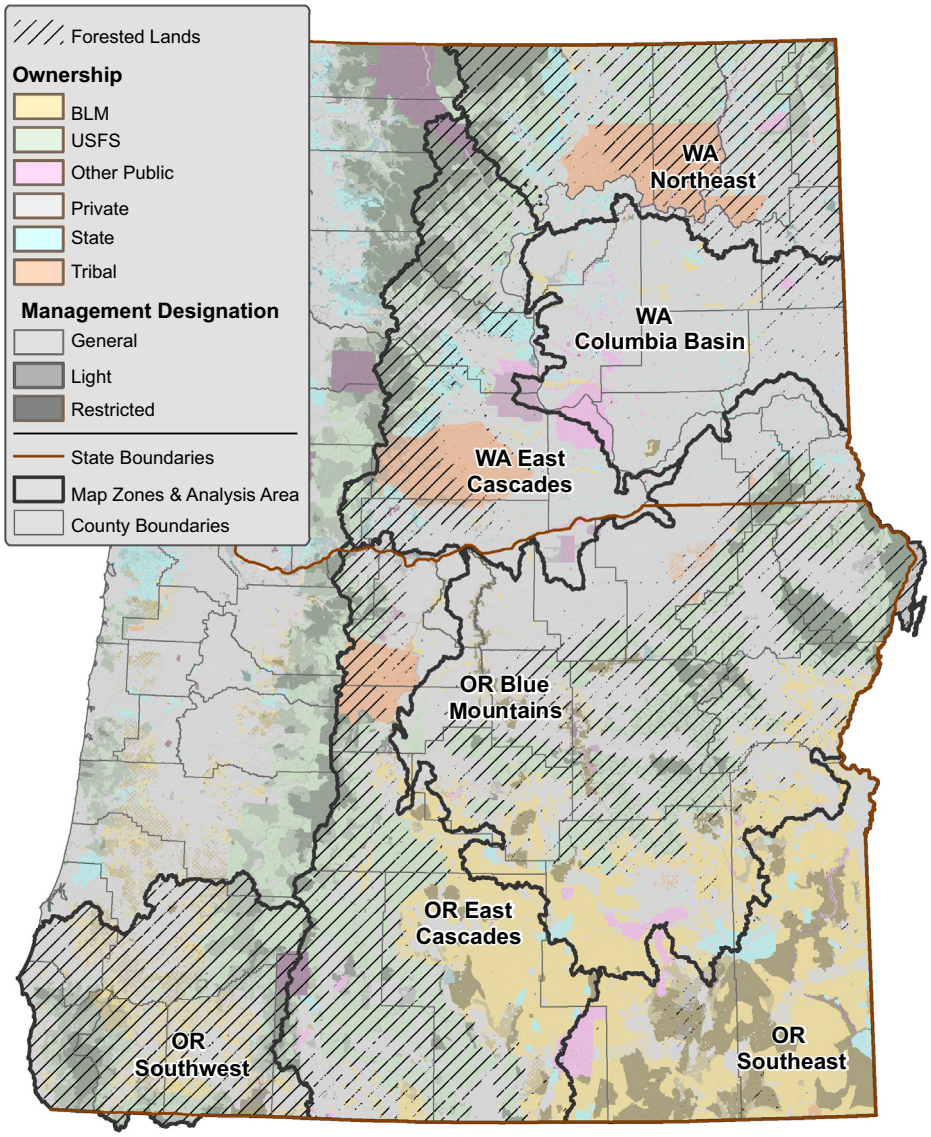


Fig. 1. Map Zones, forest ownership and forest extent in eastern Washington and eastern and southwestern Oregon.

southwestern Oregon (E. Henderson, Oregon State University, unpublished data).

A biophysical setting model from either the LANDFIRE Rapid Assessment or the later LANDFIRE National program (Rollins, 2009; Ryan and Opperman, 2013) was assigned to each PVT mapping unit (Appendix A.1). Assignments were made by staff in the US Forest Service Pacific Northwest Region Ecology Program based upon the geographic, environmental, and biological characteristics of the biophysical setting models and the PVT mapping units. We defined forests across our study area as those described as a "forest" or "forest and woodland" land cover class in the biophysical setting model. National Forest System lands are typically considered "forest" if they have >10% tree canopy cover, and this generally coincides with forest, and forest and woodland land cover classes (USDA Forest Service, 2004).

2.2.2. Natural range of variability reference conditions

Each biophysical setting model is composed of a suite of 3–5 successional/structural stages (s-classes). These classes typically include: (A) Early Development, (B) Mid-Development Closed Canopy, (C) Mid-Development Open Canopy, (D) Late Development Open Canopy, and (E) Late Development Closed Canopy. The definition of each s-class in terms of species composition, stand structure, and stand age is unique for each biophysical setting (Appendix A.2). The percentage of a biophysical setting in each s-class will differ depending on disturbance frequencies and/or intensities. The LANDFIRE and FRCC conceptual framework assumes that, given natural processes, a biophysical setting will have a characteristic range of variation in the proportion in each s-class and that an effective indicator of "ecological condition" for a given landscape is the relative abundance of each s-class within biophysical settings (Barrett et al., 2010; Keane et al., 2011).

NRV reference models describe how the relative distribution of s-classes for a biophysical setting were shaped by succession and the frequency and severity of disturbances prior to European settlement and provide a comparison to present-day forest conditions (Keane et al., 2009; Landres et al., 1999). LANDFIRE biophysical setting models are used to develop NRV estimates through the use of state-and-transition models incorporating pre-European settlement rates of succession and disturbance. Rates were determined through an intensive literature and expert review process (Keane et al., 2002, 2007; Pratt et al., 2006; Rollins, 2009).

The distribution of s-classes for each biophysical setting which results from running state-and-transition models for many time-steps (Appendix A.3) does not represent a specific historical date, but instead approximates characteristic conditions that result from

natural biological and physical processes operating on a landscape over a relatively long time period. NRV is frequently represented by a single value, the mean relative abundance of each s-class from a collection of Monte Carlo state-and-transition model simulations (e.g., Low et al., 2010; Shlisky et al., 2005; Weisz et al., 2009). However, we extended this method by developing and using ranges for each s-class resulting from the stochastic variation around the mean within the state-and-transition models. The main source of this stochastic variation was the random draw to determine whether or not a transition occurred at each time step. We ran 10 simulations for each biophysical setting state-and-transition model over 1000 cells and 1000 annual time steps (Provencher et al., 2008; Forbis, 2006). Simulations were started with an equal proportion in each s-class and it took 200–400 years for the initial trends to stabilize. We calculated the range for each s-class as ±2 standard deviations from the mean abundance from the last 500 time steps (Provencher et al., 2008). Simulations were modeled using the Vegetation Dynamics Development Tool (ESSA Technologies, 2007).

2.2.3. Landscape units

Following the LANDFIRE and FRCC conceptual framework, we defined discrete landscape units to compare present-day forests to modeled NRV reference conditions (Barrett et al., 2010; Pratt et al., 2006). Landscape units varied in size based upon their associated historical fire regimes (Hann and Bunnell, 2001; Hardy et al., 2001) as described in each biophysical setting model (Appendix A.2). To be meaningful, landscape units must be large enough to fully contain the extent of historical disturbance events and scale of other ecological dynamics, but small enough to allow detection of present day disturbance events or management activities (Keane et al., 2009; Landres et al., 1999). In a simulation study focusing on landscapes in northern Utah, USA, Karau and Keane (2007) report an optimal landscape size of ~11,500 ha for assessing vegetation dynamics within low and mixed severity fire regime biophysical settings. Historically high severity fire regime systems require much larger landscapes to evaluate vegetation dynamics. Within the Oregon Coast Range, Wimberly et al. (2000) recommend landscapes of 300,000 ha or larger to compare modeled historic and current levels of late-successional stands within forests with a high severity fire regime.

In comparison to these previous studies, we used slightly larger landscape units to ensure appropriate estimates of restoration need. Restoration needs within historical Fire Regime Group I (FRG I; Table 1) biophysical settings were calculated within watersheds (10-digit/5th level hydrologic units; average ~46,000 ha). Within historical Fire Regime Group III (FRG III; Table 1) biophysical settings we used subbasins (8-digit/4th level hydrologic units; average ~285,000 ha). For these two scales, we used watershed and subbasin delineations from the US Geological Survey Watershed Boundary Dataset (Simley and Carswell, 2009; http://nhd.usgs.gov). Finally, restoration need within historical Fire Regime Groups IV and V (FRG IV & V; Table 1) biophysical settings was assessed within "map zones" (Fig. 1; average ~3.5 million ha) modified from the Integrated Landscape Assessment Project "Model Regions" (Halofsky et al., in press). We created "map zones" by setting the boundaries of the ILAP Model Regions to subbasin boundaries in order to maintain consistent nesting of our landscape units.

Table 1
Historic fire regime groups from Barrett et al. (2010).

Fire regime group	Frequency	Description
I	0–35 years	Generally low severity fires replacing less than 25% of dominant overstory; can include mixed-severity fires that replace up to 75% of the overstory
II[a]	0–35 years	High-severity fires replacing greater than 75% of the dominant overstory vegetation
III	35–200 years	Generally mixed-severity, can also include low-severity fires
IV	35–200 years	High-severity fires
V	200+ years	Generally replacement-severity, can include any severity type in this frequency range

[a] There are no forested biophysical settings classified as Fire Regime Group II within our analysis regions.

2.2.4. Present-day forest structure and composition

We characterized present-day forest vegetation with the gradient nearest neighbor imputation (GNN; Ohmann and Gregory, 2002) datasets produced by the US Forest Service Pacific Northwest Research Station and Oregon State University Landscape Ecology, Modeling, Mapping, and Analysis research group (www.fsl.orst.edu/lemma). The 30 m pixel GNN datasets derive from a process integrating regional inventory field plots, environmental gradients, and Landsat imagery. Within Oregon and Washington the GNN datasets have become a common regional-scale measurement of present-day forest conditions (Moeur et al., 2011). Due to the Landsat imagery used to produce the GNN datasets "present-day" is year 2006 within southwest Oregon, eastern Oregon Cascades, and eastern Washington Cascades and year 2000 in all other map zones (Fig. 1).

To compare present-day forest vegetation to the NRV reference conditions, we mapped the current distribution of s-classes for each biophysical setting using GNN data. S-class mapping was based upon tree canopy cover and tree size thresholds provided for each s-class in the biophysical setting model descriptions (Appendix A.2). Quadratic mean diameter has been used in previous applications of the GNN data to classify forest size class (Moeur et al., 2011). However, simply using the GNN dataset's reported quadratic mean diameter to represent forest stand size class has been found to over represent the abundance of large and extra-large size class stands in eastern Oregon and Washington forests (M. Hemstrom and K. Mellen-McLean personal observations). Consequently, we used total canopy cover accounting for canopy overlap, and a combination of canopy cover and trees per acre by size class to classify GNN data into successional stages. We first applied a customized decision process developed to assign one of the 7 regional forest stand size classes (USDA Forest Service, 2004) to each pixel based on the GNN plot-related attributes of trees per acre by diameter class and canopy cover by diameter class (Appendix A.4). We then assigned biophysical setting s-classes by size class and total canopy cover. The first two steps of the size class decision process sets a density threshold for the number of trees >50.8 cm or >76.2 cm diameter breast height in order for a pixel to be classified as large or extra-large, respectively. These threshold values vary by biophysical setting from approximately 20–50 trees per hectare and were determined by US Forest Service Pacific Northwest Region Ecology Program specialists. We evaluated our "GNN size class decision process" using stand exam and forest inventory and analysis plot data from the Mahleur National Forest. Estimated abundance of large and very large size classes using our "GNN size class decision process" were very close to levels based stand exam and plot data (76,897 ha. versus 74,244 ha respectively; M. Hemstrom unpublished data). In contrast, simply applying the GNN dataset's quadratic mean diameter measure grossly overestimates the abundance of large and very large size classes (234,327 ha; M. Hemstrom unpublished data) compared to stand exam and plot data. All size class and s-class assignments were made using custom Python scripts (Python Software Foundation) within ArcMap 10.1 (Environmental Systems Resources Institute, 2013).

2.3. Forest restoration needs analysis

We assessed forest restoration needs based on the present-day relative abundance of s-classes compared to NRV reference conditions. Within each biophysical setting and landscape unit (stratum), we determined which s-classes were overrepresented and which were underrepresented, then how many hectares would need to transition to a different s-class in order to move the present-day distribution of all s-classes to within the NRV reference distribution (mean ± 2 SD). We categorized these specific transitions between s-classes as resulting from implementation of "disturbance only", "succession only", or "disturbance then succession" restoration categories based upon the identity of the excess and deficit classes (Fig. 2). Our analysis considered the following possible restoration categories and the resulting transitions between s-classes.

2.3.1. Disturbance only

- **Thinning/low severity fire**: Transitions between mid and late development closed canopy to open canopy s-classes through the removal of small and medium sized trees. May be accomplished through fire or mechanical treatment.
- **Opening/high severity fire**: Transition from any mid or late development s-class to "Early Development" through removal of the major proportion of medium and large trees, generally to create a clearing. May be accomplished through fire or mechanical treatment.
- **Overstory Thinning**: Transition from late development to mid development open canopy s-class through removal of overstory cohort trees and retention of smaller understory cohort trees. This transition is likely to be accomplished through mechanical treatment, insects, or disease.

2.3.2. Disturbance then succession

- **Thinning/low fire + grow with fire**: This is a two-step transition that first requires fire or mechanical treatment to transition from mid development closed canopy to mid development open canopy followed by growth with fire to transition to a late development open canopy s-class.
- **Other disturbance + growth**: Transition to mid development closed canopy from any other mid or late development s-class. The specific pathway of this uncommon transition varies by biophysical setting, but includes both disturbance and growth for all biophysical settings.

2.3.3. Succession only

- **Growth with fire**: Transitions from "Early Development" to "Mid Development Open Canopy" or from "Mid Development Open Canopy" to "Late Development Open Canopy" in Fire Regime Group I or III biophysical settings. These transitions are considered succession only as fire disturbance is not immediate required to alter the successional trajectory.
- **Growth without fire**: All other transitions from earlier to later development s-classes, typically maintaining or resulting in a closed canopy

We defined all possible transitions between s-classes within each biophysical setting (Fig. 2) described in terms of the unique characteristics of each biophysical setting's state-and-transition model and s-class descriptions. All transition definitions for a biophysical setting are captured in that setting's "rules table" (Table 2, Appendix A.5). When a transition between s-classes required more than one discrete step based upon that biophysical setting's state-transition model, we defined both a "primary" and a "secondary" transition (Fig. 2 and Table 2).

The restoration needs calculations were conducted in a stepwise fashion for each strata. For each strata, we first calculated the excess or deficit abundance of each s-class when compared to that biophysical settings' NRV reference condition. In order to incorporate the full range of conditions represented by NRV, excesses are calculated from the upper edge (mean + 2 SD) of the biophysical setting's NRV while deficits are calculated from the lower edge (mean – 2 SD; Fig. 3). Using the upper and lower edges of NRV provides a more conservative estimate of restoration need based upon the variability a biophysical setting may experience over time. Based upon the first transition (e.g. row 1) in that biophysical setting's rules table (Table 2) we determined if there was an over-abundance of hectares in the "excess" s-class and an under abundance in the "deficit"

		Deficit S-Class *Currently under-represented compared to reference condition*				
Excess S-Class *Currently over-represented compared to reference condition*		Early Devl.	Mid Closed	Mid Open	Late Open	Late Closed
	Early Devl.		Grow without fire	Grow with fire	Grow with fire	Grow without fire
	Mid Closed	Opening / high fire		Thin / low fire	Thin / low fire + grow with fire	Grow without fire
	Mid Open	Opening / high fire	Other disturbance + growth		Grow with fire	Grow without fire
	Late Open	Opening / high fire	Other disturbance + growth	Overstory thinning		Grow without fire
	Late Closed	Opening / high fire	Other disturbance + growth	Overstory thinning	Thin / low fire	

= Disturbance Only
= Succession Only
= Disturbance then Succession

Fig. 2. Default transitions used in calculations of forest structure restoration need. If there is an excess in the vertical s-class and a deficit in the horizontal s-class for particular strata (biophysical setting × landscape unit), then each intersecting cell represents the hypothetical transition needed to restore forest structure to the Natural Range of Variability (NRV). See Appendix A.3 for NRV reference conditions for each biophysical setting and Appendix A.5 for specific restoration transition definitions for each biophysical setting.

s-class. If no, we skipped that transition step. If yes, we "moved" hectares from the excess to the deficit s-class, such that the deficit s-class does not become overabundant and the excess s-class does not become under abundant relative to the NRV reference condition. These "moved" hectares were then considered "restoration hectares" and were added to the tally for that particular transition category. We then recalculated the excess or deficit abundance of each s-class following the hypothetical redistribution of acres between s-class in the previous step. Based upon the second transition in that biophysical setting's rules table (row 2) we determined if there was an overabundance in the "excess" s-class and a under abundance in the "deficit" s-class. If yes, we "moved" hectares following the same procedure as for the first priority transition and added them to the tally of restoration hectares. If no, we skipped this transition step. This process was then repeated for all transition steps for all 1729 strata. Calculations were conducted using a custom Python script (Python Software Foundation) within ArcMap 10.1 (Environmental Systems Resources Institute, 2013).

We determined the order of operation for each biophysical setting's rules table based on the following logic. First we considered disturbance transitions that were analogous to the predominant historical disturbances within that setting (e.g., thin/low fire for FRG I biophysical settings). Second we considered other disturbance transitions that were less common based on the biophysical setting's historical disturbance regime. Third we considered successional transitions analogous to that setting's historical growth dynamics. Fourth we considered other multi-step disturbance treatments, and fifth we considered multi-step successional treatments. To assess the potential bias introduced by the order of transitions we compared the number of all disturbance and all successional restoration hectares per biophysical setting and landscape unit combination calculated with the specified order of operation (Appendix A.5) versus a randomized order of operation. The absolute difference (mean ± 1 SD) in all disturbance and in all succession restoration hectares was inconsequential (1.8 ± 3.5% and 2.3 ± 4.8% of total hectares respectively per biophysical setting and landscape unit, $n = 1729$).

2.4. Forest ownership and management

Understanding how restoration needs differ amongst forest ownerships and management designations is essential to an integrated landscape scale approach to ecological restoration across ownerships. We intersected our assessment of forest restoration need with forest ownership and management allocations spatial data compiled by Halofsky et al. (in press). We considered six ownership categories (US Forest Service, US Bureau of Land Management, State, Other Public, Tribal, Private), and three levels of forest management intensity (Restricted, Limited, General). Restricted management includes forests where mechanical treatments are typically not allowed, such as Wilderness Areas, National Parks, Inventory Roadless Areas, and Research Natural Areas. Limited management includes forests in which mechanical treatments may be allowed with certain limitations, such as late successional reserves. General management refers to lands where mechanical treatments are allowed.

We used an "equal distribution" approach to determine restoration need by forest ownership and management designation at the level of map zones. Our restoration need calculations provide the percentage of total hectares for each present day sub-strata (landscape unit × biophysical setting × s-class) currently "in need" of disturbance and/or successional restoration. We also determined for each present day sub-strata the number of hectares within each ownership × management designation category. We then made the assumption that the overall percentage of a sub-strata in need of each restoration need transition applied equally across ownership × management designation categories. Consequently, we calculated the number of hectares in need of each restoration need transition for each ownership × management designation × sub-strata. Finally, we summed these values to total active and growth restoration need per ownership and management designation category per map zone. We recognize in some areas with mixed federal and private lands (e.g., checkerboard ownership configurations), a more generalized and variable allocation of restoration needs by landowners could emerge.

3. Results

3.1. Regional-wide trends in forest restoration need

We found that approximately 41% (4,742,000 ha) of all coniferous forest in eastern Washington and eastern and southwestern Oregon was in need of a transition to a different s-class in order to restore forest structure to a NRV reference condition (Table 3,

Table 2
Default restoration transitions "rule table" for biophysical settings with historic low or mixed severity fire regimes. Table describes the primary and secondary actions needed to transition from the excess to the deficit s-class. See Appendix A.5 for a complete list of rules tables for each biophysical setting.

Order	Excess S-Class	Deficit S-Class	Primary Actions	Secondary Actions	Category
1	Mid closed	Mid open	Thin/low fire		Disturbance Only
2	Late closed	Late open	Thin/low fire		Disturbance Only
3	Mid closed	Late open	Thin/low fire	Grow with fire	Disturbance then Succession
4	Late open	Mid open	Overstory thinning		Disturbance Only
5	Late closed	Mid open	Overstory thinning		Disturbance Only
6	Mid closed	Early	Opening/high fire		Disturbance Only
7	Mid open	Early	Opening/high fire		Disturbance Only
8	Late open	Early	Opening/high fire		Disturbance Only
9	Late closed	Early	Opening/high fire		Disturbance Only
10	Early	Mid open	Grow w/fire		Succession Only
11	Mid open	Late open	Grow w/fire		Succession Only
12	Early	Mid closed	Grow w/o fire		Succession Only
13	Mid closed	Late closed	Grow w/o fire		Succession Only
14	Mid open	Late closed	Grow w/o fire		Succession Only
15	Late open	Late closed	Grow w/o fire		Succession Only
16	Mid open	Mid closed	Other disturbance	Growth	Disturbance then Succession
17	Late open	Mid closed	Other disturbance	Growth	Disturbance then Succession
18	Late closed	Mid closed	Other disturbance	Growth	Disturbance then Succession.
19	Early	Late open	Grow with fire	Grow with fire	Succession Only
20	Early	Late closed	Grow without fire	Grow without fire	Succession Only

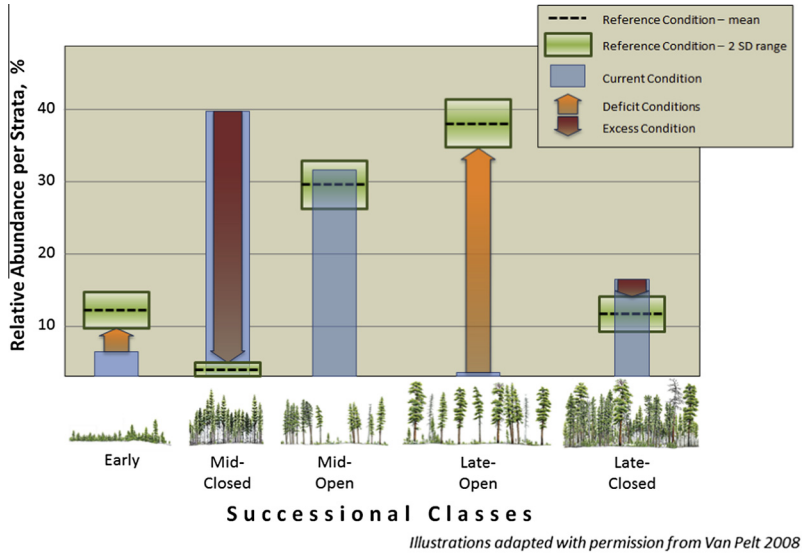


Fig. 3. Example of how the comparison of excess and deficit s-classes to natural range of variability reference conditions (NRV) are determined for a strata (biophysical setting × landscape unit). This example depicts the Dry Douglas-fir biophysical setting within the Oregon Blue Mountains – Upper Tucannon watershed (HUC 1706010706). See Appendix A.3 for NRV reference conditions for each biophysical setting. Forest illustrations adapted with permission (Van Pelt, 2008). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Figs. 4 and 5). Across these regions Disturbance then Succession was the most common restoration need category (20% of all forests, 5,678,000 ha) followed by Disturbance Only (14%, 3,920,000 ha) and Succession Only (7%, 2,120,000 ha; Table 3). On the largest individual ownership, the US Forest Service, approximately 38% (2,412,000 ha) of coniferous forests was in need of transition to a different s-class. Only (16%) of the overall restoration needs and 14% of the Disturbance Only plus Disturbance then Succession restoration needs on US Forest Service lands were within Restricted management areas. Across all US Forest Service Forests, the Disturbance Only and Disturbance then Succession categories were roughly equivalent at 15% and 17% of all national forests respectively (Table 3). Overall restoration need was higher on Bureau of Land Management, State, and Private forests (52%, 45%, and 45% of forests per respective ownership) with Disturbance then Succession, the most common restoration need category on these ownerships (Table 3).

Both the overall level and the type of restoration need varied greatly between forested biophysical settings. Specific restoration need transitions are illustrated in Fig. 2. Historical FRG 1 forests were both the most abundant (5,627,000 ha) and had the greatest overall restoration needs (2,857,000 ha, 51% of all FRG I forests, Table 4). Restoration needs within FRG I forests were dominated by the "thinning/low severity fire followed by growth" transition in the mid-development closed canopy s-class (1,695,000 ha, Table 4). We also found a substantial need for "thinning/low severity fire only" in the mid development closed canopy and late development closed canopy s-classes (390,000 and 261,000 ha respectively, Table 4). Forests historically characterized as FRG III were slightly less abundant (4,947,000 ha) and had lower overall restoration needs (33% of all FRG III forests; Table 4). "thinning/low severity fire followed by growth" in the mid-development closed canopy s-class was again the most commonly needed restoration transition (420,000 ha; Table 3). Other commonly needed transitions were "opening/high severity fire" in mid-development closed canopy s-classes (215,000 ha) and "thinning/low fire only" in late development closed canopy s-classes (223,000 ha). Historical FRG IV & V forests were the least common (1,045,000 ha) and had the lowest overall restoration needs (23% of all FRG IV & V forests, Table 4). Within FRG IV & V forests restoration needs were evenly divided between the Disturbance Only and Succession Only categories in the early and mid-development s-classes (Table 4).

3.2. Comparisons of forest restoration need among map zones

Across eastern Washington and eastern and southwestern Oregon we found the highest proportion of restoration need in the Oregon Southwest (1,321,000 ha, 51% of all forests) and

Table 3
Forest structure restoration needs by ownership for eastern Washington and eastern and southwestern Oregon. See Appendix B.2 for detailed summaries of restoration need by forest ownership–management and Map Zones.

Forest owner	Total	Disturbance only[a]		Disturbance then succession[b]		Succession only[c]	
	ha.	ha.	%	ha.	%	ha.	%
US Forest service	6,381,000	960,000	15	1,074,000	17	378,000	6
Bureau of land management	705,000	98,000	14	197,000	28	73,000	10
State	390,000	57,000	15	90,000	23	28,000	7
Other public	141,000	23,000	16	11,000	8	11,000	8
Tribal	697,000	70,000	10	143,000	20	41,000	6
Private	3,305,000	378,000	11	783,000	24	326,000	10
Total	11,619,000	1,586,000	14	2,298,000	20	858,000	7

[a] Includes the thin/low fire, opening/high fire and overstory thinning transitions.
[b] Includes the thin/low fire + growth and other disturbance + growth transitions.
[c] Includes the grow with fire and the grow without fire transitions.

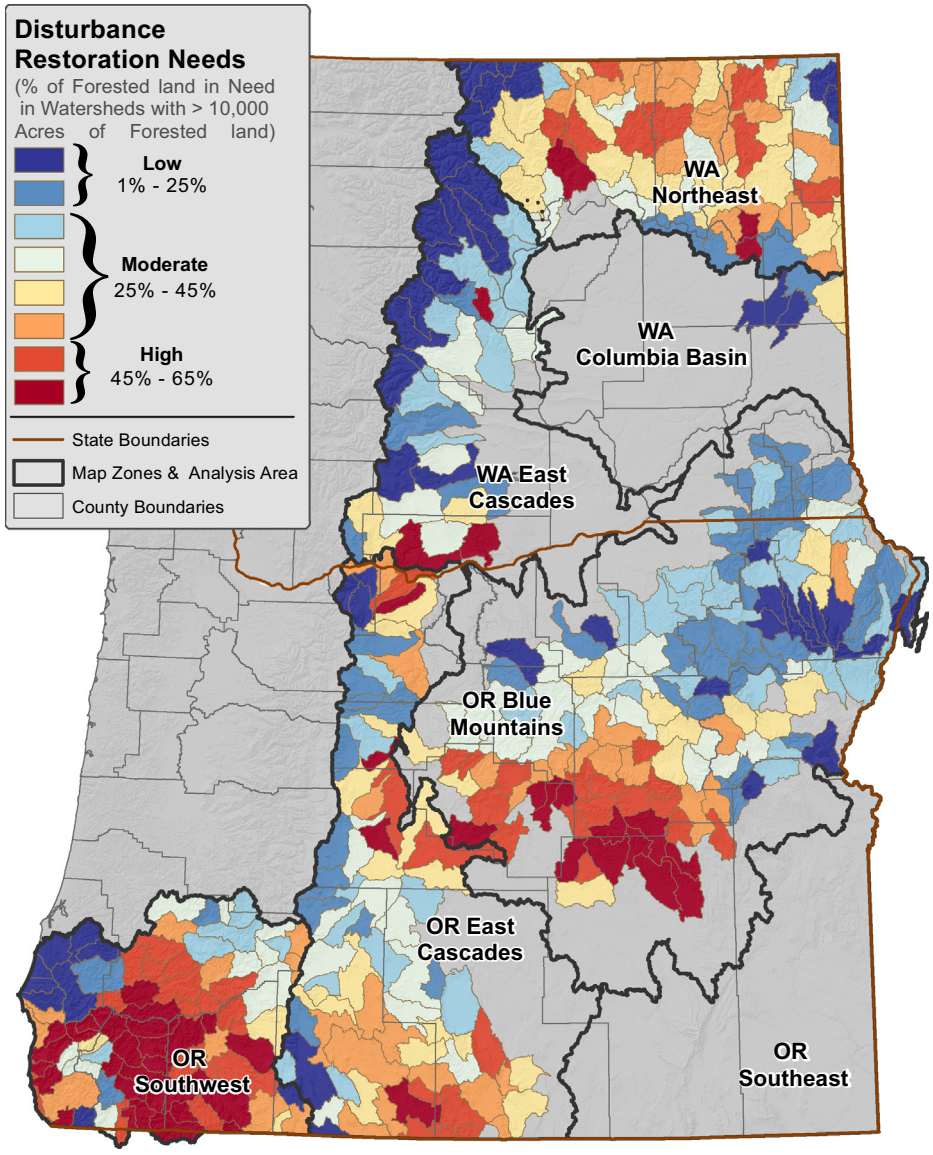


Fig. 4. All disturbance restoration needs as a percentage of forests within 10-digit/5th level hydrologic unit watersheds. Includes the thin/low fire, opening/high fire, overstory thin, thin/low fire + growth, and other disturbance + growth transitions. Within Map Zone labels WA = Washington and OR = Oregon. See Appendix B.4 for restoration need summaries per watershed.

Washington Northeast (955,000 ha, 46% of all forests) map zones (Table 5, Figs. 4 and 5). In contrast to other zones, the majority of overall Disturbance restoration needs (Disturbance Only plus Disturbance then Succession) in Oregon Southwest and Washington Northeast occurred off US Forest Service lands (Fig. 6) and were concentrated in the historically low severity fire regime forests (Fig. 7). Additionally, in both map zones the overall Succession restoration needs (Succession Only plus Disturbance then Succession) were nearly as great as the overall Mechanical/Fire restoration needs (39% vs. 33% and 23% vs. 25% of all forests in the map zone respectively; Table 5).

Compared with these map zones, the overall proportions of restoration need were slightly lower within the Oregon Blue Mountains (1,095,000 ha, 38% of all forests) and Oregon East Cascades (866,000 ha, 36% of all forests; Table 5). Restoration needs within the Oregon Blue Mountains were dominated by the Disturbance then Succession category (696,000 ha, 24% of all forests) while the Oregon East Cascades have equivalent levels of the Disturbance Only and Disturbance then Succession categories (382,000 ha, 16% and 401,000 ha, 17% respectively, Table 5). Within both zones the majority of overall Disturbance needs are on US Forest Service lands (648,000 ha, 69% and 519,000 ha, 66% respectively; Fig. 6) and were found across the FRG I and III biophysical settings (Fig. 7). This is in contrast to the Oregon Southwest and Washington Northeast zones, where sum total of needs were greatest outside the national forests.

We found the lowest overall levels of restoration need within the Washington East Cascades (476,000 ha, 30% of all forests). Similar to the Oregon East Cascades, the Washington East Cascades had equivalent levels of the Disturbance and the Disturbance then Succession (each approximately 190,000 ha/12% of all forests; Table 5). US Forest Service lands contributed only 40% (152,000 ha) of overall Disturbance restoration needs (Fig. 6), and were concentrated in the historically FRG I forests (Fig. 7).

The Oregon Southeast and Washington Columbia Basin map zones were dominated by non-forested ecosystems. Although levels of overall restoration need as a percentage of total forested area are similar to other map zones (Oregon Southeast 44%, Washington

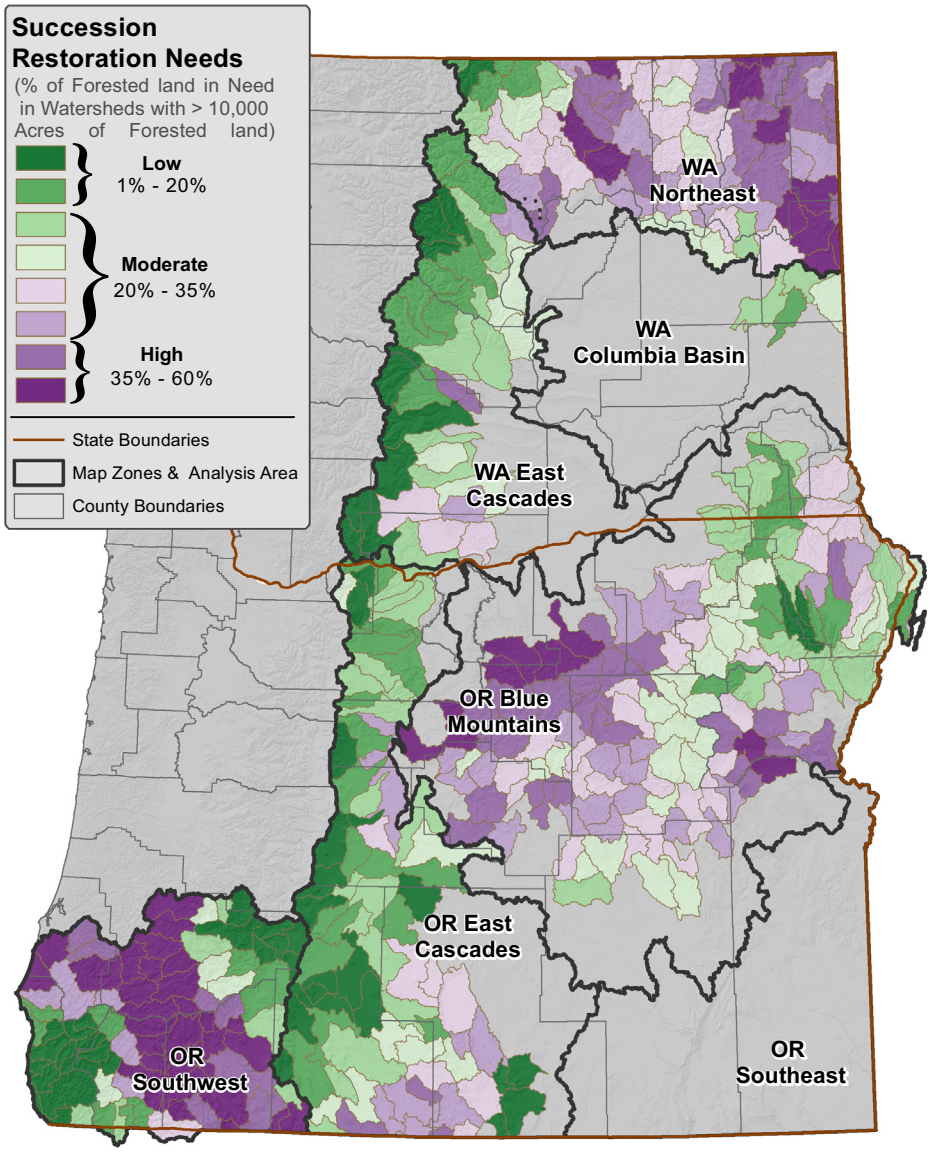


Fig. 5. All succession restoration needs as a percentage of forests within 10-digit/5th level hydrologic unit watersheds. Includes the thin/low fire + growth, other disturbance + growth, grow with fire, and grow without fire transitions. Within Map Zone labels WA = Washington and OR = Oregon. See Appendix B.4 for restoration need summaries per watershed.

Columbia Basin 37%), they contribute little to the regional-wide restoration needs (Table 5).

4. Discussion

4.1. Interpreting regional restoration needs

We found that forest structural restoration needs across eastern Washington and eastern and southwestern Oregon were dominated by the need for thinning and/or low severity fire transitions within forests historically characterized by low and mixed severity fire regimes (FRG I and III biophysical settings; Table 4). These basic findings reflect the commonly understood impacts of wildfire suppression and past management on historically fire-dependent forest ecosystems across western North America (Noss et al., 2006). However, we found substantial variation in restoration need per watershed (5th field hydrologic units) across our region with results ranging from less than 5% to greater than 80% of all forests within individual watersheds in need of disturbance transitions. The variation we observed in restoration needs was driven in large part by the distribution of forest biophysical settings, but also by patterns of forest ownership and management. We found the highest levels of restoration need at both map zone and watershed scales in locations dominated by FRG I biophysical settings and with forest ownerships that likely focused primarily on timber production, resulting in a preponderance of early and mid-development closed canopy successional classes.

Within the vast majority of the watersheds we evaluated, disturbance alone cannot restore NRV forest structure. Deficits in late development forest structure were clearly evident; succession into later development s-classes was required in over half (66%) of the total restoration needs across the region. However, the predominant late development successional classes and the successional pathways to these classes vary amongst biophysical settings and may require repeated disturbances. The map zones with the highest proportion of overall disturbance needs (Oregon Southwest and Washington Northeast) also had the highest successional restoration

Table 4
Forest structure restoration need transitions by forested biophysical setting historical fire regime group's successional classes for eastern Washington and eastern and southwestern Oregon. See Appendix B.3 for detailed summaries of restoration need by forest biophysical settings and Map Zones.

S-Class	Total forest	Disturbance only			Disturbance then succession		Succession only	
		Thin/low fire	Opening/high fire	Overstory thinning	Thin/low fire + Grow	Other Disturbance + Grow	Grow with fire	Grow without fire
	ha.	ha.	ha.	ha.	ha.	ha.	ha.	ha.
FRG I – All S-Classes								
Early	625,000	0	0	0	0	0	59,000	17,000
Mid Closed	2,797,000	390,000	132,000	0	1,695,000	0	0	160,000
Mid Open	1,303,000	0	21,000	0	0	0	46,000	40,000
Late Open	144,000	0	0	0	0	0	0	0
Late Closed	758,000	261,000	10,000	27,000	0	0	0	0
FRG III – All S-Classes								
Early	586,000	0	8000[a]	0	0	0	60,000	11,000
Mid Closed	2,007,000	77,000	215,000	0	420,000	0	0	166,000
Mid Open	1,126,000	0	58,000	0	0	174,000	55,000	125,000
Late Open	136,000	0	0	0	0	0	0	0
Late Closed	1,092,000	223,000	12,000	33,000	0	1000	0	0
FRG IV & V – All S-Classes								
Early	129,000	0	0	0	0	0	4000	31,000
Mid Closed	387,000	42,000	43,000	0	0	7,000	0	54,000
Mid Open	125,000	0	0	0	0	0	0	29,000
Late Open	53,000	0	0	9000	0	0	0	0
Late Closed	353,000	0	2000	24,000	0	0	0	0
All forests total	11,619,000	993,000	500,000	94,000	2,116,000	182,000	225,000	633,000

[a] Transition between two different early successional classes within the subalpine parkland biophysical setting.

needs (Figs. 4 and 5). In most locations, restoration programs must focus on both the application of mechanical treatments and fire while also conserving and promoting old trees and late development forest structures (Franklin and Johnson, 2012; Franklin et al., 2013; Stine et al., in press).

The historical dynamics and present day management of historical mixed severity fire regime forests has received particular attention recently by the science and management communities (e.g., Halofsky et al., 2011; Perry et al., 2011; Stine et al., in press). The complex nature of mixed severity fire regimes and long history of management for many of these forests were reflected in the variety of specific restoration transitions needs that we identified for FRG III biophysical settings (Table 3). Stine et al. (in press) argue that due to greater productivity, restoration needs within historical mixed severity fire regime forests may be even greater than historical low severity fire regime forests. While we identified a greater proportion of total forested area in need of restoration within historical FRG I forests, FRG III forests may certainly be prioritized in local restoration programs due to higher site productivity and concurrent higher fuel levels, and greater risk of high severity fire and insect/disease mortality (*see* Section 4.2).

Similarly, the historic role of high severity fire and the importance of complex early seral habitats in western forested landscapes have also received significant recent attention by the science and management communities (Hutto, 2008; Swanson et al., 2011). As a proportion of overall restoration needs, the opening/high severity fire transition was most common in historically mixed and high severity fire regime forests (e.g., FRG III, IV, & V biophysical settings). All disturbance restoration need transitions in this paper, and particularly the opening/high severity fire transition, should be interpreted with respect to historical spatial patterns at patch and landscape scales. Stand level reconstructions of frequent fire forests in western North America emphasize high levels of fine scale spatial heterogeneity in the form of individual trees, tree clumps, and openings within forest stands (Churchill et al., 2013; Larson and Churchill, 2012). At landscape scales, reconstructions of historical patch sizes from the eastern Washington Cascades reveal distributions following a negative power law, with many small ($\leqslant$10s ha) and few very large patches (1000s ha+; Hessburg et al., 2007, 2000a; Perry et al., 2011). Consequently, the majority of opening/high severity transitions that we report, particularly within historical low severity fire regime forests (e.g., FRG I biophysical settings), are likely to be represented as smaller within-stand openings. Within FRG III, IV, and V biophysical settings, the opening/high severity fire transitions may also represent larger patches of early seral habitat.

4.2. Management implications

In recent years there have been numerous calls by local, state, and federal governments, agencies, and stakeholder groups to increase the pace and scale of forest restoration treatments across Oregon and Washington (State of Oregon, 2011; The Nature Conservancy, 2012; USDA Forest Service, 2013). We have identified approximately 1.7 million ha presently in need of disturbance (including disturbance then succession) to restore forest structure NRV on US Forest Service lands outside of wilderness and inventoried roadless areas (e.g., "USFS-Restricted", Appendix Table B.2). Within our analysis area the US Forest Service averaged approximately 12,000 ha per year of hazardous fuels treatments between 2004 and 2013 and had a total of nearly 19,000 ha of forest vegetation improvements in 2013 (US Forest Service Pacific Northwest Region; unpublished data). Assuming that these treatments are additive and address disturbance restoration needs identified in this study, at these treatment rates it will take over 50 years to meet the identified disturbance restoration needs on these US Forest Service lands. These assumptions are not likely to be true for all of the recorded treatments. Furthermore, this rough comparison does not take into account the extremely important influences of wildfire, managed or otherwise, and other unplanned disturbance events or the natural growth and succession of forests. The US Forest Service Pacific Northwest Region is increasing the rate of restoration treatments, notably in the Blue Mountains. For example, acres treated in the Pacific Northwest Region increased 22% from Fiscal Year 2012 to Fiscal Year 2013 (US Forest Service Pacific Northwest Region; unpublished data). Our results indicate that such an increase in treatment rate on federal forests is warranted. However, region-wide restoration needs cannot be met through focus on unreserved US Forest Service lands alone. Coordination amongst governments, agencies, and landowners and application

Table 5
Forest structure restoration need transitions by Map Zone for eastern Washington and eastern and southwestern Oregon. See Appendix B.4 for detailed summaries of restoration need by watershed.

Map zones	Total forest	Disturbance only			Disturbance then succession		Succession only	
		Thin/low fire	Opening/high fire	Overstory thinning	Thin/low fire + Grow	Other disturbance + Grow	Grow with fire	Grow without fire
	ha.	ha.	ha.	ha.	ha.	ha.	ha.	ha.
Oregon Blue Mtns.	2,907,000	91,000	149,000	1,000	554,000	142,000	74,000	84,000
Oregon East Cascades	2,379,000	267,000	101,000	14,000	370,000	31,000	37,000	46,000
Oregon Southeast	17,000	0	0	0	3000	0	4000	1000
Oregon Southwest	2,616,000	352,000	79,000	67,000	534,000	1,000	24,000	263,000
Oregon Totals[a]	**7,919,000**	**711,000**	**329,000**	**82,000**	**1,462,000**	**175,000**	**138,000**	**394,000**
Washington Columbia Basin	54,000	7000	1000	0	5000	0	6000	1000
Washington East Cascades	1,575,000	125,000	49,000	12,000	188,000	6000	52,000	44,000
Washington Northeast	2,071,000	150,000	120,000	0	462,000	1000	29,000	194,000
Washington totals	**3,700,000**	**282,000**	**171,000**	**12,000**	**654,000**	**7000**	**87,000**	**239,000**

[a] Includes the portions of the Oregon Blue Mountains map zone within Washington State political boundaries.

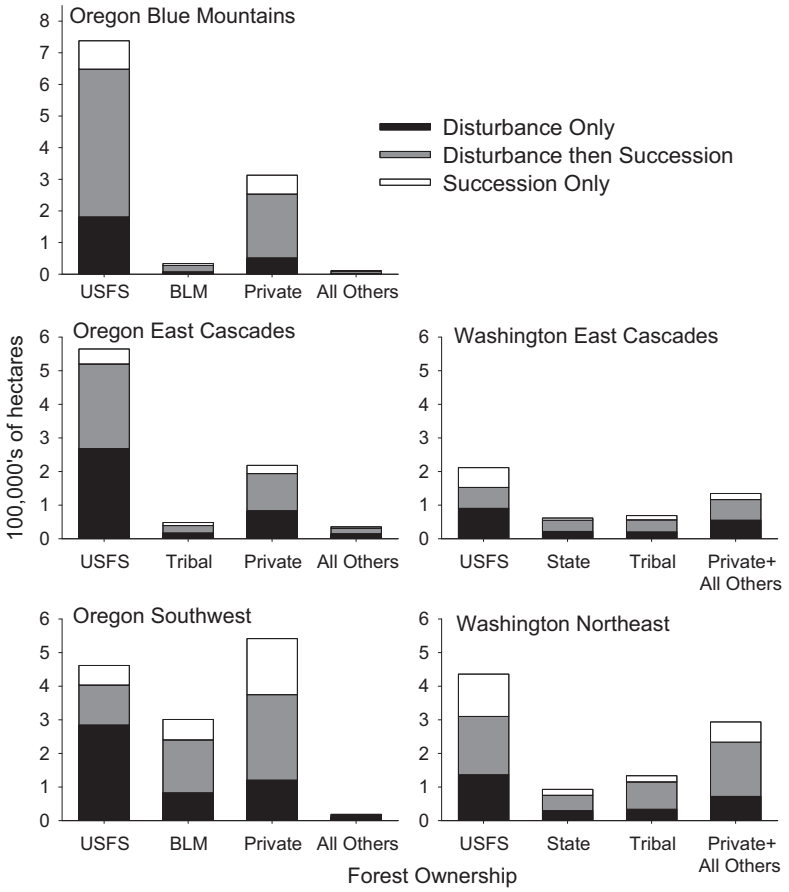


Fig. 6. Forest structure restoration needs by forest ownership per Map Zone for eastern Washington and eastern and southwestern Oregon. USFS = US Forest Service. BLM = US Bureau of Land Management. "Disturbance Only" includes the thin/low fire, opening/high fire and overstory thinning transitions. "Disturbance then Succession" includes the thin/low fire + growth and other disturbance + growth transitions. "Succession only" includes the grow with fire and grow without fire transitions. See Appendix B.2 for detailed summaries of restoration need by forest ownership–management and Map Zones.

of the entire "toolbox" (e.g., mechanical treatments, prescribed fire, managed wildfire, protection) will be required.

A primary motivation behind this study is to facilitate the ability of local land managers to incorporate regional scale, multi-ownership context into local forest management and restoration. This assessment, however, is not a replacement for the evaluation of local landscapes (1000s–10,000s of ha) and development of local landscape prescriptions. With that understanding, the results from this study may inform local landscape evaluations and development of local landscape restoration prescriptions (e.g., Hessburg et al., 2013). For example, our results provide managers with the ability to place local treatments within regional context based on relative restoration needs by biophysical settings and s-classes (Appendix B.3). Land managers may also use our results to estimate and compare overall treatment need amongst potential project areas through our watershed level summaries (Appendix B.4). However, local landscape evaluations are still required to develop on the ground restoration treatments. Ideally, these local

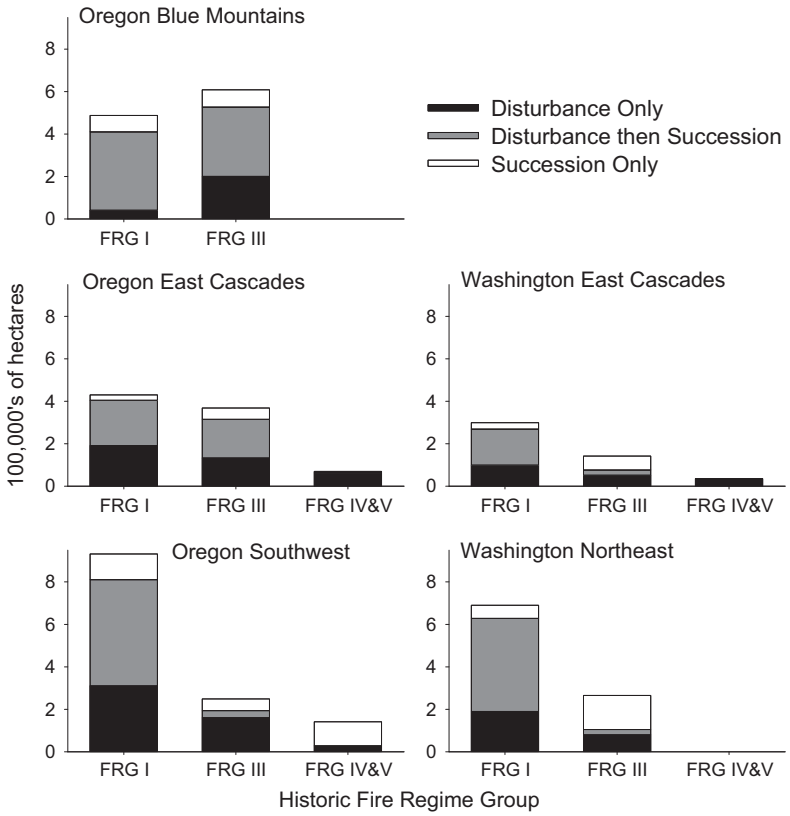


Fig. 7. Forest structure restoration need by forested biophysical setting historic fire regime groups (FRG; Table 1) per Map Zone for eastern Washington and eastern and southwestern Oregon. "Disturbance Only" includes the thin/low fire, opening/high fire and overstory thinning transitions. "Disturbance then Succession" includes the thin/low fire + growth and other disturbance + growth transitions. "Succession only" includes the grow with fire and grow without fire transitions. See Appendix B.3 for detailed summaries of restoration need by forest biophysical settings and Map Zones.

evaluations also incorporate important factors not included in our analysis such as tree species composition, forest patch size, shape, and configuration, aquatic ecosystem conditions, and specific habitat requirements. Additionally, local adjustments to the state-and-transitions models, such as changing disturbance probabilities to reflect the impact of climate, insects, disease and other natural cycles (sensu Forbis, 2006), could help refine the NRV estimates presented here. Consequently, local landscape evaluations require measurements of forest structure and composition at finer spatial resolutions (e.g., lidar, high resolution aerial photography) than are presently available for our regional scale analysis.

Forest restoration programs must consider not only patterns of vegetation and habitat, but also ecological processes such disturbance, hydrology, and migration. Our evaluation of forest restoration needs considers only half of the Fire Regime Condition Class assessment; forest structure but not contemporary fire/disturbance history (Barrett et al., 2010). However, a fundamental principle of landscape ecology is the linkage between ecological patterns and processes (Turner et al., 2001). Restoration of pattern in forested landscapes, from local to regional scales, facilitates the restoration of ecological processes. Consequently, the restoration needs identified in this study help to set the stage for the restoration of ecological processes. Finally, as better data on historical disturbance becomes available, more refined estimates of ecological departure, and associated indications for treatment, may be possible.

4.3. Appropriate uses of restoration needs results

We expect that both the results of this analysis and the conceptual framework we have introduced will be useful in providing regional context for local restoration treatments, conducting regional scale prioritizations, and assessing the scope and scale of current restoration programs. However, such uses require an understanding of the data and assumptions upon which this analysis was built. The restoration transitions we report are broad characterizations; they do not represent specific sivicultural prescriptions and are limited by both the accuracy and resolution of the current forest structure and potential vegetation type mapping we used, and by the simplified classification of each biophysical setting into five s-classes. Similarly, there are many aspects of ecological restoration, including but not limited to tree species composition and aquatic ecosystems, which our narrow focus on forest structure did not consider. Given these limitations, our results should not be interpreted below the resolution of individual watersheds (5th field hydrologic units, average ~46,000 ha).

In addition, the restoration transitions we report in this study do not directly correspond to the concepts of "active restoration" and "passive restoration" which are referenced in other discussions of forest restoration (e.g., Morrison and Lindell, 2011). Active restoration typically refers to direct intervention or manipulation, such as mechanically thinning a forest stand, whereas passive restoration typically refers to no action, such as letting a natural fire ignition burn. Yet both of these scenarios, mechanical treatment and letting a natural ignition burn, may be included in our disturbance transitions. Whether active or passive restoration means are used within a specific location to achieve identified disturbance restoration needs depends upon forest ownership and management allocation for that location. We recognize that there are many significant differences in the ecological outcomes of mechanical treatments versus prescribed fire versus wildfire (Schwilk et al., 2009). Furthermore, fire is frequently required following mechanical treatment in order to meet ecological and/or forest fuels objec-

tives (Schwilk et al., 2009). However, we consider that either mechanism is capable of achieving the coarse s-class transitions that we report in this study.

As our understanding of historical and future ecosystem dynamics, classification and mapping of biophysical settings, and measurement of current conditions across Oregon and Washington improves, new data may be incorporated into our conceptual approach to revise the results presented here. Our conceptual approach is also applicable to other regions. The basic concepts of our approach may be applied anywhere that the foundational inputs of biophysical setting classification and mapping, reference conditions, landscape units, and mapping of current conditions is available. There is great value having a consistent approach to evaluating where, how much, and what kinds of forest restoration are needed across regional scales.

Acknowledgements

We thank Darren Borgias, Miles Hemstrom, Rick Brown, Kerry Metlen, Reese Lolley, Tom Sensenig, and Patricia Hochalter, and two anonymous reviewers for providing helpful feedback during development of the potential vegetation type – biophysical setting crosswalk and on earlier versions of this manuscript. Funding was provided by the US Forest Service Pacific Northwest Region, The Nature Conservancy in Oregon, The Nature Conservancy in Washington, and the Icicle Fund.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.09.014.

References

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC.

Agee, J.K., 2003. Historical range of variability in eastern Cascades forests, Washington, USA. Landsc. Ecol. 18, 725–740. http://dx.doi.org/10.1023/B:LAND.0000014474.49803.f9.

Barrett, S., Havlina, D., Jones, J., Hann, W.J., Frame, C., Hamilton, D., Schon, K., DeMeo, T., Hutter, L., Menakis, J., 2010. Interagency Fire Regime Condition Class (FRCC) Guidebook, version 3.0. In: USDA Forest Service, US Department of the Interior, and The Nature Conservancy. <http://www.frcc.gov/>.

Brown, R.T., Agee, J.K., Franklin, J.F., 2004. Forest restoration and fire: principles in the context of place. Conserv. Biol. 18, 903–912. http://dx.doi.org/10.1111/j.1523-1739.2004.521_1.x.

Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, J.F., Hessburg, P.F., Lutz, J.A., 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. For. Ecol. Manage. 291, 442–457. http://dx.doi.org/10.1016/j.foreco.2012.11.007.

Environmental Systems Resources Institute, 2013. ArcGIS Desktop 10.1. In: ESRI, Redlands, CA.

ESSA Technologies, L., 2007. Vegetation Dynamics Development Tool User Guide, Version 6.0. In: ESSA Technologies Ltd., Vancouver, BC, p. 196.

Everett, R.L., Schellhaas, R., Keenum, D., Spurbeck, D., Ohlson, P., 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. For. Ecol. Manage. 129, 207–225. http://dx.doi.org/10.1016/S0378-1127(99)00168-1.

Forbis, T., Provencher, L., Frid, L., Medlyn, G., 2006. Environ. Manage. 38 (1), 62–83. http://dx.doi.org/10.1007/s00267-005-0089-2.

Franklin, J.F., Dyrness, C.T., 1973. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR.

Franklin, J.F., Johnson, K.N., 2012. A restoration framework for federal forests in the Pacific Northwest. J. For. 110, 429–439.

Franklin, J.F., Hemstrom, M.A., Van Pelt, R., Buchanan, J.B., Hull, S., 2008. The case for active management of dry forest types in eastern Washington: perpetuating and creating old forest structures and functions. In: Washington Department of Natural Resources, Olympia, Washington, p. 105.

Franklin, J.F., Johnson, K.N., Churchill, D., Hagmann, K., Johnson, D., Johnson, J., 2013. Restoration of dry forests in eastern Oregon: a field guide. The Nature Conservancy, Portland, OR.

Gartner, S., Reynolds, K.M., Hessburg, P.F., Hummel, S., Twery, M., 2008. Decision support for evaluating landscape departure and prioritizing forest management activities in a changing environment. For. Ecol. Manage. 256, 1666–1676. http://dx.doi.org/10.1016/j.foreco.2008.05.053.

Hagmann, R.K., Franklin, J.F., Johnson, N.K., 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. For. Ecol. Manage. 304, 492–504. http://dx.doi.org/10.1016/j.foreco.2013.04.005.

Halofsky, J.E., Donato, D.C., Hibbs, D.E., Campbell, J.L., Donaghy Cannon, M., Fontaine, J.B., Thompson, J.R., Anthony, R.G., Bormann, B.T., Kayes, L.J., Law, B.E., Peterson, D.L., Spies, T.A., 2011. Mixed-severity fire regimes: lessons and hypotheses from the Klamath-Siskiyou Ecoregion. Ecosphere 2, art40. http://dx.doi.org/10.1890/ES10-00184.1.

Halofsky, J.E., Creutzburg, M.K., Hemstrom, M.A., in press. Integrating social, economic, and ecological values across large landscapes. In: General Technical Report, US Department of Agriculture Forest Service, Pacific Northwest Research Station. Portland, OR.

Hann, W.J., Bunnell, D.L., 2001. Fire and land management planning and implementation across multiple scales. Int. J. Wildland Fire 10, 389–403. http://dx.doi.org/10.1071/WF01037.

Hardy, C.C., Schmidt, K.M., Menakis, J.P., Sampson, R.N., 2001. Spatial data for national fire planning and fuel management. Int. J. Wildland Fire 10, 353–372.

Haugo, R.D., Hall, S.A., Gray, E.M., Gonzales, P., Bakker, J.D., 2010. Influences of climate, fire, grazing, and logging on woody species composition along an elevation gradient in the eastern Cascades, Washington. For. Ecol. Manage. 260, 2204–2213. http://dx.doi.org/10.1016/j.foreco.2010.09.021.

Henderson, J.A., Lesher, R.D., Peter, D.H., Ringo, C.D., 2011. A landscape model for predicting potential natural vegetation of the Olympic Peninsula USA using boundary equations and newly developed environmental variables. In: General Technical Report PNW-GTR-841. USDA Forest Service, Pacific Northwest Research Station. Portland, OR.

Hessburg, P.F., Agee, J.K., 2003. An environmental narrative of Inland Northwest United States forests, 1800–2000. For. Ecol. Manage. 178, 23–59. http://dx.doi.org/10.1016/s0378-1127(03)00052-5.

Hessburg, P., Smith, B.G., Kreiter, S.D., Miller, C.A., Salter, R.B., McNicoll, C.H., Hann, W.J., 1999. Historical and Current Forest and Range Landscapes in the Interior Columbia River Basin and Portions of the Klamath and Great Basins. Part 1: Linking Vegetation Patterns and Landscape Vulnerability to Potential Insect and Pathogen Disturbances. In: PNW-GTR-458. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Hessburg, P.F., Smith, B.G., Kreiter, S.D., Millar, C.I., McNicoll, C.H., Wasienko-Holland, M., 2000a. Classifying plant series-level forest potential vegetation types: methods for subbasins sampled in the midscale assessment of the interior Columbia Basin. In: Research Paper PNW-RP-54. US Department of Agriculture Forest Service, Pacific Northwest Research Station. Portland, OR.

Hessburg, P.F., Smith, B.G., Salter, R.B., Ottmar, R.D., Alvarado, E., 2000b. Recent changes (1930s–1990s) in spatial patterns of interior northwest forests, USA. For. Ecol. Manage. 136, 53–83. http://dx.doi.org/10.1016/S0378-1127(99)00263-7.

Hessburg, P.F., Agee, J.K., Franklin, J.F., 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. For. Ecol. Manage. 211, 117–139. http://dx.doi.org/10.1016/j.foreco.2005.02.016.

Hessburg, P.F., Reynolds, K.M., Keane, R.E., James, K.M., Salter, R.B., 2007. Evaluating wildland fire danger and prioritizing vegetation and fuels treatments. For. Ecol. Manage. 247, 1–17. http://dx.doi.org/10.1016/j.foreco.2007.03.068.

Hessburg, P.F., Reynolds, K.M., Salter, R.B., Dickinson, J.D., Gaines, W.L., Harrod, R.J., 2013. Landscape evaluation for restoration planning on the Okanogan-Wenatchee National Forest, USA. Sustainability 5, 805–840. http://dx.doi.org/10.3390/su5030805.

Heyerdahl, E.K., Loehman, R.A., Falk, D.A., 2014. Mixed-severity fire in lodgepole pine dominated forests: are historical regimes sustainable on Oregon's Pumice Plateau, USA? Can. J. For. Res.-Rev. Can. Rech. For. 44, 593–603. http://dx.doi.org/10.1139/cjfr-2013-0413.

Hutto, R.L., 2008. The ecological importance of severe wildfires: some like it hot. Ecol. Appl. 18, 1827–1834. http://dx.doi.org/10.1890/08-0895.1.

Johnson, D.H., O'Neil, T.A. (Eds.), 2001. Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis, OR.

Karau, E.C., Keane, R.E., 2007. Determining landscape extent for succession and disturbance simulation modeling. Landsc. Ecol. 22, 993–1006. http://dx.doi.org/10.1007/s10980-007-9081-y.

Keane, R.E., Parsons, R.A., Hessburg, P.F., 2002. Estimating historical range and variation of landscape patch dynamics: limitations of the simulation approach. Ecol. Model. 151, 29–49. http://dx.doi.org/10.1016/S0304-3800(01)00470-7.

Keane, R.E., Rollins, M.G., Zhu, Z.L., 2007. Using simulated historical time series to prioritize fuel treatments on landscapes across the United States: the LANDFIRE prototype project. Ecol. Model. 204, 485–502. http://dx.doi.org/10.1016/j.ecolmodel.2007.02.005.

Keane, R.E., Hessburg, P.F., Landres, P.B., Swanson, F.J., 2009. The use of historical range and variability (HRV) in landscape management. For. Ecol. Manage. 258, 1025–1037. http://dx.doi.org/10.1016/j.foreco.2009.05.035.

Keane, R.E., Holsinger, L.M., Parsons, R.A., 2011. Evaluating indices that measure departure of current landscape composition from historical conditions. In: RMRS-RP-83. US Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins CO.

Landres, P.B., Morgan, P., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol. Appl. 9, 179–1188. http://dx.doi.org/10.2307/2641389.

Larson, A.J., Churchill, D., 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and

implications for designing fuel reduction and restoration treatments. For. Ecol. Manage. 267, 74–92. http://dx.doi.org/10.1016/j.foreco.2011.11.038.
Low, G., Provencher, L., Abele, S.L., 2010. Enhanced conservation action planning: assessing land-scape condition and predicting benefits of conservation strategies. J. Cosnser. Plan. 6, 36–60.
Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17, 2145–2151. http://dx.doi.org/10.1890/06-1715.1.
Moeur, M., Ohmann, J.L., Kennedy, R.E., Cohen, W.B., Gregory, M.J., Yang, Z., Roberts, H.M., Spies, T.A., Fiorella, M., 2011. Northwest Forest Plan, the first 15 years (1994–2008): Status and trends of late-successional and old-growth forests. In: General Technical Report PNW-GTR-853. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.
Morgan, P., Aplet, G.H., Haufler, J.B., Humphries, H.C., Moore, M.M., Wilson, W.D., 1994. Historical range of variability: a useful tool for evaluating ecosystem change. J. Sustain. For. 2, 87–111.
Morrison, E.B., Lindell, C.A., 2011. Active or passive forest restoration? Assessing restoration alternatives with avian foraging behavior. Restor. Ecol. 19, 170–177. http://dx.doi.org/10.1111/j.1526-100X.2010.00725.x.
North, M., Stine, P., O'Hara, K., Zielinski, W., Stephens, S.L., 2009. An ecosystem management strategy for sierran mixed-conifer forests. In: PSW-GTR-220. US Department of Agriculture, Pacific Southwest Research Station, Albany, CA.
Noss, R., Franklin, J.F., Baker, W.L., Schoennagel, T., Moyle, P., 2006. Managing fire-prone forests in the western United States. Front. Ecol. Environ. 4, 481–487. http://dx.doi.org/10.1890/1540-9295(2006) 4[481:MFFITW]2.0.CO;2.
Ohmann, J.L., Gregory, M.J., 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, U.S.A. Can. J. For. Res.-Rev. Can. Rech. For. 32, 725–741. http://dx.doi.org/10.1139/X02-011.
Perry, D.A., Hessburg, P., Skinner, C.N., Spies, T.A., Stephens, S.L., Taylor, A.H., Franklin, J., McComb, B., Riegel, G., 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. For. Ecol. Manage. 262, 703–717. http://dx.doi.org/10.1016/j.foreco.2011.05.004.
Peterson, D.L., Johnson, M.C., Agee, J.K., Jain, T.B., McKenzie, D., Reinhard, E.D., 2005. Forest structure and fire hazard in dry forests of the western United States. In: USDA Forest Service General Technical Report PNW-GTR-628.
Pratt, S.D., Holsinger, L.M., Keane, R.E., 2006. Using simulation modeling to assess historical reference conditions for vegetation and fire regimes for the LANDFIRE prototype project. In: Rollins, M.G., Frame, C.K. (Eds.), The LANDFIRE Prototype Project: Nationally Consistent and Locally Relevant Geospatial Data for Wildland Fire Management. General Technical Report RMRS-GTR-175. US Department of Agriculture Forest Service, Rocky Mountain Research Station. Fort Collins CO.
Provencher, L., Campbell, J.L., Nachlinger, J., 2008. Implementation of mid-scale fire regime condition class mapping. Int. J. Wildland Fire 17, 390–406. http://dx.doi.org/10.1071/WF07066.
Python Software Foundation, Python Language Reference, version 2.7.2. <http://www.python.org>.
Rasmussen, M., Lord, R., Vickery, B., McKetta, C., Green, D., Green, M., Hemstrom, M.A., Potiowsky, T., 2012. National forest health restoration an economic assessment of forest restoration on Oregon's eastside national forests. In: Prepared for Governor John Kitzhaber and Oregon's Legislative Leaders, p. 84.
Rollins, M.G., 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. Int. J. Wildland Fire 18, 235–249. http://dx.doi.org/10.1071/WF08088.
Ryan, K.C., Opperman, T.S., 2013. LANDFIRE – a national vegetation/fuels data base for use in fuels treatment, restoration, and suppression planning. For. Ecol. Manage.. http://dx.doi.org/10.1016/j.foreco.2012.11.003.
Schoennagel, T., Veblen, T.T., Romme, W.H., 2004. The interaction of fire, fuels and climate across Rocky Mountain forests. Bioscience 661, 661–676, 10.1641/0006-3568(2004)054[0661:TIOFFA]2.0.CO;2.
Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J., Bailey, J.D., Fettig, C., Fiedler, C.E., Harrod, R.J., Moghaddas, J.J., Outcalt, K.W., Skinner, C.N., Stephens, S.L., Waldrop, T.H., Yaussy, D.A., Youngblood, A., 2009. The national fire and fire surrogate study: effects of fuel reduction methods on vegetation structure and fuels. Ecol. Appl. 19, 285–304. http://dx.doi.org/10.1890/07-1747.1.
SER, 2004. The SER international primer on ecological restoration, version 2. In: Society for Ecological Restoration Science and Policy Working Group.
Shlisky, A.J., Guyette, R.P., Ryan, K.C., 2005. Modeling reference conditions to restore altered fire regimes in oak-hickory-pine forests: validating coarse models with local fire history data. In: EastFire Conference Proceedings. George Mason University, Fairfax, VA, May 12–13, 2005.
Simley, J.D., Carswell Jr., W.J., 2009. The national map – hydrography. In: U.S. Geological Survey Fact Sheet 2009–3054. <http://nhd.usgs.gov>.
Simpson, M., 2007. Forested plant associations of the Oregon East Cascades. In: Technical Paper R6-NR-ECOL-TP-03-207. US Department of Agriculture Forest Service, Pacific Northwest Region. Portland, OR.
State of Oregon, 2011. Oregon business plan: Forest management and biomass, 2011 summary of progress. In: Oregon Solutions. <http://orsolutions.org/wp-content/uploads/2012/01/Forestry-2011-Accomplishments-and-2012-Initiatives.pdf>.
Stephens, S.L., Agee, J.K., Fule, P.Z., North, M.P., Romme, W.H., Swetnam, T.W., Turner, M.G., 2013. Managing forests and fire in changing climates. Science 342, 41–42. http://dx.doi.org/10.1126/science.1240294.
Stine, P., Hessburg, P., Spies, T.A., Kramer, M., Fettig, C., Hansen, A., Lehmkuhl, J.F., O'Hara, K., Polivka, K., Singleton, P.H., Charnley, S., Merschel, A., in press. The ecology and management of moist mixed-conifer forests in eastern Oregon and Washington: a synthesis of relevant biophysical science and implications for future land management. In: General Technical Report, USDA Forest Service Pacific Northwest Research Station, Portland, OR.
Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., Dellasala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2011. The forgotten state of forest succession: early-successional ecosystems on forest sites. Front. Ecol. Environ. 9, 117–125. http://dx.doi.org/10.1890/090157.
The Nature Conservancy, 2012. Press Release. In: The Nature Conservancy, Arlington, VA. <http://www.nature.org/ourinitiatives/habitats/forests/newsroom/conservancy-applauds-forest-service.xml>.
Turner, M.G., Gardner, R.H., O'Neill, R.V., 2001. Landscape Ecology, in theory and practice. Springer, New York.
USDA Forest Service, 2004. Standards for mapping of vegetation in the Pacific Northwest Region. In: USDA Forest Service Pacific Northwest Region, Portland, OR, p. 22.
USDA Forest Service, 2011a. Watershed Condition Framework: a framework for assessing and tracking changes in watershed condition. FS-977. In: US Department of Agriculture Forest Service, Washington, DC.
USDA Forest Service, 2011b. Western Bark Beetle Strategy: human safety, recovery and resiliency. In: US Department of Agriculture Forest Service, Washington DC.
USDA Forest Service, 2012a. 36 CFR Part 219. National Forest system land management planning. Fed. Reg. 77, 21162–21276.
USDA Forest Service, 2012b. Increasing the pace of restoration and job creation on our National Forests. In: US Department of Agriculture Forest Service, Washington DC.
USDA Forest Service, 2013. Restoration of fire-dependent forest: a sense of urgency. In: USDA Forest Service Pacific Northwest Region, Portland, OR. <http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5423599.pdf>.
Van Pelt, R., 2008. Identifying Old Trees and Forests in Eastern Washington. Washington State Department of Natural Resources, Olympia, WA.
Weisz, R., Tripeke, J., Truman, R., 2009. Evaluating the ecological sustainability of a ponderosa pine ecosystem on the Kaibab Plateau in Northern Arizona. Fire Ecol. 5, 100–114.
Wimberly, M.C., Spies, T.A., Long, C.J., Whitlock, C., 2000. Simulating historical variability in the amount of old forest in the Oregon Coast Range. Conserv. Biol. 14, 167–180. http://dx.doi.org/10.1046/j.1523-1739.2000.98284.x.
Wright, C.S., Agee, J.K., 2004. Fire and vegetation history in the eastern Cascade Mountains, Washington. Ecol. Appl. 14, 443–459. http://dx.doi.org/10.1890/02-5349.

Check for updates

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Ecological Applications, 31(8), 2021, e02432
© 2021 The Authors. *Ecological Applications* published by Wiley Periodicals LLC on behalf of Ecological Society of America. This article has been contributed to by US Government employees and their work is in the public domain in the USA
This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

Wildfire and climate change adaptation of western North American forests: a case for intentional management

Paul F. Hessburg [1,2,6], Susan J. Prichard [2], R. Keala Hagmann [2,3], Nicholas A. Povak [1,4] and Frank K. Lake[5]

[1]*USDA-FS, Pacific Northwest Research Station, 1133 N. Western Avenue, Wenatchee, Washington 98801 USA*
[2]*College of the Environment-SEFS, University of Washington, Seattle, Washington 98195 USA*
[3]*Applegate Forestry LLC, Corvallis, Oregon 97330 USA*
[4]*USDA-FS, Pacific Southwest Research Station, 2480 Carson Road, Placerville, California 95667 USA*
[5]*USDA-FS, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, California 95521 USA*

Citation: Hessburg, P. F., S. J. Prichard, R. K. Hagmann, N. A. Povak, and F. K. Lake. 2021. Wildfire and climate change adaptation of western North American forests: a case for intentional management. Ecological Applications 31(8):e02432. 10.1002/eap.2432

Abstract. Forest landscapes across western North America (wNA) have experienced extensive changes over the last two centuries, while climatic warming has become a global reality over the last four decades. Resulting interactions between historical increases in forested area and density and recent rapid warming, increasing insect mortality, and wildfire burned areas, are now leading to substantial abrupt landscape alterations. These outcomes are forcing forest planners and managers to identify strategies that can modify future outcomes that are ecologically and/or socially undesirable. Past forest management, including widespread harvest of fire- and climate-tolerant large old trees and old forests, fire exclusion (both Indigenous and lightning ignitions), and highly effective wildfire suppression have contributed to the current state of wNA forests. These practices were successful at meeting short-term demands, but they match poorly to modern realities. Hagmann et al. review a century of observations and multiscale, multi-proxy, research evidence that details widespread changes in forested landscapes and wildfire regimes since the influx of European colonists. Over the preceding 10 millennia, large areas of wNA were already settled and proactively managed with intentional burning by Indigenous tribes. Prichard et al. then review the research on management practices historically applied by Indigenous tribes and currently applied by some managers to intentionally manage forests for resilient conditions. They address 10 questions surrounding the application and relevance of these management practices. Here, we highlight the main findings of both papers and offer recommendations for management. We discuss progress paralysis that often occurs with strict adherence to the *precautionary principle*; offer insights for dealing with the common problem of irreducible uncertainty and suggestions for reframing management and policy direction; and identify key knowledge gaps and research needs.

Key words: Climate Change and Western Wildfires; climate warming; forest landscape changes; Indigenous fire use; landscape realignment; landscape resilience; landscape resistance; social-ecological systems; wildfire regime changes.

Introduction

Western forests are rapidly changing

Starting in the mid-1980s, area burned in seasonally dry forests of western North America (wNA) began a steady rise (Westerling et al. 2006), despite increasing investment in fire suppression (Calkin et al. 2005). Seasonally dry forests are those pine, dry or moist mixed-conifer, and cold forests that are available to burn most years during the wildfire season (refer to forest type definitions and discussion in Hessburg et al. 2019). Increased burned area is attributed to combinations of warmer seasonal temperatures, longer wildfire seasons, drier summers, below-average winter precipitation and earlier snowmelt, and increasing human ignitions (Westerling et al. 2006, Morgan et al. 2008). The incidence of large wildfires has likewise increased across wNA over the last three decades (Schoennagel et al. 2017, Parks and Abatzoglou 2020), while burned area in the Inland Northwest and American Southwest has risen most noticeably over the last two decades (Westerling 2016). These increases are occurring not only in dry pine and mixed-conifer forests, but also in moist and cold

Manuscript received 18 November 2020; revised 17 February 2021; accepted 3 March 2021; final version received 6 July 2021. Corresponding Editor: David S. Schimel.
[6] E-mail: paul.hessburg@usda.gov

forests, and in nearby nonforest vegetation (preforest, grassland, shrubland, and sparse woodland; Parks et al. 2015). Based on climate change predictions, burned area in wNA will at least double or triple by mid-century (McKenzie et al. 2004, Westerling et al. 2011).

While increase in burned area is strongly associated with climatic warming, changes to other aspects of wildfire regimes (Table 1) more directly reflect the influence of human activities. For example, in many wNA forests, land and resource management decisions and actions led to abrupt and persistent declines in fire frequency (and hence, burned area) beginning more than 170 yr ago. Decreased fire frequency led to increased continuity and accumulation of live and dead fuels (Stephens et al. 2009), both of which contribute to increases in fire severity as burned area increases (Parks and Abatzoglou 2020). Likewise, while human-caused ignitions continue to contribute to increasing burned area (Balch et al. 2017), they also reflect contemporary land development and access patterns. With ongoing fire suppression, lengthening wildfire seasons, and the increased likelihood of extreme fire weather, fire effects are broadly becoming more severe than those experienced in the last two centuries (North et al. 2015, Parks and Abatzoglou 2020). As a result, forests developing after large contemporaneous wildfires little resemble forests evolving under a more characteristic wildfire regime (Keane et al. 2002, Hessburg et al. 2005, Coop et al. 2020).

The challenge of larger and more intense wildfires

The increasing impacts that large and intense wildfires will have on social and ecological systems will be the major challenge facing managers of seasonally dry forests over the 21st-century. Prolonged smoke production and human health effects, chronic soil erosion and mass wasting, degraded water supplies, loss of cultural and natural resources, increased greenhouse gas emissions and reduced carbon storage are all growing issues (Spies et al. 2014). Management capacity to influence how much area burns will be somewhat limited (cf. Taylor et al. 2016), but fuel reduction treatments, including prescribed burning, coupled forest thinning and prescribed burning, and managed wildfires, are proven methods to influence the ecological impacts of wildfire, and mitigate impacts of extreme fire events on social systems (Taylor et al. 2016; Prichard et al. 2021). To date, mechanical fuel reduction treatments have been applied to small portions of wNA forested landscapes (Barnett et al. 2016, Vaillant and Reinhardt 2017, Kolden 2019, Kolden and Henson 2019). One reason is that land allocations amenable to mechanical treatments (via their enabling legislation) represent a dwindling fraction of public lands (Fig. 1); another is a lack of sufficient experience with prescribed burning and managing wildfires in front or backcountry locations. However, scaling-up a broad variety of fuel reduction treatments can tip landscape dynamics in favor of more benign fire behavior and effects (Stevens et al. 2014, Parks et al. 2016, Taylor et al. 2016, Ager et al. 2020).

Table 1. Components of an active fire regime.

Component	Definition
Amount	total amount of area burned annually or decadally
Distribution (severity)	distribution of severity class patch sizes
Distribution (event areas)	distribution of fire event patch sizes
Frequency	average fire return interval, and variation around the mean
Spatial distribution	the geographic distribution of fires†
Intensity	the energy release from surface and crown fires at the flaming front
Duration	the length of time fires burn‡
Seasonality	the time of the year when fires burn

Note: Components may vary by climatic period.

†The spatial distribution of fires is dictated by biophysical setting, climate, and weather conditions, forest or nonforest type, ignition probability, and the propensity for reburning.

‡The period of fires is dependent on the climate, weather, and fuel bed characteristics.

The assertion of regional-scale adaptation needs

The need for broad-scale climate and wildfire adaptation across wNA is predicated on two main assertions. The first is that most seasonally dry forest landscapes, and some drier coastal forests (Hessburg et al. 2019), have significantly changed over at least the last two centuries under the influences of curtailed Indigenous burning before 1850 (Kay 2000, Stewart 2002); wildfire exclusion (beginning with domestic livestock grazing in the mid-1850s, Belsky and Blumenthal 1997); and decades of selection cutting of large, old, early seral tree species (Hessburg and Agee 2003, Lydersen et al. 2013). The resultant stand- to landscape-scale changes in forest structures and fuels have left these seasonally dry forests vulnerable to the direct and indirect effects of climate warming, drought, and wildfire (Allen et al. 2002, Noss et al. 2006, Keane et al. 2018, Bryant et al. 2019, Hessburg et al. 2019). The second assertion is that climate change and wildfire adaptation treatments implemented at large regional landscape scales can effectively moderate many ecosystem transitions, conserve greater area and heterogeneity of forest successional conditions (Moritz et al. 2013, Coop et al. 2020), better foster native biodiversity (Raphael et al. 2001, Bisson et al. 2003, Isaak et al. 2010, Rieman et al. 2010), and maintain essential and desirable ecosystem services and processes (e.g., see Dale et al. 2001, Millar et al. 2007, Hurteau et al. 2014).

Public land management: political and paralyzed

As with many topics in conservation biology (Soulé 1985), active or intentional management of public

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

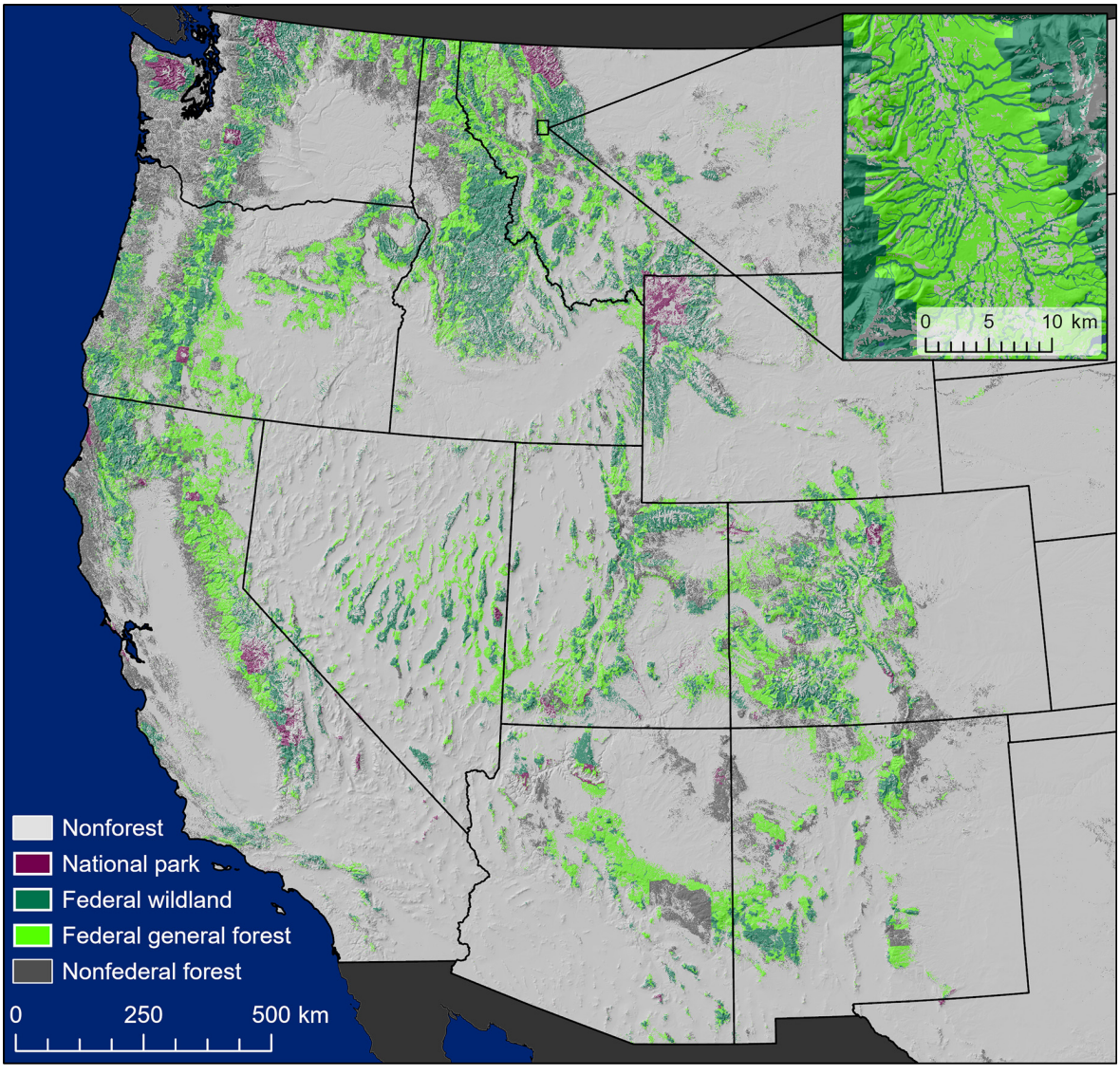


FIG. 1. Map of forested areas and their primary public land management allocations in the western United States. Federal wildlands include administratively withdrawn roadless areas, congressionally designated wilderness, and terrestrial habitat reserve networks. General forest areas are those remaining that are ostensibly amenable to mechanical thinning and prescribed burning treatments. Riparian reserves are generally not shown due to map scale, but they represent a significant area in general forest. The inset map at top right shows an example of riparian reserves in the Swan sub-basin of northwest Montana. Riparian buffers are 100 m on either side of perennial streams and 30 m on ephemeral streams. Most federal wildlands and national parks are available in concept for using managed wildfires and prescribed burning as fuel reduction treatments, but application of these tools remains uneven. Data sources for map development are (1) for forested areas, National Land Cover Database, NLCD (2006); https://www.mrlc.gov/data/nlcd-2006-land-cover-conus) for inventoried Roadless Areas (2001), https://www.fs.usda.gov/detail/roadless/2001roadlessrule/maps/?cid=stelprdb5382437, USDA-FS internal enterprise data layer name: S_USA. InvRoadlessArea_2001; (2) for Northwest Forest Plan Land Use Allocations (2013), https://www.fs.fed.us/r6/reo/landuse/, USDA-FS internal enterprise data layer name: S_R06.NWFP_LandUseAllocation_2013; (3) for designated Wilderness Areas (2020), USDA-FS internal enterprise data layer name: S_USA.Wilderness; (4) for Other National Designated Areas (2020), USDA-FS internal enterprise data layer name: S_USA.PADUS_DESIGNATION; (5) for US National Atlas Federal and Indian Land Areas (last updated 2004), USDA-FS internal enterprise data layer name: S_USA.OtherNationalDesignatedArea.

forestlands often devolves into value-laden discussions and politicized views of appropriate contexts and frames of reference (Peery et al. 2019). Here, we define intentional management as the planned application of silvicultural and prescribed fire treatments and managed wildfire to meet a variety of specific landscape-level objectives in predefined conditions and contexts. This can include opportunities in Indigenous communities for more decentralized stewardship practices related to resource tending, subsistence activities, and spiritual or

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

religious observances (Norgaard 2014). In contrast, under passive management (i.e., continued fire suppression with little intentional forest or fuel management), many assume that existing conditions and processes will naturally sort out an effective remedy without benefit of intentional management (Carey 2006).

Owing to extensive 20th-century harvest of large trees and old-growth forests, public trust in forest management eroded. In response, an emphasis emerged to conserve the victims of that history, large trees and old forests, and native species and their habitats, by minimizing further forest management actions. This emphasis is commonly underscored with policies that emphasize riparian and terrestrial habitat reserves and related conservation areas (Spies et al. 2019, Stephens et al. 2019), by legal injunction of active management projects (Prichard et al. 2021), and by maintaining a relatively small footprint of areas available for active management (Fig. 1). Opposition to active forest management is reflected in statements like "active forest management is unwarranted because the effects of fire exclusion and forest changes are overstated; . . .is ineffective and counterproductive; . . . should be focused on the wildland urban interface; or wildfires alone can do the work of fuel treatments." On the other hand, support for active management from the commercial sector suggests that "forest thinning alone can mitigate wildfire severity; forest thinning and prescribed burning can solve the problem; or managed wildfires hold no real promise." Each statement polarizes debates and oversimplifies the problems and the solutions (Prichard et al. 2021). Given rapid climate change and a legacy of excluding most natural and Indigenous ignitions, effective forest landscape restoration and adaptation strategies are more complex and nuanced than any of these statements imply.

Advocacy and objectivity: is it one or the other?

The polarization and politicization of scientific evidence impedes implementation of effective land management plans, policies, and management by raising the volume of the disagreement; obscuring the line between facts, opinions, and legal requirements; creating the impression that knowledge is more uncertain than it is; and increasing the time to resolution. Wellerstein (2018) argue that the premise of science as apolitical is simply a myth, since all science takes place and is supported within a highly political environment. Nonetheless, when scientists affiliate themselves with one-sided or partisan views and activism, they inevitably minimize their value and that of the applied science (Lackey 2007, Pielke 2007).

Scientists are increasingly asked to comment on forest policy and management recommendations. Facilitating communication among stakeholders of public land management by providing practical access to the best-available science can more effectively ensure scientifically credible decision-making (Komatsu and Kume 2020). However, while some encourage scientists to be responsible informants for species or ecosystem conservation (e.g., Lach et al. 2003), others worry that their objectivity in conservation or ecological research may be compromised (e.g., Scott et al. 2007), especially during volatile times, and with arguments that are already polarized or politicized.

Garrard et al. (2016) argue that scientists are not compromised when they transparently evaluate policies or recommendations for their consistency with the best available science, its weight of evidence, and any associated uncertainties. A systematic evaluation of best available science would include careful examination of Indigenous and western data, information, knowledge, and wisdom from a variety of locally and regionally relevant sources (Varghese and Crawford 2020). Garrard et al. (2016) further suggest that in the face of serious societal, economic, or existential issues, "the standard of debate about conservation is impoverished when scientists with relevant knowledge remain silent outside the pages of their academic journals."

Peery et al. (2019) provide a framework for evaluating agenda-driven science and a case example of controversy in the scientific literature that has impacted management of the California spotted owl and its habitats. They discuss professional norms for scientist engagement with management and policy issues and conclude "that intentionally engaging in activities outside of these professional norms to promote desired political outcomes, as part of either the production or dissemination of science . . .constitute[s] agenda-driven science."

Recent controversy involving the creation and dissemination of agenda-driven science is creating uncertainty for forest managers and policy-makers throughout wNA. Contributing to the controversy are publications that challenge the significance of forest condition and wildfire regime changes, and the advisability of proactive management without addressing the core arguments (e.g., compare Hessburg et al. [2020] and Mildrexler et al. [2020] and their discussion of trade-offs between wildfire dynamics, carbon sequestration, and forest adaptation to climate warming). To aid those engaged in designing, evaluating, and implementing science-based adaptation options, we examine the strength of evidence pertaining to these topics.

We first provide a framework for characterizing and evaluating changes in forest conditions and fire regimes in Hagmann et al. (2021). We then review the strength of evidence documenting changes or lack thereof. Similarly, in Prichard et al. (2021), we review the strength of evidence surrounding the usefulness of various passive and active management treatments to provide remedies to current conditions. We then discuss 10 key questions related to application of methods as viable treatments.

Forest Conditions and Wildfire Regimes

Advances in fire and landscape science over the past several decades enable rigorous multi-proxy and multi-

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

scale assessments of variation in historical fire regime and forest vegetation conditions. These insights build on more than a century of assessment of changing fire behavior and forest landscape conditions. Beginning in the 1930s, fire histories based on tree-ring and fire-scar records have provided high-resolution, cross-dated, multi-centenary evidence of the spatial point patterns of fires, which have enabled precise interpretations of fire frequency associated with recorder trees. While fire-scar records remain a primary means of exploring historical fire ecology, more recently developed methodologies and multi-proxy assessments have expanded the potential to evaluate broader temporal and spatial patterns. New insights into complex relations between variations in climate, fire, and vegetation emerge from multi-proxy and trans-disciplinary studies that combine sedimentary pollen and charcoal records (Higuera et al. 2007), large-scale tree cohort analyses (Schoennagel et al. 2011), early 20th-century land system inventories and surveys (Hagmann et al. 2013, 2014, Levine et al. 2017), landscape reconstructions from historical black and white photographic imagery (oblique, panoramic, stereo photo pairs, Hessburg et al. 1999, 2000, Stockdale et al. 2015, 2019), forest inventories and land system surveys (Williams and Baker 2012, cf. Fulé et al. 2014, Odion et al. 2014, cf. Stevens et al. 2016), and simulation modeling of landscape succession and disturbance regimes (Keane et al. 2004, 2018, McGarigal and Romme 2012). Additionally, trans-disciplinary studies that employ fire-scar research, climate, archaeological, and ethnographic studies show that many different Indigenous cultures were significant contributors to the magnitude and extent of fire influence on the wNA landscape (e.g., see Taylor et al. 2016, Lightfoot et al. 2013).

Over the past two decades, a series of publications using novel techniques has suggested that 19th- to 21st-century changes in western forests and their fire regimes have been less substantial than a much larger and more diverse body of scientific evidence has long indicated. Hagmann et al. (2021) provide a comprehensive review of these papers and studies that directly evaluated them. They show that methods and inferences in these articles failed independent validation by other research groups and lend their support to the findings of the larger body of evidence.

The evidence for change in forest conditions

Hagmann et al. (2021) relied on several hundred research articles from research groups throughout wNA that examined historical changes to seasonally dry forests patterns and processes to illustrate key departures from conditions that existed prior to European colonization. They found that changes in forest successional landscapes are significant in all forest types, whether dry, moist, or cold. Changes are prominent at tree, patch, and local and regional landscape levels, and these changes explain important shifts in numerous habitats and ecosystem processes. Conditions of nonforest vegetation (grasslands, shrublands, sparse woodlands) are likewise altered as a consequence of fire exclusion and forest encroachment. While some forest and nonforest ecosystems may not have been directly altered by fire exclusion, the magnitude of changes suggests that it is likely that all were indirectly impacted by alteration of the landscape ecology and disturbance regimes that surround them. Based on a preponderance of scientific evidence, there can be little doubt that long-term fire exclusion and other associated social-ecological influences contributed to extensive modification of landscapes across wNA, and that the magnitude of the departures in fire regimes and landscape conditions has increased the vulnerability of contemporary forested landscapes to fire and drought-related stressors.

The evidence for change in fire regimes

Hagmann et al. (2021) also review the evidence for changes in the dimensions of fire regimes (Table 1). Fire exclusion has reduced fire frequency in all forest types, with the degree of change generally declining with increasing elevation, owing to orographic effects on moisture and temperature, and topo-edaphic effects on insolation. As a consequence, surface and ladder fuel abundance generally increased in historically fuel-limited frequent-fire forests, while forest cover at higher elevations expanded and became more successionally homogenized (Fig. 2). In both cases, crownfire vulnerability increased. Long-term fire exclusion reduced the total amount and spatial distribution of wildfires resulting in a nearly universal fire deficit in forests (Parks et al. 2015, Parks and Abatzoglou 2020).

Adapting Forests to Wildfires and Climate Change

Prichard et al. (2021) address 10 key questions surrounding active forest management, address the assumption that historical fire regimes were "natural" rather than cultural, and describe conditions where specific management actions are appropriate and effective for adapting current forests to wildfires and climate change. The authors again use a strength of scientific evidence approach to show why the answers to the 10 questions are relatively straightforward. In addition to evaluating the efficacy of diverse treatments to moderate expected fire severity, they discuss these questions in the context of their consistency with more holistic climate- and wildfire-adaptation strategies that are designed to achieve many social and ecological benefits. Moreover, they discuss how methods designed to achieve a single objective often fail given contemporary goals for multi-objective landscape management. We summarize their responses to the 10 questions here.

1) *Are the effects of fire exclusion overstated? If so, are treatments unwarranted and even counterproductive?*

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

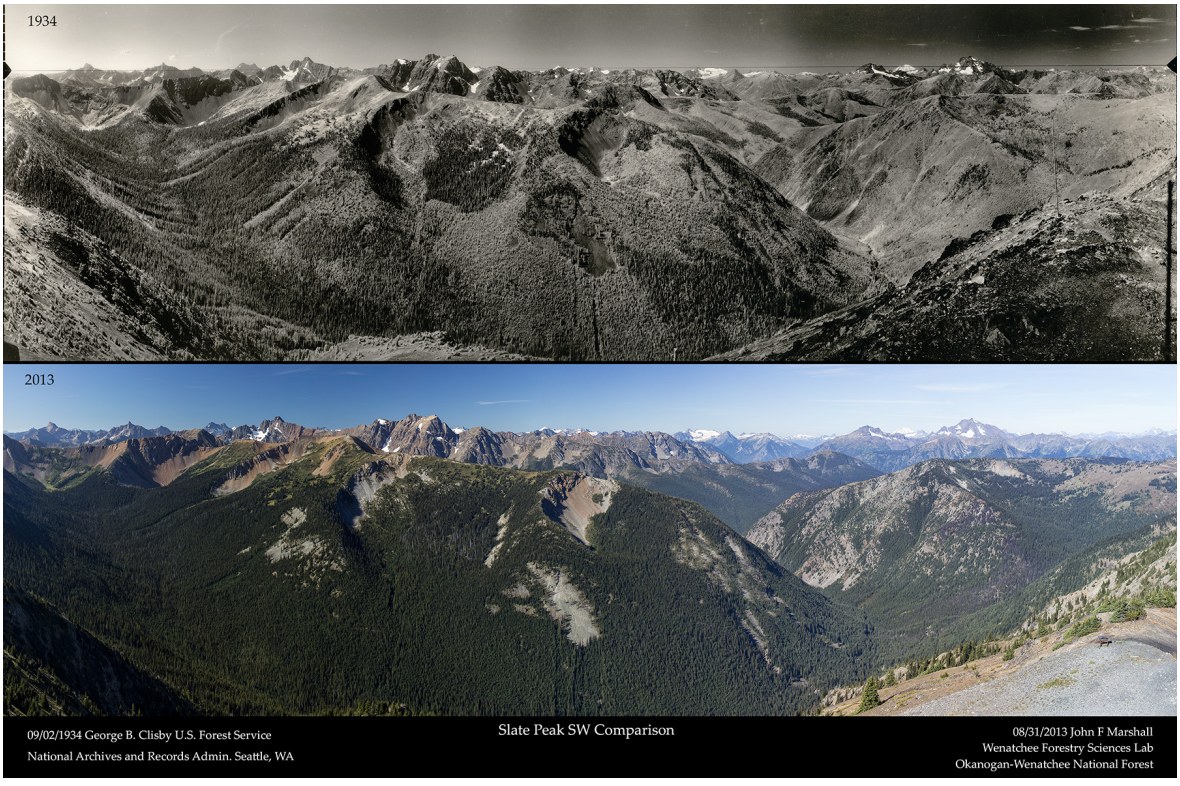


FIG. 2. Top photo: View from atop Slate Peak in northeastern Washington, looking southwest, 1934, George Clisby photograph, National Archives, Seattle, Washington, USA. The 1934 panoramic view shows extensive evidence of prior wildfires, varied age classes of cold forest, and recently burned and recovering areas. In the same view nearly eight decades later (bottom photo, 2013, John Marshall Photography), note the complete absence of recent fire evidence, widespread ingrowth creating denser forests, loss of nonforest, and lack of forest successional heterogeneity.

Prichard et al. (2021) dispute all parts of this question. They reveal four crucial components in their answer, not the least of which is that increasing forest resilience and resistance to wildfires and climate change provides positive societal and ecosystem benefits, which overwhelm uncertainties about prior historical conditions. They also show that intentional forest management is effective and corrective where practiced, but its pace and footprint are insufficient to current needs.

2) *Is forest thinning alone sufficient to mitigate wildfire hazard?* Whether forest thinning achieves adaptation objectives depends on several factors, including its timing, location, rate, and spatial scale. Reducing canopy layering and density limits crownfire potential, but unless the abundance and connectivity of surface fuels and fuel ladders is also reduced, thinning can have limited effectiveness in mitigating wildfire severity, and may make matters worse. In forest thinning for adaptation to climate change and wildfires, emphasis is placed on residual forest structure, composition, and understory fuels rather than on the trees that are removed (Larson and Churchill 2012, Churchill et al. 2013).
3) *Can forest thinning and prescribed burning achieve climate adaptation?* Coupled thinning and prescribed burning treatments are proven approaches to mitigating wildfire severity in many seasonally dry forests, but they are not appropriate to all forest types, land allocations, and conditions. These treatments require regular maintenance application of prescribed or cultural burning to maintain low surface fuel levels and remove developing fuel ladders. The vast scale of ongoing fuel reduction necessitates wise use of naturally ignited future fires during moderate fire weather as well.
4) *Should active forest management, including forest thinning, be concentrated in the wildland urban interface (WUI)?* Fuel treatments in the WUI are critically important as is reducing continued development in high fire danger areas (Balch et al. 2017, Radeloff et al. 2018). People living in the WUI have ample incentive to reduce their vulnerability to wildfires (Cohen 2000), and many resources are available to

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

help them do so (Syphard et al. 2012; *resources available online*).[7,8] However, this logic, concentrating treatments in WUI, fails to address interconnectedness between social and ecological systems in landscapes beyond the WUI. Examples include wildfire emissions and broad-scale smoke movement in the atmosphere; water quality and quantity provided by municipal watersheds distant from population centers; ember attack on WUI areas from wildfires burning several kilometers away; wildfire effects on power, WIFI, and broadband transmission and distribution networks; and tribal connections to ancestral territories and resources. It also avoids core decisions related to human social values for forested landscapes and long-term ecosystem dynamics. Alternatively, intentional forest management both within and beyond the WUI offers the greatest social and ecological benefits.

5) *Can wildfires on their own do the work of fuel treatments?* Many forests are experiencing rapid WUI expansion, leaving land managers and citizens increasingly unwilling to accept the risks of managed wildfires In the backcountry, some wildfires are allowed to burn under specified conditions to achieve incident and resource management objectives. However, the effects of fire exclusion are varied and extensive, and managed wildfire is a spatially imprecise tool. To increase predictability of outcomes, application during benign to moderate fire weather may be preferred; this, however, necessitates numerous follow-up treatments to meet objectives, and it broadens the period of landscape vulnerability to more extreme wildfires. Considering the narrow seasonal operating window and spatial imprecision concerns, managed wildfires cannot be a cure-all, but can be one of several options in a broader toolkit.
6) *Is the primary objective of fuel reduction treatments to assist in future firefighting response and containment?* The central objective of fuel treatments is to moderate fire behavior when fire inevitably returns, not to stop fire spread or reduce ignitions If fuel treatments simply improve suppression success, less area is burned in the short term but more area will escape control in the future, resulting in deferred risk and contributing to larger and more often severe wildfires.
7) *Do fuel treatments work under extreme fire weather?* Many studies show that fuel reduction treatments are effective at moderating subsequent fire severity, even under extreme weather Far fewer experimental or empirical studies challenge this premise. Moreover, there is strong evidence that some prior burn and reburn mosaics reduce landscape contagion, which limits subsequent spread and severity of wildfires.
8) *Is the scale of the problem too great? Can we ever catch up?* Given the scale of the area burned by wildfires each decade compared to area treated, some surmise that fuel treatments are futile Nevertheless, a large body of work shows that fuel reduction treatments, including portions of some past wildfires, effectively mitigate subsequent fire behavior and effects. It follows that strategies can be developed to increase rather than decrease the role of fuel reduction treatments. The key to defining the locations, spatial scale, timing, rate of treatment, and methods used is the desired forest–nonforest conditions that result, their degree of adaptation to changing climate and fire regime conditions, and the degree of comfort with spatial uncertainty of outcomes. Moreover, coupling Indigenous cultural burning, fuel reduction, and prescribed fire treatments furthers Indigenous fire stewardship and food security (Sowerwine et al. 2019*a*,*b*), and recovers opportunities for tribal engagement in resource management within their ancestral territories (Long and Lake 2018, Long et al. 2020).
9) *Will planting more trees in wNA forests help to mitigate climate change?* Widespread tree planting has been proposed as a key climate change mitigation (Bastin et al 2019). This premise has poor scientific support in many fire-prone regions of the world (e.g., Grainger et al. 2019, Lewis et al. 2019, Veldman et al. 2019). An increasing body of evidence reveals that proactive management to restore more resilient forest and nonforest structure and composition over large areas, and diversifying tree planting species mixes, can more effectively maintain or increase carbon stores relative to the effects of modern wildfires (e.g., see Hof et al. 2017).
10) *Is post-fire management needed or even ecologically justified?* Prior to fire exclusion, historical landscapes in seasonally dry regions of wNA were the product of complex mosaics of low-, moderate- and high-severity fire patches, which yielded highly variable patterns of surviving forest and scattered fire refugia (ie., unburned patches that functioned as seed sources for postfire tree regeneration in their vicinity). After contemporaneous wildfires, this mosaic is often simplified by large high-severity fire patches, and fire refugia are operationally burned out in closing suppression actions. Within one to two decades after a high-severity fire, dead wood accumulations contribute to uncharacteristically high surface fuel loads. Post-fire removal of the dead understory stems (i.e., those that had previously colonized the landscape during the lengthy period of fire exclusion) by harvest or reburning can mimic this historical reburn influence, thereby minimizing surface fuels in some developing new forests (Stevens-Rumann and Morgan 2016), and reducing future wildfire vulnerability (Coppoletta et al. 2016). The ecological justification for this post-fire removal of the smaller dead understory trees can be

[7] https://www.nfpa.org/Public-Education/Fire-causes-and-risks/Wildfire/Preparing-homes-for-wildfire.
[8] https://www.usfa.fema.gov/wui_toolkit/wui_planning.html.

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

observed in the low surface fuel loads associated with the frequent reburning of pre-management era landscapes and modern-day wilderness areas. It is also clearly revealed in intentional Indigenous cultural burning practices. Indigenous fire stewardship actively mediated post-fire landscape effects to stagger the availability of desired resources and species over time, and ensure their quality, quantity, and abundance (Boyd 1999, Lake and Christianson 2019).

Strategies for Adapting Western Landscapes

Changes in forested landscapes throughout wNA are somewhat unique geographically, as are the stories of change. To consider appropriate climate and wildfire adaptation strategies, managers are compelled to evaluate current vegetation and fuel conditions, the influences that precipitated changes in conditions, the magnitude of the changes, ecological and social constraints to adaptation, patch to landscape vulnerability to changing climatic and wildfire regimes, and nonnative species and any sensitive or endangered species concerns.

Stephens et al. (2010) recommend four strategies for adapting western landscapes to changing climatic and wildfire regimes, and they can be applied in a variety of contexts. They define *resistance* work as that which mitigates expected wildfire effects and protects valued resources, while *realignment* work modifies existing conditions to restore key ecosystem patterns and the processes they drive. Creating *resilient* conditions improves the natural capacity of an ecosystem to respond favorably when unplanned disturbances occur. Finally, they present *response* work as any intentional facilitation to achieve socially and ecologically desirable results that are otherwise difficult to achieve. Each of these strategies can play a role in proactive management going forward. Where their application also considers Indigenous cultural adaptations to climate, vital ecosystem processes, and active cultural use of fire, there will be greater likelihood that resulting vegetation conditions are strongly linked to culturally valued resources and services (Power et al. 2018).

Whether reactive or proactive fire management

Modern wildfire suppression extinguishes essentially all fire starts except those that overwhelm fire suppression capacity and can only be extinguished when aided by a significant change in the weather (North et al. 2015). Fires burning under extreme fire weather often burn vast areas, much larger than the current footprint of managed wildfires and other fuel treatment projects. As a consequence, wildfires that escape initial suppression efforts burn under the most extreme fire weather conditions and do most of the vegetation management in wNA ecosystems (Calkin et al. 2005, North et al. 2015). Appropriately designed thinning, burning, and managed wildfire treatments, that are tailored to topo-edaphic conditions would be helpful additions to this scenario (sensu Taylor and Skinner 2003, Hessburg et al. 2015). Such treatments would prepare landscapes for wildfires that will inevitably follow.

Managing wildfires that burn under extreme fire weather is a blunt management response, which most often results in failure to meet resource management or conservation objectives. Science-based strategies for forest and fuel management are well known, but lack of social license and sufficient financial and personnel resources currently limit fuel reduction programs to a small percentage of wNA forestlands (Hessburg et al. 2020). Increasing costs of fire suppression and lack of control during large fire growth days reveals a reactive management posture that is progressively prone to failure, despite ever-increasing investments (North et al. 2015, Stephens et al. 2020). Thus, a business-as-usual approach to wildfire in fire-prone regions will not solve the current wildfire dilemma (Moreira et al. 2020). Strategic management of regional landscapes is needed that establishes topographically sensible (sensu Povak et al. 2018 and Taylor and Skinner 2003), fire-maintained, control and anchor points (e.g., see Wei et al. 2019). This would improve fire manager usage of future wildfires as adaptation tools.

A more proactive and evidence-based management goal is to restore active wildland fire regimes and landscape resilience to climate change, and actively enable future wildland fires, prescribed and cultural burning, and managed wildfire to provide a higher standard of social-ecological work. To achieve this goal, massive progress and investment are needed (Madeira and Gartner 2018) to transition management from a reactive to a proactive, forward-looking stance. Such an approach allows for the direct adaptation of wildfire regimes by intentionally crafting landscape patterns that drive more benign fire behavior and less severe drought effects. This will require radically increasing the areal extent of restorative and adaptive fuel reduction treatments as is appropriate to conditions and land allocations. It will also require increased use of natural wildfire ignitions (as above) under moderate fire weather conditions, to recapture the once extensive moderate influences of wildfires, and then maintain that progress with controlled (prescribed and cultural) burning and thinning as needed.

The nested character of regional landscapes holds adaptation clues

The hierarchical organization of historical wNA landscapes influences countless ecosystem functions, including scale-dependent spatial and temporal controls that drive wildfire behavior and effects, and the cross-connection between levels of organization. Characteristics of this organization and its influence on ecosystem

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

functions can inform realignment of current systems with early 21st-century and projected future climates (Hessburg et al. 2016, 2019). Three important ideas associated with that nested structure are that (1) at a fine spatial scale, species traits and adaptations drive within-patch structure, composition, and response to disturbances; (2) cross-connections between fine-scale patch structure and composition and meso-scale landscape patchworks influence fire frequency and severity because they form the percolation surface where disturbance propagates, and the manner of propagation; and (3) cross-connections between non-forest and forested landscapes mediate broad spatial patterns of fire behavior attributes and their effects. These three ideas help shape a scientifically supported landscape adaptation framework (Hessburg et al. 2015, 2019).

Additionally, we are learning through integration of western science with traditional ecological knowledge that Indigenous fire use and broader landscape stewardship practices were upheld in tribal communities as human services for ecosystems. Indigenous tribes acknowledged and promoted multi-generational contributions to foster landscape resistance and resilience. Trans-generational fire use also promoted post-fire recovery of landscapes and habitats where culturally valued drought-tolerant, fire-adapted plant species were adversely influenced by a fire (Huffman 2013).

Beyond the Precautionary Principle

The precautionary principle holds that when the potential for adverse effects is unknown or difficult to quantify; the burden of proof rests on the proponent of an activity to demonstrate that lack of harm is the most likely outcome. However, it is virtually impossible to demonstrate lack of harm for most any activity, including no action, especially in a rapidly changing environment. Moreover, one-sided, or single-issue application of the principle can overlook desired ecosystem services, species, and processes that proactive work could have protected. Given human influence on climate and wildfire regimes the world over, a no-action alternative that purports to let so-called natural processes like modern wildfires operate unfettered is grossly misleading. These processes are operating within a human-influenced template globally, and their regime characteristics and fuel conditions have been altered by humans, increasing the likelihood that large portions of many modern wildfires are unnatural.

Modern wildfire management dominated by fire suppression is perceived by many as a no-action alternative when compared to active restoration and adaptation in planning and management. However, active suppression of 98% of wildfire ignitions (North et al. 2015) hardly qualifies as no action, as we have shown earlier. The small proportion of wildfires that escape containment all too often rapidly and indiscriminately convert forest to non-forest conditions. This is an altogether unevaluated planning outcome, and the recovery of forest structure and processes can take decades to centuries, if it occurs at all. Furthermore, fire suppression costs currently exceed US$2 billion annually, not including loss of life and property, and detrimental impacts to lifeways, human health, and livelihoods, while the total annualized economic burden of wildfires ranges from US$71 billion to US$347 billion (Thomas et al. 2017; data *available online*).[9]

The precautionary principle is indeed useful guidance, but it must be applied equally to what are often mistakenly perceived as no-action alternatives. Lacking this clarity, broad application of the precautionary principle as a conservation approach can result in greater long-term harm than more ecologically intuitive remedies, as can be seen within the Northwest Forest Plan area of the eastern Cascade and Klamath Mountain regions (Spies et al. 2019, Stephens et al. 2019). There, networks of late-successional reserves (LSRs) for the northern spotted owl in seasonally dry, historically frequent-fire forests increase the likelihood of their elimination by extreme wildfire events (Henson et al 2013, Spies et al. 2018, 2019). There is simply too much at stake to require unattainable certainty about potential risk of harm or losses (Wood and Jones 2019).

The precautionary principle can become the "paralyzing principle" given irreducible uncertainty about risk of loss associated with action and no-action alternatives (Sunstein 2003). The loss of ˜30 million mature and old pine trees during a recent extreme drought in south-central California (Asner et al. 2016) is a stark reminder of the pitfall of requiring unduly high certainty despite decades of established science showing the efficacy of treatments that foster resilient forest structure and composition (Henson et al. 2018, Fettig et al. 2019). Absent 150–170 yr of frequent fires, overgrown forest density conditions produced a massive and predictable die-off event, facilitated by tree-killing bark beetles and drought, that proactive implementation of climate- and wildfire-adaptation strategies could have mitigated (Stephens et al. 2018, Fettig et al. 2019). Remedying such conditions would have required careful consideration of changes over the period of fire exclusion, the effects of climatic changes looking forward, and any related ESA (Endangered Species Act) concerns.

Dealing with uncertainty

There is much uncertainty to science, including that surrounding our knowledge of historical and contemporary forest ecology, future conditions, and adaptive forest management. In that light, active forest management projects with objectives of restoring more resilient and resistant structure and composition can be assessed using a set of questions to address the relative

[9] https://www.nifc.gov/fireInfo/fireInfo_documents/SuppCosts.pdf.

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

uncertainty associated with proactive versus reactive treatment alternatives. For example, in the context of changing wildfire regimes and climatic conditions, what are the uncertainties, trade-offs, and likely consequences to U.S., Canadian, and Mexican Indigenous and non-indigenous people, infrastructure, ecosystems, native species and habitats of

1) Restoring active fire regimes to dry, moist, and cold forest ecosystems,
2) Continued fire suppression in these same forest types,
3) Proposed proactive, reactive, and no-action management alternatives,
4) Post-fire forest regeneration under action and no-action alternatives, and
5) Post-fire harvest/non-harvest of the younger fire-killed trees to mimic reburns?

Reframing Management and Policy

As demonstrated in literature reviews, the disturbance ecology of an ecosystem may still be the most valuable lens through which climate-related events and outcomes may be understood (Long 2009, Newman 2019, Franklin and Johnson 2013). Over millennia, Indigenous fire use in many areas amplified fire frequency to reduce the likelihood of more extreme wildfires and their effects on culturally valued resources and conditions. This culturally modified disturbance regime increased the resilience and resistance of vegetation and landscape conditions to changing climatic conditions and associated disturbances.

More recently, ecological forestry principles recognize the value of management planning that incorporates the influence of natural disturbance processes on forest dynamics (Franklin et al. 2018). Additionally, as shown by Indigenous experience, natural lightning ignitions can be supplemented to achieve desired conditions. In uncertain times, management might better focus on the long-term persistence of that native biodiversity that evolved within the local, culturally enhanced, disturbance regime, and will likely go extinct with rapid or extreme changes to those regime properties (Newman 2019). Where possible, adapting local landscapes to conserve key aspects of culturally enhanced disturbance regimes could be vital to preserving functioning ecosystems and to the native biodiversity that requires non-extreme disturbance for its continued existence (Franklin and Johnson 2012, North et al. 2014), even where single-species conservation and broader ecosystem goals may appear to be in conflict at other scales (Henson et al. 2013).

Managers and scientists have repeatedly proposed management directions that incorporate knowledge of disturbance ecology and methods that adequately mimic and recover local disturbance regimes; however, socioeconomic challenges have impeded widespread implementation of these strategies (Long 2009). Effective direction would be proactive rather than reactive, recognizing that just as with human society, all desired ecological outcomes are not possible in the same place, at the same time.

Recommendations

In this light, what constitutes adaptation of wNA forests in these uncertain times? Is bias for action rather than inaction recommended?

Scientific knowledge is always growing and incomplete. However, a preponderance of evidence suggests that proactive management can prepare many landscapes for future wildfires and the maintenance work they can provide. This would also reduce emphasis on high-maintenance solutions and the overarching and increasingly burdensome role of wildfire suppression and its expenditures.

Emphasize whole landscape and multi-scale adaptation.—Stand management as applied to western U.S. and Canadian public lands typically emphasizes forested areas where there are commercial opportunities for mechanical treatments in specific stands of trees. This focus misses many locations where proactive treatments may be most useful to adapting an entire landscape. Conducting whole landscape evaluations of forest conditions, fire regime departures, and expected future climate and weather conditions can powerfully aid in defining those places that would most benefit from adaptation treatments (North et al. 2009, Hessburg et al. 2013, 2016, Meyer et al. 2021).

Ongoing collaborative partnerships also recommend that emphasis on timber volume production from public lands has a negative influence on partner support for projects and trust maintenance (Hessburg et al. 2020), and it tends to force the hand of managers to rank commercial treatments over others that may be more truly adaptive. Alternatively, management and planning that emphasizes area restored and adapted could build trust and a broader base of support, while still providing timber volume to sustain rural mills and economies (Rummer et al. 2005). Increasingly, collaborative restoration partnerships with Indigenous communities, having tribes as part of the leadership and management, can increase opportunities for reinstating tribal stewardship practices, with tribes, local communities, and the broader society as beneficiaries of active management that achieves shared values (Lake et al. 2018, Long and Lake 2018).

Large and old trees.—Most research reveals that broadly conserving large and old fire-resistant trees and replacing those that were removed or killed by harvest, drought, insects, pathogens, and wildfires provides a strong backbone of resilient structure and habitat to seasonally dry pine and mixed-conifer ecosystems (Spies et al. 2018, 2019).

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Clumped and gapped trees.—As is appropriate to local seasonally dry forest types, restoring tree clump and gap patterns, and increasing area of these conditions will provide a solid patch-to-local landscape bet-hedging strategy in a warming future with increasing burned area (Larson and Churchill 2012, Churchill et al. 2013, LeFevre et al. 2020).

Successionally heterogeneous forests.—Successional heterogeneity, whether fine-, meso-, or coarse-grained, was an historical consequence of patterns of environmental productivity and fire–climate interactions with vegetation. It reinforced a continual shifting of diverse but similar patterns of heterogeneity at each scale of observation. As is appropriate to forest types and physiographic domains, restoring and maintaining forms of this heterogeneity will encourage a wider variety of wildfire and habitat outcomes, and reduce the need for aggressive fire suppression in many areas (Perry et al. 2011). This can be accomplished by adapting current spatial patterns of seral stages to more frequent burning and reburning (Stephens et al. 2020). Indigenous and Western knowledge can jointly aid in determining how best to adapt current and projected future conditions.

Using the topo-edaphic template.—Throughout wNA, topography, geomorphology, lithologies, and soils provide the template for spatially varying forest cover types, structural conditions, and their variations (Taylor and Skinner 2003, Hessburg et al. 2015). Fire exclusion and other influences have weakened connections to this template. Realigning spatial patterns of nonforest and forest successional pattern conditions (e.g., open vs. closed canopy, fire-tolerant vs. intolerant species) to this template will aid in adapting landscapes to changing climatic and wildfire regimes. For example, restoring non-forest and low-density forest cover patches to south-facing slopes and ridgetops and higher-density forest cover patches on north aspects and valley bottoms are examples of strengthening connections to the topographic template (Hessburg et al. 2015, 2019). These underlying conditions continually co-create the environments for disturbance and revegetation as the climate changes (Taylor and Skinner 2003, Hessburg et al. 2015, 2016).

Forests and their nonforests.—Meadows, shrublands, savannahs, and preforest conditions result from natural succession, disturbance dynamics, and reburning (Prichard et al. 2017). Restoring more characteristic nonforest-forest patterns in and among all forest types at fine, meso, and broad scales could significantly realign primary ecosystem processes, carbon storage, and hydrologic regimes with the warming climate (Shakesby and Doerr 2006). As recent history has shown, many pre-fire-suppression era nonforest areas throughout wNA became forested absent active fire regimes during the mild mid-20th-century climatic period (Hessburg et al. 2019).

Research Needs

The reviews of Hagmann et al. (2021) and Prichard et al. (2021) show deepening understanding of the fire and landscape ecology of wNA forests; however, substantive knowledge gaps remain. Here, we discuss the following research needs that emerged from this review:.

1) *Fortifying future vegetation and wildfire projections with insights from landscape ecology research* Most continental to regional projections of climate influence on biotic conditions and physical processes use a range of intuitive climatic drivers to explain responses to warming (Rosenzweig et al. 2008, Parks et al. 2015, Abatzoglou and Williams 2016). Outcomes are presented as ostensibly unaffected by bottom-up or meso-scale spatial variation in biotic, environmental, disturbance history, or topoedaphic conditions inherent to the system(s) of interest. From the standpoint of landscape ecology theory and practice, this approach misses key cross-scale interactions between the climate system and highly varying biophysical settings, which are known to modify climate system inputs and alter spatial and temporal patterns of realized conditions (Wu and Loucks 1995). Hurteau et al. (2019) for example, showed that future projections of burned area under climate change, which accounted for interactions among prior fires on surface and canopy fuel availability, reduced area burned by 14.3% in the Sierra Nevada compared to projections where only climate drivers were considered. Hybrid research and modeling are needed among climate change scientists and landscape ecologists to improve projections of vegetation and burned area changes, and species ranges.
2) *Multi-proxy evidence is more informative than single proxy* Observing and integrating knowledge of the multi-level dimensions of forest landscapes and their wildfire regimes provides deeper insight into how patterns influence processes, and it improves change detection (Hagmann et al. 2021). Some regions are already represented by multi-level studies, but in some cases, they could be better integrated. Multiscale and multi-proxy historical reconstructions are still needed for other regions of wNA to better understand variations in forest–nonforest relations and successional heterogeneity that are better aligned with changing climatic and wildfire regimes. With these insights, managers and policy-makers will be better able to understand how warming and drying may affect adaptation strategies.
3) *More wildfire–forest dynamics carbon research is needed* Recent studies show that strategies for adapting current forests to wildfires and climate change may result in more terrestrial carbon storage than business-as-usual scenarios. The reason is that large fuel buildup under fire exclusion renders forest carbon stores vulnerable to large, high-severity fire

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

events (Liang et al. 2018, Hurteau et al. 2019). This nascent inquiry area deserves significant investment and increased scope to determine suitable landscape management strategies, and where they may best apply.

4) *Disturbance–fish-and-wildlife-habitat connections* As Newman (2019) suggests, native species and their habitats are tied to disturbance regimes of local and regional landscapes. Our current knowledge of these species-disturbance regime linkages is weak in many areas and could be much better understood. Even where 25 yr of research is available for one of the most intensively studied bird species, that knowledge is not preventing population declines for Northern Spotted Owls (Spies et al. 2019, Stephens et al. 2019). As a result, Henson et al. (2018) advocated a coarse-filter approach that incorporates disturbance ecology in management for spotted owl habitat. Understanding and managing spatial domains to restore these more functional disturbance regimes is an intuitive coarse-filter conservation strategy for terrestrial and aquatic species.
5) *A role for decision support tools* Predicting future vegetation, climate, and wildfire conditions, and trade-offs among various habitats and resources across a set of potential management scenarios is intellectually and computationally challenging. Considering the large number of data layers, the one-to-many and many-to-one interactions among conditions represented by these layers, and variation in these relationships by scenario thwarts careful evaluation by even the best planning intellects. Decision support tools are designed for this complex and integrated planning environment and are useful for evaluating trade-offs among changing conditions, outcomes, and management scenarios (Kangas and Kangas 2005, Reynolds et al. 2014). Using such tools, managers and scientists can observe trade-offs and related positive and negative cascades associated with varied management scenarios and discover their primary drivers.
6) *Innovation and investment in multi-party monitoring and adaptive management* Adaptive forest management has been recommended by scientists and managers for decades (Lee 1999), however, it has functioned more as an abstraction than an applied reality (Bormann et al. 2007). While adaptive management provided the core of Indigenous landscape management methods (Anderson 2013), there are several key reasons for delayed application in contemporary management. Adaptive management depends on watchful learning; what we today call ecosystem monitoring, which can be time consuming and expensive, and results often come after lengthy delays. Sufficient monitoring is rarely budgeted for, and consequently, an adaptive process is inhibited. Without agreement on the monitoring questions and goals of management, disputes remain unresolved. Innovation and investment are needed in this area to develop better methods of multi-party goal setting, and efficient and inexpensive means of monitoring; for example, multi-scale photography or remote sensing in addition to intensive plot and survey application. Another monitoring approach proposed by Tribes is to use cultural keystone species as indicators of ecosystem integrity and function (Garibaldi and Turner 2004). Results from monitoring a representative subset of forest conditions and projects could be extrapolated to similar conditions. This would enable more rapid learning and implementation, which are core concerns. Effective learning of this sort will become more essential as expanding human populations search for better ways to live sustainably on increasingly dynamic wNA landscapes.

Conclusions

Here, we have described how policy and management choices of the last two centuries yielded forest conditions throughout much of wNA that are vulnerable to the effects of rapid climatic warming, including increasing fire and drought severity. We summarized core messages of Hagmann et al. (2021) and Prichard et al. (2021), detailing widespread changes in forested landscapes and wildfire regimes since the influx of European colonists, and addressing popular questions about the capacity of management practices to reverse or mitigate the worst effects of these changes. We address concerns about the influence of agenda-driven science and reiterate that the *precautionary principle* can become the *paralyzing principle* given uncertainty about the risk of losses associated with action and no-action alternatives. We discussed the near impossibility of demonstrating lack of harm for most any action, including inaction, especially in a rapidly changing environment.

We provided recommendations for reframing forest and fire management and their related policy underpinnings, emphasizing (1) whole landscape and multi-scale adaptation; (2) protection of large and old fire- and drought-tolerant trees and old forests; (3) restoration of clumped and gapped tree patterns at fine and meso spatial scales; (4) creation of successionally heterogeneous forests; (5) use of topography to realign current conditions to the biophysical template; and (6) restoration of nonforest conditions. Climate change will create more nonforest and more young open canopy forest conditions (Parks et al. 2016, Hessburg et al. 2019, Coop et al. 2020); the opportunity for management is to place those conditions and patch sizes in locations that provide the greatest social and ecological benefits while conserving and recruiting old trees and old forest where possible.

Some today call for cultivating pyrodiversity to advance biodiversity (Parr and Andersen 2006, Taylor et al. 2012, Bowman et al. 2016). However, not all heterogeneity is equally well adapted to the topography, soils, and varied environmental settings and fire

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

regimes of wNA landscapes, and thus may endanger native biodiversity. Climate and wildfire adaptation requires structural and compositional patterns and pattern variations that are in synch with biophysical settings, reinforce the desired fire regimes, and reduce undesirable impacts of climatic warming to socioecological communities.

We close our review with a short list of research needs. Key among them is the need to better understand the disturbance regimes that native plants and animals evolved with and through which persistence occurred even as we act proactively to restore pattern–process interactions and adapt these landscapes to warming climate. Most legal battles concerning forest management today are about native biodiversity, old tree or old forest conservation, conservation of threatened and endangered species, and impacts of timber harvesting. Yet, native species and their habitats are tied to disturbance regimes of local and regional landscapes and their pattern variations. Our current knowledge of these species-disturbance regime linkages is weak, yet these dynamics might become a focal means of biodiversity conservation (Henson et al. 2013).

Finally, we discussed how some of these climatic and fire regime effects were common to landscapes inhabited by the Indigenous people of wNA, and in closing, we return to those ideas. Because of significant vulnerabilities linked to native wildfire regimes, Indigenous people intentionally managed wildfire for millennia to provide a broad variety of life-supporting resources, food and medicine security, protect lifeways, sacred places, and deeply held traditions, and to increase personal safety. This intentional management was a transgenerational commitment; prior generations took responsibility for the quality and abundance of desired conditions they passed on to subsequent generations. Since the mid-1850s, the majority of EuroAmerican colonists and present-day citizens have neither practiced this intentional management nor passed on a transgenerational commitment. Yet, we are ever more dependent as a society on the ecosystem services that functional fire-adapted landscapes provide. Given the known risks of modern wildfires and climate change, embracing the role of fire and a return to intentional transgenerational management is of critical importance.

Acknowledgments

The authors acknowledge constructive reviews by Keith Reynolds, Jamie Rosen, Derek Churchill, Gavin Jones, and two anonymous reviewers. We are grateful to David Schimel for the invitation to publish this small collection of papers, and to Brion Salter for cartography. We appreciate funding by the U.S. Fish and Wildlife Service, The Wilderness Society; The Nature Conservancy, Oregon; Conservation Northwest; The Ecological Restoration Institute; Washington State Department of Natural Resources; USDA-FS, the Pacific Northwest and Pacific Southwest Research Stations, and the California Department of Forestry and Fire Protection in support of these reviews.

Disclaimer

The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service or the USDA Forest Service.

Literature Cited

Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences USA 113:11770–11775.

Ager, A. A., A. M. Barros, R. Houtman, R. Seli, and M. A. Day. 2020. Modelling the effect of accelerated forest management on long-term wildfire activity. Ecological Modelling 421:108962. https://doi.org/10.1016/j.ecolmodel.2020.108962

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications 12:1418–1433.

Anderson, M. K. 2013. Tending the wild: Native American knowledge and the management of California's natural resources. University of California Press, Berkeley, California, USA.

Asner, G. P., P. G. Brodrick, C. B. Anderson, N. Vaughn, D. E. Knapp, and R. E. Martin. 2016. Progressive forest canopy water loss during the 2012–2015 California drought. Proceedings of the National Academy of Sciences USA 113:E249–E255. https://doi.org/10.1073/pnas.1523397113

Balch, J. K., B. A. Bradley, J. T. Abatzoglou, R. C. Nagy, E. J. Fusco, and A. L. Mahood. 2017. Human-started wildfires expand the fire niche across the United States. Proceedings of the National Academy of Sciences of the United States of America 114:2946–2951.

Barnett, K., S. A. Parks, C. Miller, and H. T. Naughton. 2016. Beyond fuel treatment effectiveness: characterizing interactions between fire and treatments in the US. Forests 7:237. https://doi.org/10.3390/f7100237

Bastin, J. F., Y. Finegold, C. Garcia, D. Mollicone, M. Rezende, D. Routh, C. M. Zohner, and T. W. Crowther. 2019. The global tree restoration potential. Science 365:76–79.

Belsky, A., and D. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. Conservation Biology 11:315–327.

Bisson, P. A., B. E. Rieman, C. Luce, P. F. Hessburg, D. C. Lee, J. L. Kershner, G. H. Reeves, and R. E. Gresswell. 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. Forest Ecology and Management 178:213–229.

Bormann, B. T., R. W. Haynes, and J. R. Martin. 2007. Adaptive management of forest ecosystems: did some rubber hit the road? BioScience 57:186–191.

Bowman, D. M., G. L. Perry, S. I. Higgins, C. N. Johnson, S. D. Fuhlendorf, and B. P. Murphy. 2016. Pyrodiversity is the coupling of biodiversity and fire regimes in food webs. Philosophical Transactions of the Royal Society B 371:20150169.

Boyd, R. 1999. Indians, fire and the land. Pages 54. Oregon State University Press, Corvallis, Oregon, USA.

Bryant, T., K. Waring, A. Sánchez Meador, and J. B. Bradford. 2019. A framework for quantifying resilience to forest disturbance. Frontiers in Forests and Global Change 2:56. https://doi.org/10.3389/ffgc.2019.00056

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Calkin, D. E., K. M. Gebert, J. G. Jones, and R. P. Neilson. 2005. Forest service large fire area burned and suppression expenditure trends, 1970–2002. Journal of Forestry 103:179–183.

Carey, A. B. 2006. Active and passive forest management for multiple values. Northwestern Naturalist 87:18–30. https://doi.org/10.1898/1051-1733(2006)87[18:AAPFMF]2.0.CO;2

Churchill, D. J., A. J. Larson, M. C. Dahlgreen, J. F. Franklin, P. F. Hessburg, and J. A. Lutz. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. Forest Ecology and Management 291:442–457.

Cohen, J. D. 2000. Preventing disaster: home ignitability in the wildland-urban interface. Journal of Forestry 98:15–21. https://doi.org/10.1093/jof/98.3.15

Coop, J. D., et al. 2020. Wildfire-driven forest conversion in Western North American landscapes. BioScience 70:659–673.

Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecological Applications 26:686–699.

Dale, V. H., et al. 2001. Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. BioScience 51:723–734. https://doi.org/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2

Fettig, C. J., L. A. Mortenson, B. M. Bulaon, and P. B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, US. Forest Ecology and Management 432:164–178. https://doi.org/10.1016/j.foreco.2018.09.006

Franklin, J. F., and K. N. Johnson. 2012. A restoration framework for federal forests in the Pacific Northwest. Journal of Forestry 110:429–439.

Franklin, J. F., and K. N. Johnson. 2013. Ecologically based management: A future for federal forestry in the Pacific Northwest. Journal of Forestry 111:429–432.

Franklin, J. F., K. N. Johnson, and D. L. Johnson. 2018. Ecological forest management. Pages 646. Waveland Press, Long Grove, Illinois, USA.

Fulé, P. Z., et al. 2014. Unsupported inferences of high-severity fire in historical dry forests of the western United States: response to Williams and Baker. Global Ecology and Biogeography 23:825–830.

Garibaldi, A., and N. Turner. 2004. Cultural keystone species: implications for ecological conservation and restoration. Ecology and Society 9:1.

Garrard, G. E., F. Fidler, B. C. Wintle, Y. E. Chee, and S. A. Bekessy. 2016. Beyond advocacy: making space for conservation scientists in public debate. Conservation Letters 9:208–212.

Grainger, A., L. R. Iverson, G. H. Marland, and A. Prasad. 2019. Comment on "The global tree restoration potential". Science 366:eaay8334.

Hagmann, R. K., et al. 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. Ecological Applications e02431. https://doi.org/10.1002/eap.2431

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. Forest Ecology and Management 304:492–504.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2014. Historical conditions in mixed-conifer forests on the eastern slopes of the northern Oregon Cascade Range, USA. Forest Ecology and Management 330:158–170.

Henson, P., J. Thrailkill, B. Glenn, B. Woodbridge, and B. White. 2013. Using ecological forestry to reconcile spotted owl conservation and forest management. Journal of Forestry 111:433–437.

Henson, P., R. White, and S. P. Thompson. 2018. Improving implementation of the Endangered Species Act: finding common ground through common sense. BioScience 68:861–872. https://doi.org/10.1093/biosci/biy093

Hessburg, P. F., et al. 2015. Restoring fire-prone Inland Pacific landscapes: seven core principles. Landscape Ecology 30:1805–1835.

Hessburg, P. F., et al. 2016. Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. Forest Ecology and Management 366:221–250.

Hessburg, P. F., et al. 2019. Climate, environment, and disturbance history govern resilience of western North American forests. Frontiers in Ecology and Evolution 7:239. https://doi.org/10.3389/fevo.2019.00239

Hessburg, P. F., et al. 2020. The 1994 Eastside Screens large-tree harvest limit: review of science relevant to forest planning 25 years later. Pages 114. General Technical Report PNW-GTR-990. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Hessburg, P. F., and J. K. Agee. 2003. An environmental narrative of inland northwest United States forests, 1800–2000. Forest Ecology and Management 178:23–59.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211:117–139.

Hessburg, P. F., K. M. Reynolds, R. B. Salter, J. D. Dickinson, W. L. Gaines, and R. J. Harrod. 2013. Landscape evaluation for restoration planning on the Okanogan-Wenatchee National Forest, USA. Sustainability 5:805–840. https://doi.org/10.3390/su5030805

Hessburg, P. F., B. G. Smith, and R. B. Salter. 1999. Detecting change in forest spatial patterns from reference conditions. Ecological Applications 9:1232–1252.

Hessburg, P. F., B. G. Smith, R. B. Salter, R. D. Ottmar, and E. Alvarado. 2000. Recent changes (1930s–1990s) in spatial patterns of interior northwest forests, USA. Forest Ecology and Management 136:53–83. https://doi.org/10.1016/S0378-1127(99)00263-7

Higuera, P. E., M. E. Peters, L. B. Brubaker, and D. G. Gavin. 2007. Understanding the origin and analysis of sediment-charcoal records with a simulation model. Quaternary Science Reviews 26:1790–1809. https://doi.org/10.1016/j.quascirev.2007.03.010

Hof, A. R., C. C. Dymond, and D. J. Mladenoff. 2017. Climate change mitigation through adaptation: the effectiveness of forest diversification by novel tree planting regimes. Ecosphere 8:e01981.

Huffman, M. R. 2013. The many elements of traditional fire knowledge: synthesis, classification, and aids to cross-cultural problem solving in fire-dependent systems around the world. Ecology and Society 18:3.

Hurteau, M. D., J. B. Bradford, P. Z. Fulé, A. H. Taylor, and K. L. Martin. 2014. Climate change, fire management, and ecological services in the southwestern US. Forest Ecology and Management 327:280–289.

Hurteau, M. D., S. Liang, A. L. Westerling, and C. Wiedinmyer. 2019. Vegetation-fire feedback reduces projected area burned under climate change. Scientific Reports 9:1–6.

Isaak, D. J., C. H. Luce, B. E. Rieman, D. E. Nagel, E. E. Peterson, D. L. Horan, S. Parkes, and G. L. Chandler. 2010. Effects of climate change and wildfire on stream temperatures

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

and salmonid thermal habitat in a mountain river network. Ecological Applications 20:1350–1371.

Kangas, J., and A. Kangas. 2005. Multiple criteria decision support in forest management—the approach, methods applied, and experiences gained. Forest Ecology and Management 207:133–143. https://doi.org/10.1016/j.foreco.2004.10.023

Kay, C. E. 2000. Native burning in western North America: implications for hardwood forest management. Pages 19–27 *in* A. D. Yaussy, comp. Proceedings: Workshop on Fire, People, and the Central Hardwoods Landscape. General Technical Report NE-274. US Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania, USA.

Keane, R. E., G. J. Cary, I. D. Davies, M. D. Flannigan, R. H. Gardner, S. Lavorel, J. M. Lenihan, C. Li, and T. S. Rupp. 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. Ecological Modelling 179:3–27. https://doi.org/10.1016/j.ecolmodel.2004.03.015

Keane, R. E., R. A. Loehman, L. M. Holsinger, D. A. Falk, P. Higuera, S. M. Hood, and P. F. Hessburg. 2018. Use of landscape simulation modeling to quantify resilience for ecological applications. Ecosphere 9:e02414.

Keane, R. E., K. C. Ryan, T. T. Veblen, C. D. Allen, J. A. Logan, and B. Hawkes. 2002. The cascading effects of fire exclusion in Rocky Mountain ecosystems, Chapter 7. Pages 133–152 *in* J. Baron, editor. Rocky Mountain futures: An ecological perspective. Island Press, Washington, D.C., USA.

Kolden, C. A. 2019. We're not doing enough prescribed fire in the Western United States to mitigate wildfire risk. Fire 2:30. https://doi.org/10.3390/fire2020030

Kolden, C. A., and C. Henson. 2019. A socio-ecological approach to mitigating wildfire vulnerability in the wildland urban interface: a case study from the 2017 Thomas Fire. Fire 2:9.

Komatsu, H., and T. Kume. 2020. Modeling of evapotranspiration changes with forest management practices: A genealogical review. Journal of Hydrology 585:124835.

Lach, D., P. List, B. Steel, and B. Shindler. 2003. Advocacy and credibility of ecological scientists in resource decision-making: a regional study. BioScience 53:170–178. https://doi.org/10.1641/0006-3568(2003)053[0170:AACOES]2.0.CO;2

Lackey, R. T. 2007. Science, scientists, and policy advocacy. Conservation Biology 21:12–17.

Lake, F. K., and A. C. Christianson. 2019. Indigenous fire stewardship. Pages 1–9 *in* S. Mazello, editor. Encyclopedia of wildfire and wildland-urban interface (WUI) fires. Springer, Cham, Switzerland. https://doi.org/10.1007/978-3-319-51727-8_225-1

Lake, F. K., J. Parrotta, C. P. Giardina, I. Davidson-Hunt, and Y. Uprety. 2018. Integration of traditional and Western knowledge in forest landscape restoration. Pages 214–242 *in* S. Mansourian and J. Parrotta, editors. Forest landscape restoration: integrated approaches to support effective implementation. Routledge, Abingdon-on-Thames, UK.

Larson, A. J., and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management 267:74–92.

Lee, K. N. 1999. Appraising adaptive management. Conservation Ecology 3:1–21.

LeFevre, M. E., D. J. Churchill, A. J. Larson, S. M. Jeronimo, J. Bass, J. F. Franklin, and V. R. Kane. 2020. Evaluating restoration treatment effectiveness through a comparison of residual composition, structure, and spatial pattern with historical reference sites. Forest Science 66:578–588.

Levine, C. R., C. V. Cogbill, B. M. Collins, A. J. Larson, J. A. Lutz, M. P. North, C. M. Restaino, H. D. Safford, S. L. Stephens, and J. J. Battles. 2017. Evaluating a new method for reconstructing forest conditions from General Land Office survey records. Ecological Applications 27:1498–1513.

Lewis, S. L., E. T. Mitchard, C. Prentice, M. Maslin, and B. Poulter. 2019. Comment on "The global tree restoration potential". Science 366:eaaz0388.

Liang, S., M. D. Hurteau, and A. L. Westerling. 2018. Large-scale restoration increases carbon stability under projected climate and wildfire regimes. Frontiers in Ecology and the Environment 16:207–212.

Lightfoot, K. G., et al. 2013. Anthropogenic burning on the central California coast in Late Holocene and early historical times: findings, implications, and future directions. California Archaeology 5:371–390.

Long, J. N. 2009. Emulating natural disturbance regimes as a basis for forest management: a North American view. Forest Ecology and Management 257:1868–1873.

Long, J. W., and F. K. Lake. 2018. Escaping social-ecological traps through tribal stewardship on national forest lands in the Pacific Northwest, United States of America. Ecology and Society 23:10.

Long, J. W., F. K. Lake, R. W. Goode, and B. M. Burnette. 2020. How traditional tribal perspectives influence ecosystem restoration. Ecopsychology 12:71–82.

Lydersen, J. M., M. P. North, E. E. Knapp, and B. M. Collins. 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Reference conditions and long-term changes following fire suppression and logging. Forest Ecology and Management 304:370–382.

Madeira, L., and T. Gartner. 2018. Forest resilience bond sparks innovative collaborations between water utilities and wide-ranging stakeholders. Journal American Water Works Association 110:42–49. http://doi: 10.1002/awwa.1097

McGarigal, K., and W. H. Romme. 2012. Modeling historical range of variation at a range of scales: an example application. Pages 128–145 *in* J. Wiens, C. Regan, G. Hayward, and H. Safford, editors. Historical environmental variation in conservation and natural resource management. Wiley, New York, New York, USA.

McKenzie, D., Z. E. Gedalof, D. L. Peterson, and P. Mote. 2004. Climatic change, wildfire, and conservation. Conservation Biology 18:890–902.

Meyer, M. D., J. W. Long, and H. D. Safford. 2021. Postfire restoration framework for national forests in California. Pages 204. General Technical Report PSW-GTR-270. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Mildrexler, D. J., L. T. Berner, B. E. Law, R. A. Birdsey, and W. R. Moomaw. 2020. Large trees dominate carbon storage in forests east of the cascade crest in the United States Pacific Northwest. Frontiers in Forests and Global Change 3. http://dx.doi.org/10.3389/ffgc.2020.594274

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17:2145–2151.

Moreira, F., et al. 2020. Wildfire management in Mediterranean-type regions: paradigm change needed. Environmental Research Letters 15:011001.

Morgan, P., E. K. Heyerdahl, and C. E. Gibson. 2008. Multi-season climate synchronized forest fires throughout the 20th century, northern Rockies, USA. Ecology 89:717–728.

Moritz, M. A., M. D. Hurteau, K. N. Suding, and C. M. D'Antonio. 2013. Bounded ranges of variation as a framework for future conservation and fire management. Annals of the New York Academy of Sciences 1286:92–107.

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Newman, E. A. 2019. Disturbance ecology in the Anthropocene. Frontiers in Ecology and Evolution 7:147.

Norgaard, K. M. 2014. The politics of fire and the social impacts of fire exclusion on the Klamath. Humboldt Journal of Social Relations 36:77–101.

North, M., B. Collins, J. Keane, J. W. Long, C. Skinner, and B. Zielinski. 2014. Synopsis of emergent approaches. Pages 55–70 *in* J. W. Long, L. Quinn-Davidson, and C. N. Skinner, editors. Science synthesis to support socioecological resilience in the Sierra Nevada and southern Cascade Range. General Technical Report PSW-GTR-247. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.

North, M. P., S. L. Stephens, B. M. Collins, J. K. Agee, G. Aplet, J. F. Franklin, and P. Z. Fule. 2015. Reform forest fire management. Science 349:1280–1281.

North, M., P. Stine, K. O'Hara, W. Zielinski, and S. Stephens. 2009. An ecosystem management strategy for Sierran mixed-conifer forests. Pages 49. General Technical Report PSW-GTR-220 (Second printing, with addendum). US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. Frontiers in Ecology and the Environment 4:481–487.

Odion, D. C., et al. 2014. Examining historical and current mixed-severity fire regimes in ponderosa pine and mixed-conifer forests of western North America. PLoS ONE 9:e87852.

Parks, S. A., and J. T. Abatzoglou. 2020. Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985 to 2017. Geophysical Research Letters 47:e2020GL089858. https://doi.org/10.3389/ffgc.2021.629198

Parks, S. A., C. Miller, J. T. Abatzoglou, L. M. Holsinger, M. A. Parisien, and S. Z. Dobrowski. 2016. How will climate change affect wildland fire severity in the western US? Environmental Research Letters 11:035002.

Parks, S. A., C. Miller, M. A. Parisien, L. M. Holsinger, S. Z. Dobrowski, and J. Abatzoglou. 2015. Wildland fire deficit and surplus in the western United States, 1984–2012. Ecosphere 6:1–13. https://doi.org/10.1890/ES15-00294.1

Parr, C. L., and A. N. Andersen. 2006. Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. Conservation Biology 20:1610–1619.

Peery, M. Z., G. M. Jones, R. J. Gutiérrez, S. M. Redpath, A. B. Franklin, D. Simberloff, M. G. Turner, V. C. Radeloff, and G. C. White. 2019. The conundrum of agenda-driven science in conservation. Frontiers in Ecology and the Environment 17:80–82. http://doi:10.1002/fee.2006

Perry, D. A., P. F. Hessburg, C. N. Skinner, T. A. Spies, S. L. Stephens, A. H. Taylor, J. F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. Forest Ecology and Management 262:703–717.

Pielke, R. 2007. The honest broker: making sense of science in policy and politics. Cambridge University Press, London, UK.

Povak, N. A., P. F. Hessburg, and R. B. Salter. 2018. Evidence for scale-dependent topographic controls on wildfire spread. Ecosphere 9:e02443.

Power, M. J., B. F. Codding, A. H. Taylor, T. W. Swetnam, K. E. Magargal, D. W. Bird, and J. F. O'Connell. 2018. Human fire legacies on ecological landscapes. Frontiers in Earth Science 6:151.

Prichard, S. J., et al. 2021. Adapting western US forests to wildfires and climate change: ten common questions. Ecological Applications. http://dx.doi.org/10.1002/eap.2433

Prichard, S. J., C. S. Stevens-Rumann, and P. F. Hessburg. 2017. Tamm review: shifting global fire regimes: lessons from reburns and research needs. Forest Ecology and Management 396:217–233.

Radeloff, V. C., et al. 2018. Rapid growth of the US wildland-urban interface raises wildfire risk. Proceedings of the National Academy of Sciences USA 115:3314–3319.

Raphael, M. G., M. J. Wisdom, M. M. Rowland, R. S. Holthausen, B. C. Wales, B. G. Marcot, and T. D. Rich. 2001. Status and trends of habitats of terrestrial vertebrates in relation to land management in the interior Columbia River Basin. Forest Ecology and Management 153:63–87.

Reynolds, K. M., P. F. Hessburg, and P. S. Bourgeron. 2014. Making transparent environmental management decisions. Springer, Berlin and Heidelberg, Germany.

Rieman, B. E., P. F. Hessburg, C. Luce, and M. R. Dare. 2010. Wildfire and management of forests and native fishes: conflict or opportunity for convergent solutions? BioScience 60:460–468.

Rosenzweig, C., et al. 2008. Attributing physical and biological impacts to anthropogenic climate change. Nature 453:353–357.

Rummer, B., et al. 2005. A strategic assessment of forest biomass and fuel reduction treatments in Western States. Pages 17. General Technical Report RMRS-GTR-149. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Schoennagel, T., et al. 2017. Adapt to more wildfire in western North American forests as climate changes. Proceedings of the National Academy of Sciences USA 114:4582–4590.

Schoennagel, T., R. L. Sherriff, and T. T. Veblen. 2011. Fire history and tree recruitment in the Colorado Front Range upper montane zone: implications for forest restoration. Ecological Applications 21:2210–2222.

Scott, J. M., J. L. Rachlow, R. T. Lackey, A. B. Pidgorna, J. L. Aycrigg, G. R. Feldman, L. K. Svancara, D. A. Rupp, D. I. Stanish, and R. K. Steinhorst. 2007. Policy advocacy in science: prevalence, perspectives, and implications for conservation biologists. Conservation Biology 21:29–35.

Shakesby, R. A., and S. H. Doerr. 2006. Wildfire as a hydrological and geomorphological agent. Earth-Science Reviews 74:269–307.

Soulé, M. E. 1985. What is conservation biology? BioScience 35:727–734. https://doi.org/10.2307/1310054

Sowerwine, J., D. Sarna-Wojcicki, M. Mucioki, L. Hillman, F. K. Lake, and E. Friedman. 2019*a*. Enhancing indigenous food sovereignty: a five-year collaborative tribal-university research and extension project in California and Oregon. Journal of Agriculture, Food Systems, and Community Development 9:167–190. https://doi.org/10.5304/jafscd.2019.09B.013

Sowerwine, J., M. Mucioki, D. Sarna-Wojcicki, and L. Hillman. 2019*b*. Reframing food security by and for Native American communities: a case study among tribes in the Klamath River basin of Oregon and California. Food Security 11:579–607. https://doi.org/10.1007/s12571-019-00925-y

Spies, T. A., et al. 2014. Examining fire-prone forest landscapes as coupled human and natural systems. Ecology and Society 19:9. http://dx.doi.org/10.5751/ES-06584-190309

Spies, T. A., et al. 2019. Twenty-five years of the Northwest Forest Plan: what have we learned? Frontiers in Ecology and the Environment 17:511–520.

Spies, T. A., P. F. Hessburg, C. N. Skinner, K. J. Puettmann, M. J. Reilly, R. J. Davis, J. A. Kertis, J. W. Long, and D. C. Shaw. 2018. Old growth, disturbance, forest succession, and management in the area of the Northwest Forest Plan. Pages 95–243, 966 *in* T. A. Spies, P. A. Stine, R. Gravenmier, J. W. Long, and M. J. Reilly, tech. coords. Synthesis of science to inform

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

land management within the Northwest Forest Plan area. General Technical Report PNW-GTR-966. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Stephens, S. L., et al. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. Ecological Applications 19:305–320. https://doi.org/10.1890/07-1755.1

Stephens, S. L., et al. 2019. Is fire "for the birds"? How two rare species influence fire management across the US. Frontiers in Ecology and the Environment 17:391–399. https://doi.org/10.1002/fee.2076

Stephens, S. L., C. I. Millar, and B. M. Collins. 2010. Operational approaches to managing forests of the future in Mediterranean regions within a context of changing climates. Environmental Research Letters 5:024003.

Stephens, S. L., B. M. Collins, C. J. Fettig, M. A. Finney, C. M. Hoffman, E. E. Knapp, M. P. North, H. Safford, and R. B. Wayman. 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. BioScience 68:77–88.

Stephens, S. L., A. L. Westerling, M. D. Hurteau, M. Z. Peery, C. A. Schultz, and S. Thompson. 2020. Fire and climate change: conserving seasonally dry forests is still possible. Frontiers in Ecology and the Environment 18:354–360.

Stevens, J. T., H. D. Safford, and A. M. Latimer. 2014. Wildfire-contingent effects of fuel treatments can promote ecological resilience in seasonally dry conifer forests. Canadian Journal of Forest Research 44:843–854.

Stevens-Rumann, C., and P. Morgan. 2016. Repeated wildfires alter forest recovery of mixed-conifer ecosystems. Ecological Applications 26:1842–1853.

Stevens, J. T., et al. 2016. Average stand age from forest inventory plots does not describe historical fire regimes in ponderosa pine and mixed-conifer forests of western North America. PLoS One 11:e0147688.

Stewart, O. C. 2002. Forgotten fires: native Americans and the transient wilderness. University of Oklahoma Press, Norman, Oklahoma, USA.

Stockdale, C. A., C. Bozzini, S. E. MacDonald, and E. Higgs. 2015. Extracting ecological information from oblique angle terrestrial landscape photographs: performance evaluation of the WSL Monoplotting Tool. Applied Geography 63:315–325. https://doi.org/10.1016/j.apgeog.2015.07.012

Stockdale, C. A., S. E. MacDonald, and E. Higgs. 2019. Forest closure and encroachment at the grassland interface: a century-scale analysis using oblique repeat photography. Ecosphere 10:e02774. https://doi.org/10.1002/ecs2.2774

Sunstein, C. 2003. The paralyzing principle: Does the precautionary principle point us in any helpful direction?. Regulation, Winter, 2002–2003.

Syphard, A. D., J. E. Keeley, A. B. Massada, T. J. Brennan, and V. C. Radeloff. 2012. Housing arrangement and location determine the likelihood of housing loss due to wildfire. PLoS ONE 7:e33954.

Taylor, A. H., and C. N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications 13:704–719.

Taylor, A. H., V. Trouet, C. N. Skinner, and S. L. Stephens. 2016. Socioecological transitions trigger fire regime shifts and modulate fire–climate interactions in the Sierra Nevada, USA, 1600–2015 CE. Proceedings of the National Academy of Sciences USA 113:13684–13689.

Taylor, R. S., S. J. Watson, D. G. Nimmo, L. T. Kelly, A. F. Bennett, and M. F. Clarke. 2012. Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? Diversity and Distributions 18:519–529.

Thomas, D., D. Butry, S. Gilbert, D. Webb, and J. Fung. 2017. The costs and losses of wildfires. NIST Special Publication 1215. http://dx.doi.org/10.6028/NIST.SP.1215

Vaillant, N. M., and E. D. Reinhardt. 2017. An evaluation of the Forest Service Hazardous Fuels Treatment Program—Are we treating enough to promote resiliency or reduce hazard? Journal of Forestry 115:300–308.

Varghese, J., and S. S. Crawford. 2021. A cultural framework for Indigenous, Local, and Science knowledge systems in ecology and natural resource management. Ecological Monographs 91:e01431.

Veldman, J. W., et al. 2019. Comment on "The global tree restoration potential". Science 366:eaay7976.

Wei, Y., M. P. Thompson, J. H. Scott, C. D. O'Connor, and C. J. Dunn. 2019. Designing operationally relevant daily large fire containment strategies using risk assessment results. Forests 10:311. https://doi.org/10.3390/f10040311

Wellerstein, A. 2018. The myth of apolitical science. Science 362:1006. http://doi.org/ 10.1126/science.aav4900

Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society B 371:20150178.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313:940–943. http://doi.org/10.1126/science.1128834

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences USA 108:13165–13170.

Williams, M. A., and W. L. Baker. 2012. Spatially extensive reconstructions show variable-severity fire and heterogeneous structure in historical western United States dry forests. Global Ecology and Biogeography 21:1042–1052.

Wood, C. M., and G. M. Jones. 2019. Framing management of social-ecological systems in terms of the cost of failure: the Sierra Nevada, USA as a case study. Environmental Research Letters 14:105004.

Wu, J., and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Review of Biology 70:439–466. https://doi.org/10.1086/419172

19395582, 2021, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2432, Wiley Online Library on [30/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Ecological Applications, 19(1), 2009, pp. 163–180
© 2009 by the Ecological Society of America

Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage

Tara Hudiburg,[1] Beverly Law, David P. Turner, John Campbell, Dan Donato, and Maureen Duane

Department of Forest Science, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. Net uptake of carbon from the atmosphere (net ecosystem production, NEP) is dependent on climate, disturbance history, management practices, forest age, and forest type. To improve understanding of the influence of these factors on forest carbon stocks and flux in the western United States, federal inventory data and supplemental field measurements at additional plots were used to estimate several important components of the carbon balance in forests in Oregon and Northern California during the 1990s. Species- and ecoregion-specific allometric equations were used to estimate live and dead biomass stores, net primary productivity (NPP), and mortality. In the semiarid East Cascades and mesic Coast Range, mean total biomass was 8 and 24 kg C/m^2, and mean NPP was 0.30 and 0.78 kg C·m^{-2}·yr^{-1}, respectively. Maximum NPP and dead biomass stores were most influenced by climate, whereas maximum live biomass stores and mortality were most influenced by forest type. Within ecoregions, mean live and dead biomass were usually higher on public lands, primarily because of the younger age class distribution on private lands. Decrease in NPP with age was not general across ecoregions, with no marked decline in old stands (>200 years old) in some ecoregions. In the absence of stand-replacing disturbance, total landscape carbon stocks could theoretically increase from 3.2 ± 0.34 Pg C to 5.9 ± 1.34 Pg C (a 46% increase) if forests were managed for maximum carbon storage. Although the theoretical limit is probably unattainable, given the timber-based economy and fire regimes in some ecoregions, there is still potential to significantly increase the land-based carbon storage by increasing rotation age and reducing harvest rates.

Key words: carbon cycle; climate regime; coarse woody debris, CWD; inventory data; management; mortality rates; net primary production; west-coast forests, USA.

Introduction

The amount of carbon sequestered by forest ecosystems plays an important role in regulating atmospheric levels of carbon dioxide (Canadell et al. 2007, Denman et al. 2007). Factors affecting the amount and rate at which forests sequester carbon include climate, disturbance, management, land use history, and species composition (Peet 1981, Harcombe et al. 1990, Law et al. 2004, Krankina et al. 2005, Gough et al. 2007). Pending and future forest management policies are attempting to offset anthropogenic carbon dioxide emissions by increasing and maintaining land-based sinks of carbon (IPCC 2007). Thus, it is important to quantify current and potential forest carbon pools and fluxes, and to understand factors that account for geographic variation.

Of particular interest is examination of age-specific trends. Commonly accepted patterns of live biomass accumulation and NPP in relation to stand age show a stabilization or decline as stands age (Bormann and Likens 1969, Odum 1969, Peet 1981). These patterns have been identified using a variety of small-scale ecological studies that tend to select homogeneous stands (McCune and Menges 1986). However, because federal inventory plots are located in all types of stands (including transitional forests, uneven-aged stands, and areas that have experienced partial disturbances), the patterns of growth that emerge from inventory data may not follow idealized trends. The distinction between patterns elucidated from a sample of forest plots selected based on defined structural criteria, and a sample of stands selected regularly from the entire population is important when validating process models applied across landscapes (e.g., Jenkins et al. 2001). For this reason the patterns of carbon pools and fluxes over time, identified in inventory data, are uniquely powerful in that they can reveal collective trends (i.e., average values) in addition to idealized trends (i.e., upper bounds or maximum values).

In this study, data from supplemental field plots (i.e., foliage and fine-root metrics) and federal inventory data (FIA) were used to examine patterns of NPP, mortality, and live and dead carbon stores in different ecoregions of Oregon and Northern California, USA. The objectives were to: (1) identify age-related patterns of mean and maximum live biomass, dead biomass, NPP, and mortality; (2) determine the influence of forest type,

Manuscript received 6 December 2007; revised 11 April 2008; accepted 14 May 2008. Corresponding Editor: A. D. McGuire.
[1] E-mail: tara.hudiburg@oregonstate.edu

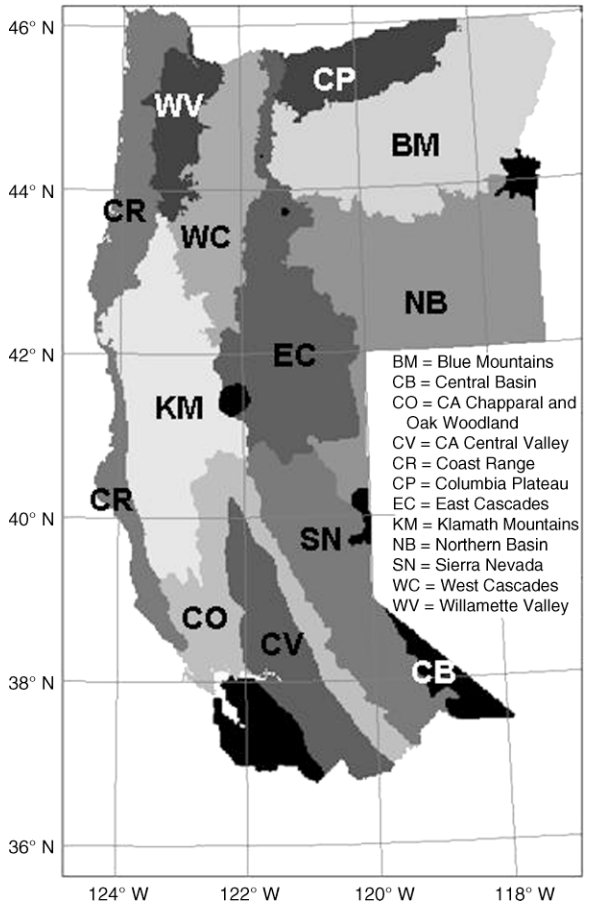


FIG. 1. ORCA study region (Oregon and Northern California, USA) divided by Omernik Level III ecoregions (Omernik 1987); different shades of gray show the different ecoregions.

ecoregion (climate), and ownership (management) on these patterns; (3) quantify total and theoretical forest carbon stocks and NPP over the study region; and (4) investigate the potential for increased land-based carbon sequestration in Oregon and Northern California forests. We examined differences in carbon pools and fluxes due to species composition, climate, and management indicated by forest type, ecoregion, and ownership, respectively. We used the patterns to determine the current land-based total stocks (excluding forest floor and soil carbon) and NPP, as well as the theoretical stocks and NPP in the absence of stand-replacing disturbance. The theoretical estimates are representative of the potential for carbon sequestration in this region through management practices. This study complements studies by Hicke et al. (2007) and Van Tuyl et al. (2005) by including additional carbon pools and fluxes (dead wood and shrub biomass, NPP, and mortality), examining possible causes of variation due to management and climate, and by further refining the estimates of carbon stocks using supplemental data and species- and ecoregion-specific allometrics.

METHODS

Study area

The ORCA project is part of the North American Carbon Program (NACP), where the goal is to quantify and understand the carbon balance of North America. The study area is the entire state of Oregon and the northern half of California (Fig. 1). The disturbance history of the region includes frequent windthrow near the coast, relatively short harvest cycles, and centuries-long fire cycles west of the Cascade crest, moderate-length harvest cycles with more frequent natural fire cycles to the drier east, and livestock grazing in the Great Basin.

The area was divided into 12 ecoregions using the U.S. EPA Level III Omernik classification scheme (Omernik 1987). The ecoregions are classified according to similar biotic and abiotic characteristics, including dominant land cover type, climate, soils, and topography. They encompass several cover types such as chaparral, juniper woodlands, coastal Douglas-fir and hemlock, and true fir alpine forests. Age-related patterns of biomass accumulation, NPP, and mortality were only examined for the dominant six ecoregions (Table 1). Totals and means were calculated for all ecoregions (Appendix: Tables A1 and A2). Approximately 50% of this area is forested land, with 56% under public ownership and 44% under private ownership (Table 1). There is a steep west to east climatic gradient, with annual precipitation ranging from 2510 mm in the Coast Range to 120 mm in the Central Basin.

Data were used from several different inventories collected by federal and state agencies and our field crews. Within plots, allometric calculations were made for each individual tree, shrub, and woody detritus record and summations were made to obtain plot total live and dead biomass carbon estimates per unit ground area and an NPP and mortality estimate per unit ground area per year.

FIA database

The federal inventory program (FIA, Forest Inventory and Analysis) has undergone recent changes in sampling protocols starting in 2001. Historically, states were measured in subsections with a complete inventory of the states completed within 10–12 years (referred to as periodic inventories). The last complete inventory (1991–1999) in Oregon and California is summarized in the Integrated Database version 2.0 or IDB (Waddell and Hiserote 2005). Under a more recent protocol (annual inventory), portions of each subsection are completed each year, with a complete inventory expected by 2010. We chose to use the earlier periodic database because it is the most recent complete cycle and thus more representative of the study region. Our results thus approximate conditions in the mid-1990s.

TABLE 1. Ecoregion mean annual precipitation (MAP), mean winter and summer temperature (MAT), total and forested area, and stand age.

Ecoregion†	No. plots	MAT (°C) (winter/summer)	MAP (mm)	Total area (ha)	Forested area (ha)	Mean stand age (yr)‡			All plots, and plots >200 yr old (%)	
						All	Private	Public	Private	Public
BM	1266	−2/17	630	6 206 770	2 852 987	195 (3)	121 (9)	204 (3)	10, <1	90, 42
CR	737	7/18	2500	3 633 280	3 280 871	128 (4)	83 (3)	156 (6)	35, <1	65, 14
EC	1834	−3/17	500	4 795 480	2 971 042	185 (2)	133 (5)	190 (3)	8, 1	92, 36
KM	1526	3/21	1500	4 850 310	4 076 569	219 (4)	132 (6)	231 (4)	11, 1	89, 47
SN	1268	5/15	1500	3 931 700	3 059 246	196 (4)	146 (7)	201 (4)	9, 1	91, 38
WC	1896	4/16	2200	3 038 260	2 889 914	248 (4)	105 (36)	254 (4)	4, <1	96, 57
CB	26	4/11	150	834 689	165 932	210 (27)	84	219 (28)	4, 0	96, 50
CO	116	4/30	630	4 222 085	1 773 527	120 (6)	117 (7)	113 (14)	70, 7	30, 3
CP	4	0/21	250	1 756 090	40 046	145 (45)	145 (45)	...	100, 25	...
CV	0	10/17	450	2 656 190	49 832	...	...	...	...	...
NB	36	−1/18	250	6 556 370	174 125	150 (21)	184 (54)	177 (26)	17, 3	83, 22
WV	46	4/20	1270	1 373 040	504 923	109 (13)	86 (7)	162 (36)	70, 0	30, 9
Total	8755	2/18	1075	43 854 264	21 839 014	201 (2)	115 (2)	213 (1.5)	31, 1	41

Note: Ellipses in cells indicate that no data are available.

† BM, Blue Mountains; CR, Coast Range; EC, East Cascades; KM, Klamath Mountains; SN, Sierra Nevada; WC, West Cascades; CO, California Chaparral and Oak Woodlands; WV, Willamette Valley; NB, North Basin and Range; CB, Central Basin and Range; CP, Columbia Plateau; CV, Central California Valley.

‡ Standard errors in parentheses.

§ The first value is the percentage of total plots in private vs. public ownership. The second value after the comma is the percentage of total plots that are >200 years old in private vs. public ownership.

There were 14 188 plots with live tree data and 12 380 plots with woody detritus and understory data within the study area boundary (Fig. 1). The inventory design consists of 0.404-ha (1-acre) plots systematically placed across the landscape, encompassing a representative range of stand ages, disturbance histories, ownerships, and land cover types. The inventory data include tree diameter (dbh), actual height, wood increment, age, and species. Understory woody shrub data include percent cover, height, and species. Coarse woody debris and snag data include diameter, decay class, and species. We excluded plots that did not have enough increment data (1290 plots) to suitably calculate a stand age or a radial growth. One or more condition classes were assigned to plots that had more than one ownership, forest type, or disturbance history. Because we were interested in differences due to ownership and forest type, we chose to use plots with only one condition class. There were 4143 multi-condition plots distributed throughout the study area. A separate analysis of live biomass that included the multi-condition plots was done to determine if exclusion of these plots affected the overall results. The ecoregion means for total live biomass were slightly higher in the majority of areas, equivalent in some, and lower in the Coast Range by 0.90 kg C/m^2 (Appendix: Table A3). The regression of the 5-year age bin means for all plots vs. the corresponding single-condition bin means had values ranging from $r^2 = 0.75$ in the Blue Mountains to $r^2 = 0.91$ in the West Cascades.

After exclusions, 8755 plots remained with live tree and understory data, of which 8135 plots had measured woody detritus data. These plots were used to analyze NPP, mortality, and biomass for age-related trends as influenced by ecoregion, management, and forest type. To evaluate and augment the federal inventory plots, we also used data from 170 supplemental field plots systematically dispersed among the ecoregions in the study area. Although these 1-ha plots cover a larger spatial area, the subplot and transect layouts, measurement protocols, and data collected met or exceeded the minimum standards of the federal inventory. Our plot locations were selected using a hierarchical random sampling design based on climate, forest type, and age (Law et al. 2006). The additional sampling was designed to allow a more comprehensive assessment of the carbon stocks and fluxes (Law et al. 2004, Sun et al. 2004, Van Tuyl et al. 2005, Law et al. 2006) by measuring foliage and soil carbon and nitrogen, leaf retention time, foliage and fine-root biomass and production (on selected plots), leaf area index, and litter stocks.

Stand age

Plot stand age was computed as the mean of the oldest 10% of trees (Spies and Franklin 1991, Van Tuyl et al. 2005). In cases where there were fewer than three trees in the oldest 10%, a mean of all aged trees on the plot was used. Stands older than 600 years were grouped into a single age class to account for an increasing trend in within plot variation. Although this method is the appropriate metric to best detect trends in growth and mortality, it is different than age based on time since disturbance and does not include effects of delayed establishment that vary widely (and probably with ecoregion, forest type, and ownership).

Ownership and forest types

Ownership was used as a surrogate for management practices because anthropogenic disturbances (i.e.,

clearcut harvest and thinning) have been more common on privately owned lands than on publicly owned lands in this region (Spies et al. 1994, Cohen et al. 2002). Public lands are defined as all non-private lands (federal, tribal, state, county, and so on). Private lands include small ownerships to large industrial properties.

Inventory plots were assigned a forest type code based on the dominant species on the plot. We grouped forest types into seven classes: (1) fir/Douglas-fir/hemlock, (2) larch and cedar/sequoia/redwood, (3) juniper, (4) spruce, (5) pine, (6) hardwoods, and (7) non-stocked. Non-stocked forest types are assigned to plots with a large percentage of ground area that is unsuitable for growth (i.e., rocky substrates).

Biomass

A database of volume and biomass allometric equations was compiled from prior studies (e.g., Means et al. 1994, Law et al. 2001, Van Tuyl et al. 2005) and new literature. We aimed to apply as many species-specific and ecoregion-specific equations as possible. Biomass estimates for trees included bole, bark, branch, foliage, and coarse roots (Appendix: Table A4). Species-specific wood densities (Maeglin and Wahlgren 1972, Forest Products Laboratory 1974) from wood cores obtained on our 170 supplemental plots were used to convert bole and coarse-root volume to biomass. For standing dead trees, wood densities were reduced according to decay class (Waddell 2002). Tree component biomass estimates were converted to kilograms per unit of ground area by multiplying by the tree-specific trees per hectare (TPH) and by 0.51 to obtain units of carbon (Law et al. 2001). TPH is a scaling factor for each tree record that is based on the sampled area and is supplied by the IDB specifically for generating plot-scale biomass estimates (Waddell and Hiserote 2005).

Fine-root biomass was estimated using an equation from earlier studies (Van Tuyl et al. 2005; Appendix: Table A4) relating leaf area index (LAI) and fine-root biomass. LAI is not measured on inventory plots, but was calculated by dividing foliage biomass (from the allometric equations) by the leaf mass per unit leaf area (LMA). LMA was obtained from a look-up table of species-specific values derived from measurements on the supplemental plots in each of the ecoregions. In some cases, a species-specific value was not available so a closely related (i.e., congeneric) species was used.

The conversion of shrub volume to biomass was from a database of allometric equations based on shrubs harvested at our supplemental plots. In total, 12 species were harvested, covering a wide range of morphology, leaf type, and leaf longevity, allowing for substitution of equations for all species where an equation could not be found. Shrub volume was calculated as the product of the recorded fraction of plot cover, plot area, and height. Coarse woody debris biomass was estimated following Waddell (2002). Biomass was calculated using piece volume, species-specific wood density, and a decay-class density reduction factor.

NPP and mortality

To calculate NPP for a plot, a radial increment is necessary for every tree on the plot. Federal inventory includes stem increment cores for a subsample of the trees on each plot. For our estimates, trees on a plot were divided into dbh quartiles and the mean radial increment of cored trees in each quartile was assigned to all other trees in the same quartile (Sun et al. 2004, Van Tuyl et al. 2005).

Net primary production of all tree woody components was estimated as the difference in biomass at two points in time and was divided by the remeasurement interval (usually about 10 years). A previous dbh and height for each tree were necessary to calculate a previous biomass. Previous dbh was derived by back-calculation from current dbh and the radial increment, and previous height was recorded for remeasured trees or was modeled for unmeasured trees in the previous inventory using height–diameter regression equations from our supplemental plot data and BioPak (Means et al. 1994).

Woody shrub, foliage, and fine-root NPP were calculated using look-up tables constructed from supplemental plot data. Foliage NPP was calculated by dividing foliage biomass per tree by the average foliage retention time (average number of years of foliage that a stand carries). An ecoregion species-specific look-up table of foliage retention values was constructed from data gathered on the supplemental plots. Woody shrub NPP was calculated as a percentage increase in biomass per year. Increment disks from several shrub species were collected on the supplemental plots to produce a look-up table of average percentage increase in biomass for the species in each ecoregion. Fine-root NPP was calculated as the product of fine-root biomass and average fine-root turnover (1.2 $year^{-1}$) obtained from the literature and supplemental plot data (Keyes and Grier 1981, Campbell et al. 2004).

Mortality in kilograms of carbon per meter squared per year was only computed for trees. The IDB has assigned a mortality rate, the probability (0–1) that a given tree may die in one year due to natural causes, to each tree record. It is derived from a ratio of dead-to-live trees that were tallied on plots throughout the inventory area and developed for different groups by species and/or location (Waddell and Hiserote 2005). The amount of mortality expressed as the biomass loss per year can be estimated by multiplying the total live tree biomass by the location and/or species-specific mortality rate.

Statistical analysis

S-PLUS version 7.02 (S-PLUS 2005) was used for all statistical analysis. The questions of interest were addressed by comparing the coefficients of the response functions fit to the age-based distributions. Plots with

stand ages greater than 600 years were grouped into a single age group. Because less than 1% of plots on private land had age groups greater than 200 years, statistical analysis for comparisons between ownerships were restricted to plots aged 200 years or less for both public and private land.

Historically, private land ownership has tended to be located in lower elevation forested areas characterized by higher productivity. We confirmed this difference by comparing mean site index (a measure of site potential productivity) across ownerships for the stand area. We found a significantly higher mean site index value for private lands ($P < 0.01$, by permutation test). To isolate effects of differences in stand age distribution between ownerships from differences in site potential, the public land data set in each ecoregion was randomly subsampled using a constrained range and distribution of site indexes that was defined by private land distributions in the same ecoregion. This distribution was then used for the comparisons across ownerships.

To compare the coefficients of the fitted functions, the data for each ecoregion, ownership, or forest type were first binned into 25-year age groups and a stratified random sample of observations was chosen to ensure that the sample included data points from the entire age range. The appropriate functions were then fit to the sample data set. The sampling process and curve fitting were repeated to obtain 10 different estimates of each coefficient (used to produce a stand error) for each ecoregion and for ownership and forest type within ecoregion. A weighted one-way ANOVA using the coefficient standard errors as the weight was run for each coefficient to test for significant differences. To determine the relative influence of ecoregion, ownership, and forest type on biomass stores, NPP, and mortality across the entire study area and within ecoregion, the data were $\log_e$-transformed and linear regression models were compared using Akaike's information criterion (AIC). For the entire study area, model weights for age only, age + ownership, age + forest type, and age + ecoregion were calculated and ranked to determine the most influential explanatory variable (Burnham and Anderson 2002). Within ecoregion, model weights were calculated for age only, age + ownership and age + forest type.

Chapman-Richards functions (Pienaar and Turnbull 1973) were fit to live biomass and mortality data to compare the amount (mean and maximum) of carbon stored in biomass as a function of age:

$$\text{biomass} = a[1 - \exp(-b \times \text{stand age})]^c \quad (1)$$

where parameter a is the asymptote, or the maximum amount of biomass carbon; parameter b determines the rate in years that it takes to reach the maximum amount; and c is a shaping parameter that gives a Chapman-Richards relationship the characteristic sigmoid shape. Because we were interested in the age at which NPP peaked and started to decline, a peak function (three-parameter, log-normal) was fit to the NPP data:

$$\text{NPP} = a \times \exp\left\{-0.5[\ln(\text{stand age}/c)/b]^2\right\} \quad (2)$$

where parameter a is the asymptote or the maximum NPP; b is the rate to reach maximum; and c represents the age of initial NPP decline.

Woody detritus data can be fit with a standard decay function plus a Chapman-Richards function (Janisch and Harmon 2002). Stands typically start with large stores of legacy dead wood from prior stand development or downed wood caused by disturbance and then start to accumulate dead biomass as they age. The decay function quantifies the decay of the legacy dead wood in clearcut/burned and very young stands and the Chapman-Richards function quantifies the accumulation of dead wood as the stand ages:

$$\text{biomass} = d \times \exp(-e \times \text{stand age}) + a[1 - \exp(-b \times \text{stand age})]^c \quad (3)$$

where parameter d is the initial carbon stores and e is the decay rate in years. Although we were able to fit this function to all of the data in each ecoregion, we were unable to detect a U-shaped pattern with stand age in the smaller random samples used to compare the coefficients of the fitted function. Therefore, the data were divided into three age classes and a permutation test for a difference of means in each age class (by ecoregion or ownership) was used.

All of the above-mentioned curves were fit to both the mean values in each 5-year age bin and to the 99th percentile (hereafter "upper bound") of each age bin. Curves fit to the mean values represent the average realized trends of biomass, mortality, and NPP, whereas the curve fit to the upper bounds should represent the maximum values of stands in the ecoregion given minimal disturbance and ideal site and growing conditions. Curves fit to the upper bounds could also represent what many ecological field studies have documented and therefore what many modelers have used to parameterize and validate model results.

Regional-scale analyses

Total biomass, NPP, and mortality estimates for each ecoregion, state, and the total ORCA study area were obtained as the sum of the product of the relevant forested area using land cover data from Advanced Very High Resolution Radiometer (AVHRR) composite images recorded during the 1991 growing season (USDA Forest Service and U.S. Geological Survey 2002) and the corresponding mean values across all plots. The same procedure was used with GIS ownership coverages (from USGS National Land Cover Data 1992) to isolate patterns by public and private ownerships. Theoretical values for live biomass, dead biomass, and NPP were determined for each forest type × ecoregion combination using the parameter estimates for the maximum (parameter a) from the curve fit to the mean values of the data (note that this was from the

mean trend, not the upper bounds). Although these values should represent the maximum amounts, given a range of site productivities, and also should allow for partial disturbance, the amounts calculated assume the absence of stand-replacing disturbance through full harvest or catastrophic wildfire. Uncertainty estimates for regional stocks and NPP were calculated with a Monte Carlo procedure using the ecoregion mean and standard errors for the current values and the ecoregion parameter *a* estimates and standard errors for theoretical values. Simulations were run using a random normal distribution. We tested the independence assumption by using correlation coefficients for no correlation (0.0) and perfect correlation (1.0). Because the results did not vary significantly, uncertainty estimates for the simulations assuming no correlation are reported. Maps (ArcGIS version 9.1; ESRI 2005) of current mean and potential maximum carbon stocks and NPP were produced using the above results and a forest type land cover layer (USDA Forest Service and U.S. Geological Survey 2002).

Results

Ecoregion patterns

There is strong evidence ($P < 0.001$) that maximum amounts of live biomass and rate of accumulation differ by ecoregion (Fig. 2). The Chapman-Richards function appeared to be a good general equation to describe biomass accumulation (Appendix: Table A5), especially for the upper bounds data in the West Cascades. When fit to the mean values, the maximum amount of live biomass (*a* in Eq. 1) is highest in the Coast Range and Klamath Mountains (33–44 kg C/m^2) and lowest in the East Cascades and Blue Mountains (7–10 kg C/m^2). The rate (*b* in Eq. 1) at which biomass reaches the maximum is lowest in the Klamath Mountains, with maximum stores still increasing at 600 years. Rates are higher in the other ecoregions, yet biomass is still increasing in stands over 300 years in the Coast Range, the Sierra Nevada, and the West Cascades.

We were unable to measure the inputs to or outputs from dead biomass, but we were able to compare the dynamic balance between these processes across ecoregions as measured by the standing mass of dead wood in three age groups (Table 2). There is strong evidence ($P < 0.001$, from a permutation test) that mean dead biomass differs among ecoregions for young, mature, and old stands. The Coast Range and West Cascades had the highest mass of dead wood in all age groups (ranging from 3.1 kg C/m^2 in the young to 4.7 kg C/m^2 in the old). The East Cascades had the lowest mass of dead wood in all age groups (ranging from 0.8 to 1.7 kg C/m^2) and the Klamath Mountains and Sierra Nevada had intermediate levels (ranging from 0.8 to 2.7 kg C/m^2).

The theoretical U-shaped pattern of dead biomass over time (high levels initially after disturbance, followed by low levels as this legacy wood decays, then by high levels as new dead wood is recruited) was mostly apparent in the West Cascades when fit to the upper bounds (Appendix: Table A6), and slightly apparent in the East Cascades and Sierra Nevada (Fig. 3). The pattern was only slightly apparent in the West Cascades when fit to the mean values.

There is strong evidence ($P < 0.001$) that maximum NPP differs among ecoregions (Fig. 4). Maximum NPP peaks earliest in the Coast Range and West Cascades at about 80 years. The most obvious cases of late-successional decline in NPP for the upper-bound data were in the ecoregions with highest maximum NPP (Coast Range, West Cascades, and Klamath Mountains). Interestingly, the Coast Range was the only case of a conspicuous decline in mean NPP with age.

There was strong evidence ($P < 0.001$) that both maximum mortality and the rate at which it is reached differs among ecoregions (Appendix: Table A5). Maximum mortality was highest in the Sierra Nevada, followed by the West Cascades and Klamath Mountains for both the mean trend and upper bounds of the data (Fig. 5). Mortality appeared to increase with stand age and become less predictable in older stands. As a percentage of live biomass, mortality ranged from 0.50% in the Coast Range to 1.20% in the Sierra Nevada for stands younger than 80 years, from 0.35% in the Coast Range to 1.30% in the Sierra Nevada for mature (80–200 year old) stands, and from 0.35% in the Coast Range to 1.35% in the Blue Mountains for old stands (>200 years old).

Ownership patterns

Stand ages varied from 0 to over 1000 years, with a higher frequency of younger stands on private land than public land and more old stands on public lands (Fig. 6). Mean stand age for private ownership ranged from 83 years in the Coast Range to 146 years in the Sierra Nevada (Table 1). Public ownership mean ages ranged from 156 years in the Coast Range to 244 years in the West Cascades, where most of the land is public. There are very few stands older than 250 years on private land.

After accounting for site index, there is strong evidence that mean and maximum biomass differed between ownerships in all but the Blue Mountains and East Cascades ($P < 0.001$), with generally higher values on public lands (parameter *a* in Eq. 1, Appendix: Table A7). Dead biomass was not as consistently influenced by ownership as was live biomass (Table 2).

There is also strong evidence that mean NPP differed between ownerships ($P < 0.001$), being generally lower on public lands. Maximum NPP (parameter *a* in Eq. 2) was lower on public lands in the Coast Range, East Cascades, and the West Cascades and showed no difference in the Blue Mountains and Klamath Mountains (Appendix: Table A7). The number of years required to reach maximum rates of NPP was higher on public land ($P < 0.01$) in the Blue Mountains, East Cascades, and Sierra Nevada. Maximum mortality was

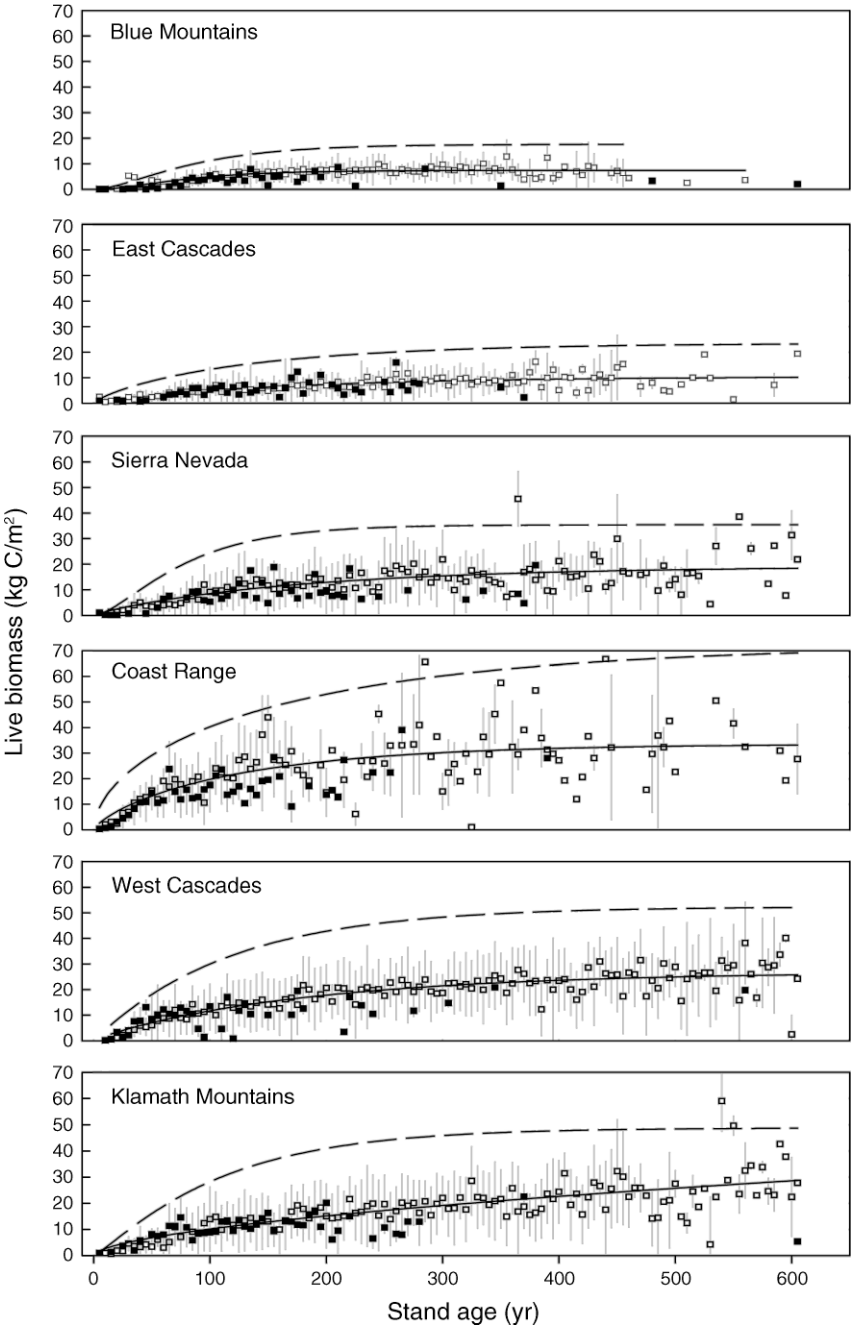


FIG. 2. Live biomass (trees and understory woody shrubs) vs. stand age. The dashed line (upper bounds) and solid line (mean trend) were fit using a Chapman-Richards function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray vertical lines are the standard deviations in each bin. Note that, for clarity, plot mean values for the upper-bounds (99th-percentile) curve of the data are not shown on the figure.

higher on public land in the Blue Mountains and Sierra Nevada, but lower in the Coast Range.

Forest type patterns

Forest type differences were examined for live biomass and NPP. There was strong evidence ($P < 0.001$) that forest types within an ecoregion differ in maximum live biomass accumulation, maximum NPP, years required to reach maximum NPP, and age at initial decline of NPP (Appendix: Table A8). The overall variation in age-related patterns of biomass accumulation was reduced in some ecoregions when the Chapman-Richards functions were fit to the data separated by forest type. Douglas-fir forest types had the highest

TABLE 2. Estimates (mean with SD in parentheses) by age group, maximum of mean trend, and age at which maximum is reached for biomass, NPP, and mortality in each ecoregion and by ownership.

Ecoregion	Young	Mature	Old	Maximum	Age at max. (yr)	Young		Mature	
						Private	Public	Private	Public
Live biomass (kg C/m^2)									
BM	1.9 (2.1)	5.9 (3.6)	7.4 (4.1)	7.1 (0.2)	180	3.0 (2.7)	3.1 (2.3)	4.8 (2.9)	6.5 (3.7)
CR	10.9 (6.9)	22.7 (12.4)	30.0 (14.5)	33.4 (3.0)	310	10.5 (7.9)	12.7 (6.6)	16.1 (7.8)	25.9 (12.9)
EC	3.0 (2.7)	6.2 (4.6)	8.7 (5.5)	10.1 (0.8)	310	3.1 (2.9)	3.2 (2.1)	6.4 (4.5)	5.6 (3.7)
KM	5.2 (5.0)	13.0 (8.9)	20.0 (11.9)	44.2 (33.0)	600+	8.3 (6.0)	7.3 (6.2)	12.4 (7.3)	15.0 (9.4)
SN	3.8 (3.5)	11.1 (7.3)	14.9 (9.6)	19.4 (0.7)	500	3.2 (4.3)	3.8 (3.4)	9.4 (5.0)	11.7 (7.3)
WC	6.2 (5.2)	14.6 (9.8)	22.1 (11.9)	26.9 (2.0)	430	7.9 (5.6)	7.0 (5.5)	11.3 (7.1)	16.4 (10.7)
Dead biomass (kg C/m^2)									
BM	1.0 (0.9)	1.9 (1.8)	2.1 (1.9)	2.1 (1.9)	200+	0.6 (0.0)	1.0 (0.8)	1.6 (1.2)	1.8 (1.8)
CR	3.1 (2.7)	3.6 (2.9)	4.7 (4.8)	4.7 (4.8)	200+	3.2 (2.5)	3.2 (2.8)	2.9 (2.4)	3.8 (3.0)
EC	0.8 (0.8)	1.3 (1.2)	1.7 (1.6)	1.7 (1.6)	200+	1.9 (1.3)	0.7 (0.7)	1.3 (1.2)	1.3 (1.1)
KM	1.5 (1.4)	1.6 (1.5)	2.6 (2.3)	2.6 (2.3)	200+	2.0 (1.2)	1.9 (2.1)	1.9 (1.5)	1.6 (1.5)
SN	0.8 (0.8)	1.9 (1.7)	2.7 (2.2)	2.8 (0.2)	200+	2.4 (1.7)	0.8 (0.7)	1.9 (1.4)	1.7 (1.6)
WC	3.1 (3.1)	2.5 (2.2)	4.9 (4.1)	9.5 (5.2)	200+	4.0 (3.6)	3.2 (3.2)	3.2 (2.6)	2.7 (2.2)
NPP (kg C·m^{-2}·yr^{-1})									
BM	0.16 (0.12)	0.27 (0.10)	0.29 (0.09)	0.30 (0.01)	125	0.23 (0.15)	0.23 (0.12)	0.28 (0.11)	0.29 (0.07)
CR	0.75 (0.31)	0.80 (0.24)	0.77 (0.27)	0.82 (0.03)	60	0.75 (0.36)	0.79 (0.23)	0.91 (0.29)	0.78 (0.19)
EC	0.24 (0.15)	0.33 (0.19)	0.36 (0.15)	0.38 (0.01)	155	0.25 (0.18)	0.25 (0.10)	0.37 (0.18)	0.29 (0.12)
KM	0.45 (0.33)	0.63 (0.34)	0.62 (0.27)	0.65 (0.01)	110	0.66 (0.30)	0.65 (0.44)	0.70 (0.28)	0.73 (0.38)
SN	0.29 (0.19)	0.48 (0.22)	0.49 (0.20)	0.51 (0.01)	125	0.25 (0.23)	0.30 (0.19)	0.50 (0.19)	0.46 (0.21)
WC	0.46 (0.26)	0.52 (0.21)	0.49 (0.15)	0.54 (0.01)	65	0.59 (0.31)	0.50 (0.24)	0.59 (0.26)	0.54 (0.21)
Mortality (kg C·m^{-2}·yr^{-1})									
BM	0.02 (0.02)	0.07 (0.02)	0.10 (0.08)	0.10 (0.00)	140	0.03 (0.03)	0.03 (0.02)	0.05 (0.04)	0.08 (0.07)
CR	0.05 (0.05)	0.06 (0.04)	0.08 (0.04)	0.09 (0.01)	270	0.06 (0.06)	0.05 (0.03)	0.08 (0.05)	0.05 (0.02)
EC	0.03 (0.03)	0.07 (0.09)	0.10 (0.12)	0.11 (0.01)	270	0.02 (0.02)	0.03 (0.03)	0.06 (0.06)	0.05 (0.05)
KM	0.03 (0.04)	0.08 (0.09)	0.13 (0.11)	0.29 (0.27)	600+	0.06 (0.05)	0.03 (0.02)	0.07 (0.07)	0.06 (0.04)
SN	0.04 (0.02)	0.13 (0.12)	0.17 (0.14)	0.20 (0.02)	250	0.03 (0.03)	0.04 (0.05)	0.10 (0.08)	0.13 (0.13)
WC	0.04 (0.03)	0.10 (0.08)	0.14 (0.09)	0.17 (0.01)	310	0.02 (0.02)	0.04 (0.03)	0.05 (0.04)	0.10 (0.07)

Notes: Age groups are defined as young, <80 years old; mature, 80–200 years old; and old, >200 years old (information is not available for private land for the "old" group). Ecoregion codes are as in Table 1. Means for each ownership type (last four columns) were calculated with site-index-corrected data, resulting in higher means than for the entire data set (described in *Methods: Statistical analysis*).

maximum NPP, whereas pine forest types had the oldest age of initial decline of NPP.

Regional-scale analyses

Across the entire ORCA study region and after accounting for stand age, variation in live biomass (model weights 0.0–1.0) and mortality (model weights 0.12–0.88) was most explained by forest type, whereas variation in dead biomass (model weights 0.40–0.60) and NPP (model weights 0.02–0.98) was most explained by ecoregion (Appendix: Table A9). Within each ecoregion or climate zone, forest type was the most important explanatory variable in all cases except for mortality in the Coast Range, where ownership was most important (higher on private lands).

Total live biomass of forests in the ORCA study region (4.4×10^7 ha of forest land) is estimated at 2.71 ± 0.28 Pg C, mean ± SD (Appendix: Table A1; Figs. 7 and 8a). Understory biomass ranged from 1% to 5% of live biomass in most ecoregions and exclusion would not have resulted in a significant underestimation of biomass. Private land accounts for 35% of live biomass (and 44% of the forested area), with nearly one-third of the regional biomass in the predominantly privately owned Coast Range. The total live biomass, assuming that all stands are at maximum carbon storage as determined by the mean trend of the data, would nearly double to 5.19 ± 1.34 Pg C (Fig. 8b). Although it would take hundreds of years to reach these theoretical levels in all ecoregions, land-based stocks could increase by 15% in just 50 years (i.e., if all stands increased in age by 50 years). Total dead biomass for the ORCA study regions is estimated at 0.51 ± 0.19 Pg C (Fig. 8c). Total dead biomass stores would increase by 36% to 0.80 ± 0.15 Pg C at maximum levels from the mean trend of the data (Fig. 8d). Total mortality of biomass for the ORCA study regions is estimated at 0.021 Pg C/yr. Total NPP of forest in the ORCA study region is estimated at 0.109 ± 0.001 Pg C/yr, mean ± SD (Fig. 9a) and total NPP would increase to 0.118 ± 0.002 Pg C/yr, assuming that all stands were at maximum NPP (Fig. 9b).

DISCUSSION

Trends with age

The expected age related ecological patterns (i.e., Chapman-Richards logistic growth for biomass accumulation, U-shaped pattern for dead biomass accumulation, and a marked decline in NPP with stand age)

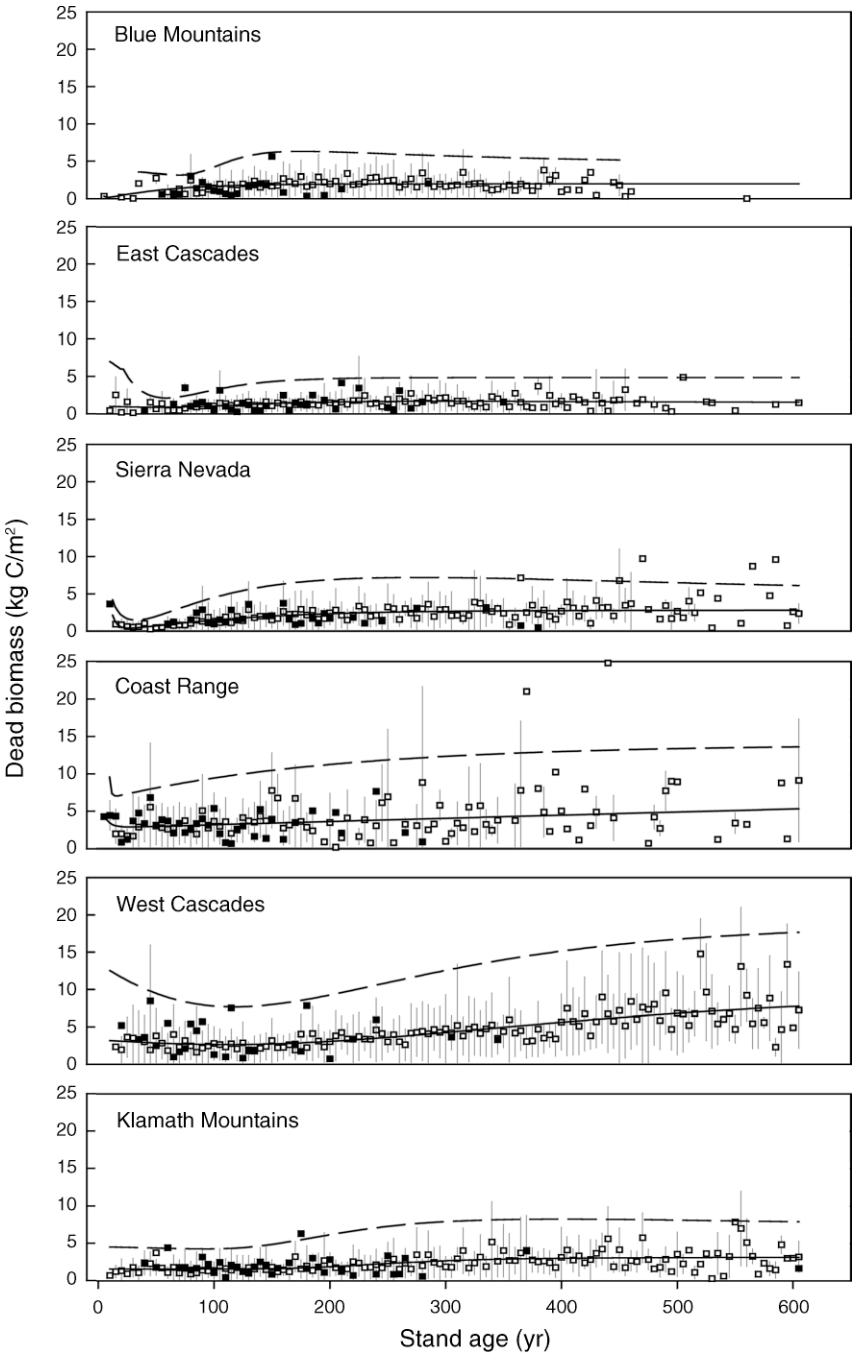


FIG. 3. Dead biomass (coarse woody debris [CWD] and standing dead trees) vs. stand age. The dashed line (upper bounds) and solid line (mean trend) were fit using a decay plus a Chapman-Richards function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray vertical lines are the standard deviations in each bin. Note that, for clarity, plot mean values for the upper-bounds (99th-percentile) curve of the data are not shown on the figure.

were generally more distinguishable in the upper bounds of the data rather than in the age-specific mean values. In almost all cases, the West Cascades plot data were most suitably fit by these age related patterns. This is not surprising when considering that the ecological studies and data that were used to elucidate these patterns deliberately and appropriately targeted productive, smaller scale, undisturbed, mature plots, especially in the West Cascades (Acker et al. 2002, Janisch and Harmon 2002). In contrast, federal inventory sampling, by design, includes the full suite of factors that cause a given forest to grow at the full range of rates.

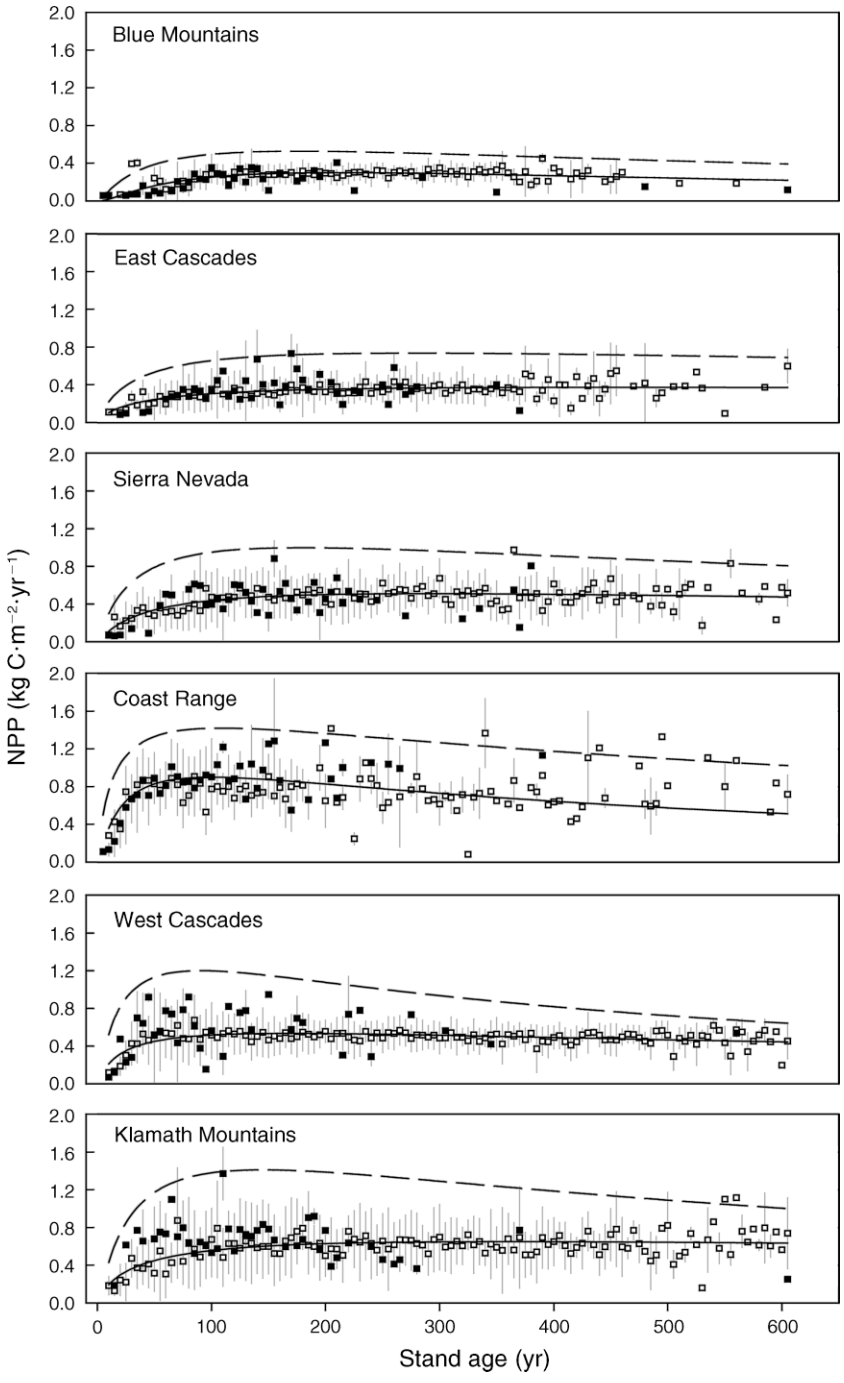


FIG. 4. Net primary productivity, NPP, of trees and understory woody shrubs vs. stand age. The dashed line (upper bounds) and solid line (mean trend) were fit using a Peak (three-parameter log-normal) function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray vertical lines are the standard deviations in each bin. Note that, for clarity, plot mean values for the upper-bounds (99th-percentile) curve of the data are not shown on the figure.

With respect to coarse woody debris (CWD), the idealized U-shaped pattern arising from the combined and lagged effects of legacy wood decay and the recruitment of new dead wood (Harmon et al. 1986) was most apparent in the upper bounds. Coarse woody debris biomass stores may be underestimated because the federal inventory CWD data required a minimum diameter measurement of 12.5 cm, rather than the 10 cm used by ecological studies or the 7.6 cm used by fire studies. Federal inventory data also do not include

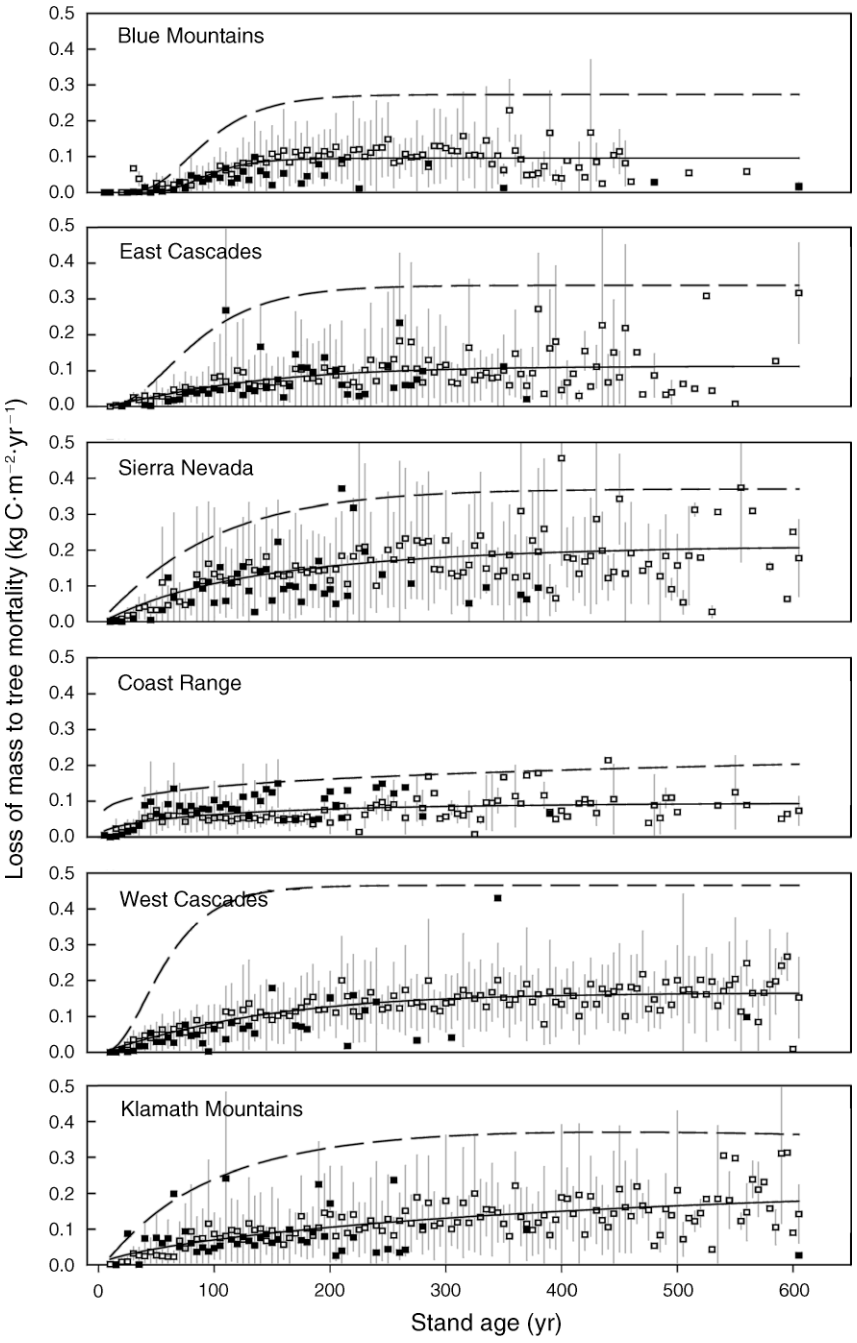


FIG. 5. Mortality of trees (loss of live carbon mass due to the death of trees) vs. stand age. The dashed line (upper bounds) and solid line (mean trend) were fit using a Chapman-Richards function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray vertical lines are the standard deviations in each bin. Note that, for clarity, plot mean values for the upper-bounds (99th-percentile) curve of the data are not shown on the figure.

stumps, which would increase biomass in recently harvested (young) stands causing the curve to follow a more U-shaped pattern.

Because mortality affects both the inputs to dead biomass and the rate of loss from live biomass, it is important to characterize the factors controlling it. Our analysis shows mortality (expressed as an amount) increasing with stand age and stabilizing in late succession (Fig. 5). Expressed as a fraction of live biomass, we found that mortality tends not to be a constant. For example, mortality increases nonlinearly with stand age in most ecoregions and then reaches equilibrium while live biomass continues to increase. Carbon cycle models that have been applied in the

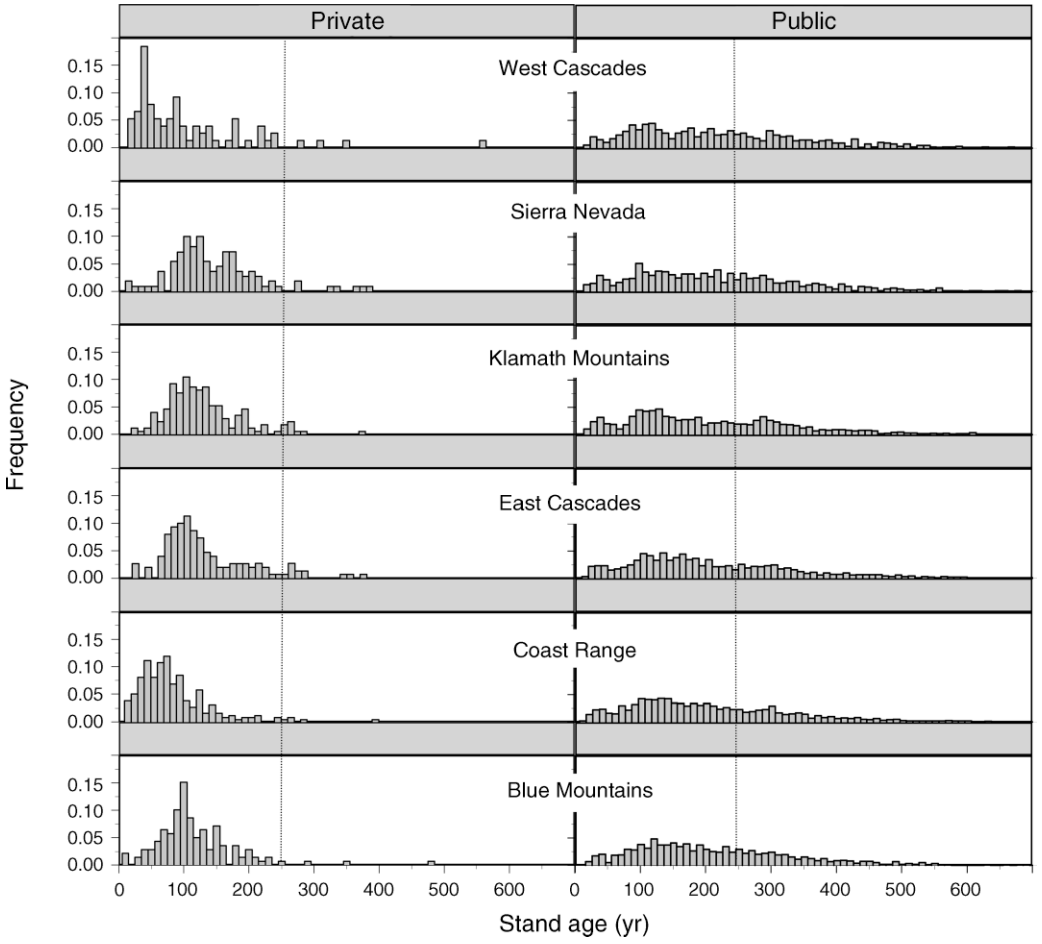


FIG. 6. Frequency distributions of stand age by ecoregion and ownership class (private vs. public). Forests on private land tend to have more stands in lower age classes than stands on public lands. The light vertical lines delineate stands older vs. younger than 250 years.

Pacific Northwest (e.g., Turner et al. 2004) often represent mortality as a fixed percentage of live biomass and our results support the implementation of a dynamic mortality function in these models.

Increased mortality and decreased net primary production have been reported as equally responsible for late-successional stabilization of bole wood biomass in the West Cascades (Acker et al. 2002).The ecological studies upon which that conclusion is based are most relevant to our upper bound lines, and our results support these findings in some ecoregions (e.g., Coast Range, West Cascades, and Klamath Mountains). In those cases, upper bound NPP peaks at approximately 80 years and then declines (Fig. 4), and mortality (Fig. 5) increases with age to a stable rate that approximates bole-wood production. The FIA data suggest that in the most productive ecoregions, biomass continues to accumulate at low rates in very old stands.

In other ecoregions, there is less marked decline in NPP with age, or no apparent decline in NPP. For instance, pine forests in the Blue Mountains, East Cascades, and Klamath Mountains experienced NPP declines at significantly older ages than did other forest types in these ecoregions (Appendix: Table A5). The traditional explanation for NPP decline with age in forests, i.e., stable GPP and increasing autotrophic respiration, has largely been rejected in PNW forests (Ryan et al. 2004). The fact that decline is most apparent in the upper bound lines and least apparent for the relatively low productivity, more open-grown, pine forest type lends support to the hypothesis that competition-related changes in stand structure (Binkley et al. 2002) may be the critical driving factor.

Ecoregion patterns

In general, wetter ecoregions west of the Cascade Mountains crest (Klamath, Coast Range, and West Cascades) had much higher NPP and biomass stores at a given age than the drier ecoregions east of the crest (East Cascades and Blue Mountains). Despite the relatively high NPP and live biomass in the Klamath Mountains, dead biomass stores were 50–60% lower than in the

Coast Range and West Cascades. Although mortality rates are generally higher for both the Coast Range and West Cascades vs. the Klamath Mountains, the difference does not account for the large difference in dead biomass stores. Dead wood biomass is either being removed or consumed in the Klamath ecoregion at a much higher rate than in other ecoregions west of the Cascade crest. One explanation is differential decomposition rates. Decomposition is thought to be higher in the Klamath than in other west-side forests because of sufficient moisture and warm temperatures, but with fewer prolonged periods of moisture saturation, which can limit log decomposition (Harmon 1992). Others have proposed that historically frequent surface fires in the Klamath (every 5–75 years) consumed much of the coarse woody debris (Skinner 2002). It is most likely a combination of faster decomposition and shorter pre-suppression-era fire return intervals that underlie the lower amounts of dead biomass in the Klamath (Wright et al. 2002).

A consideration in interpreting biomass dynamics across ecoregions is the potential influence of 20th century fire exclusion, which has likely varied among regions. In dry forest types of some ecoregions (e.g., East Cascades, Sierra Nevada), fire suppression has resulted in long recent fire intervals relative to historical fire regimes that included frequent low-intensity surface fires (Agee 1993). These long intervals may allow greater live and dead biomass accumulations than under shorter fire intervals, as well as increases in stem densities that may affect patterns of stand productivity. By contrast, in wetter ecoregions (e.g., West Cascades, Coast Range), the fire suppression era has been brief relative to characteristic fire return intervals and probably has had little effect on biomass dynamics (Noss et al. 2006). Note that the chronosequence approach taken in our study is sensitive to the changes in disturbance regime over the last century. The effect of fire exclusion (and restoration) on carbon dynamics in different forest types remains an important direction for future research.

Ownership patterns and management implications

Forest management has always been somewhat different on private and public lands in the Coast Range, West Cascades, and Klamath Mountains (Spies et al. 1994), and reduced timber cut on federal lands in these ecoregions after implementation of the Northwest Forest Plan in 1990 has intensified the differences. Private lands in these ecoregions have, on average, less live biomass per unit area than do public lands because the typical harvest rotation (80 years) is much less than the age at which maximum biomass is reached (300 years). The frequency distribution of stand age could largely explain the differences in both live and dead biomass on public and private lands (Van Tuyl et al. 2005). Mean stand age of publicly owned forests is 50–150 years older than privately owned forests and mean carbon stores are 30–50% higher. Despite the fact that

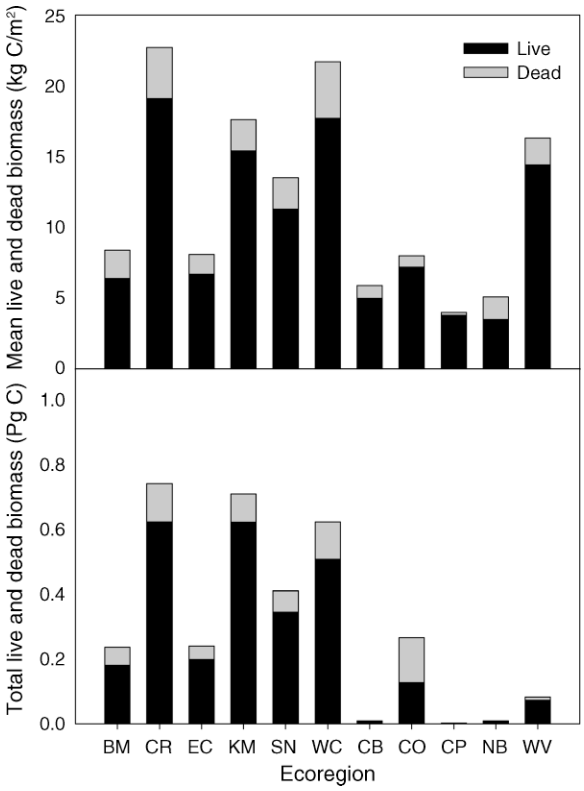


FIG. 7. Current mean and total carbon stocks in each ecoregion; mean and total live and dead biomass include trees, understory woody shrubs, and coarse woody debris.

the Coast Range has the highest percentage of private land (twice that of any other ecoregion), the lowest mean stand age, and the highest rate of removals by harvest (Law et al. 2004), it has the largest amount of biomass stored per unit area, presumably due to high NPP (climate), low natural mortality rates, and lack of recent major wildfires. Coast Range forests are among the most productive temperate forests in the world (Smithwick et al. 2002) and aboveground carbon stocks are comparable with tropical forest stocks (Houghton 2003, Sierra et al. 2007). Thus, there is high potential for increased land-based carbon storage with increased rotation age or reduction in harvest rates (Fig. 8b).

It is expected that management would affect NPP in younger stands because they are being managed for harvest and maximum wood volume production. After accounting for site index, our results supported this hypothesis, with maximum annual NPP of forests higher on private land than public land in all but the Blue Mountains and Klamath Mountains. An explanation for the lack of difference in these two ecoregions is difficult to ascertain because site index was accounted for in the analysis. There was also no difference in maximum live and dead biomass stores in the Blue Mountains. Maximum mortality is higher on public lands in the Blue Mountains, which could partially account for the decreased live biomass, but it may also

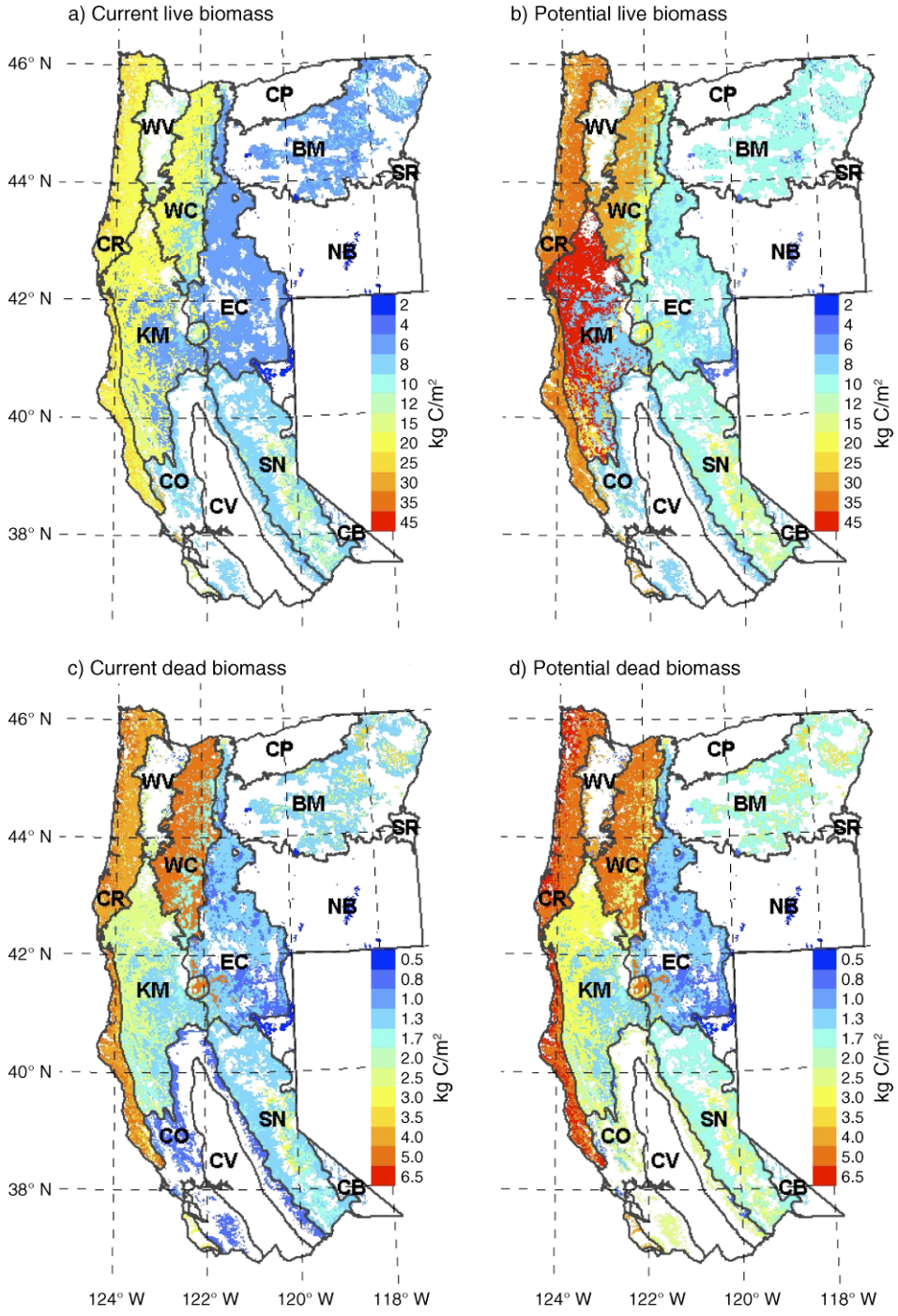


FIG. 8. Current and potential carbon stocks by forest type within ecoregion. Potential stocks were calculated using the mean trend maximums by forest type (Appendix: Table A6).

be that management practices are more similar on public and private land, as this ecoregion was also not affected by the Northwest Forest Plan.

Because ownership is associated with differences in mean biomass levels, a shift from current management on public land to a regime more like that on private land would gradually reduce mean carbon stocks on the land base. Decreasing rotation age to 50 years (i.e., mean age to 25 years) on all forested land in the Coast Range, Klamath Mountains, and West Cascades would reduce land-based live carbon stores by 53%. Some carbon can be sequestered in wood products derived from harvesting. However, due to manufacturing losses, only about 60% of the carbon harvested enters the products pool

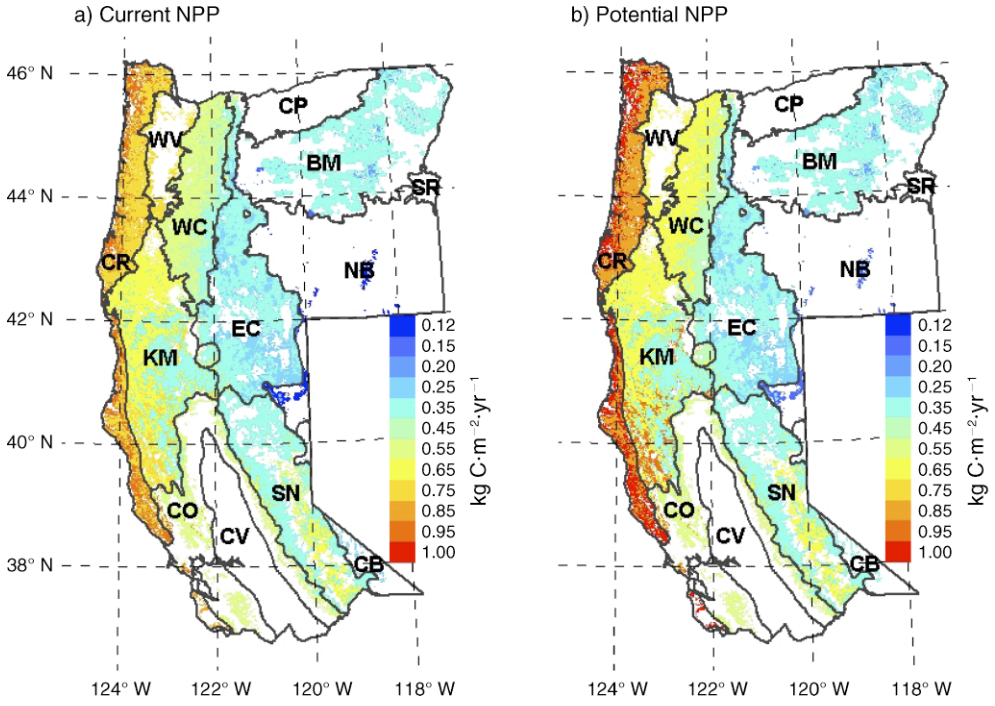


FIG. 9. Current and potential NPP by forest type within ecoregion. Potential NPP was calculated using the mean trend maximums of NPP by forest type (Appendix: Table A6).

(Harmon et al. 1996) and there are significant emissions from older products decomposing in landfills that tend to offset this carbon sink. Furthermore, with full carbon accounting there is a large carbon cost to the initial conversion of a landscape dominated by old forests to one dominated by young forests (Harmon et al. 1990).

Managing forests to maximize NPP may not have a positive effect on maximum regional carbon storage. Maximum NPP is reached much earlier in stand development than maximum biomass in all ecoregions (by hundreds of years) and limiting biomass accumulation to rotation ages based on maximum NPP would reduce land-based stocks. Examining current and potential productivity across the region is important when deciding regions where accumulation of biomass stores is most efficient. Highly productive ecoregions with infrequent fire such as the Coast Range are most likely to reach the potential stocks if managed for maximum biomass accumulation.

Modeling implications

As this study reaffirms, the processes driving forest carbon balance vary with stand age and forest type. Therefore estimates of regional carbon fluxes from modeling efforts depend in large part on our ability to accurately characterize stand age and forest type across the region (Turner et al. 2007). Including forest types as species groups in model parameterization could help further constrain model output for a specific area. Spatially explicit maps of age can be derived from remote imagery (Cohen et al. 2002), but the accuracy of these maps is dependent on pronounced canopy structural development (Law et al. 2006). Until accurate age maps can be developed for the entire region, the distribution of forest age among inventory plots is uniquely valuable in developing probabilistic-based maps of age (e.g., Ohmann et al. 2007).

Ecological studies have identified patterns of response in biomass and productivity with age that are based on homogeneous forests growing under ideal conditions, and in this study, we found that those patterns are more evident in the upper bounds of biomass or productivity for a given age rather than mean response. The structure of many process models used for scaling NEP is often developed based on ecological trends elucidated from field studies on idealized study plots or the upper bounds. Depending on exactly how a process model is structured, it may be best to parameterize it with curves fit to the upper maximum of the inventory data because these trends reflect the unconstrained behavior of vegetation in a given ecoregion. This is especially true for trends such as age-related mortality, age-related allocation, and age-related declines in NPP that need to be explicitly enforced, because these high-order trends fail to otherwise emerge in standard simulations. Mean trends in the inventory data, on the other hand, have a different, but equally important value to modeling since after incorporating the constraints of disturbance and climate across a region, model output is best validated against the mean trends apparent in the inventory data.

TABLE 3. Forest carbon stocks in different regions.

Region	Stocks (kg/m^2)	Components	Source
Oregon and N. California	6.5–19†,||	total tree biomass	this study
Oregon and N. California	17–70‡	total tree biomass	this study
West Coast USA	9.1–13.5†,||	total tree biomass	Woodbury et al. (2007)
PNW, Coast Range	63‡	total tree biomass	Smithwick et al. (2002)
PNW, Cascades	58‡	total tree biomass	Smithwick et al. (2002)
PNW, Eastside	12‡	total tree biomass	Smithwick et al. (2002)
Northern Rockies	8†	total tree biomass	Hicke et al. (2007)
Colorado Rockies	<8†	total tree biomass	Hicke et al. (2007)
Mid-Atlantic USA	16–29‡	total tree biomass	Jenkins et al. (2001)
Mid-Atlantic USA	7–11†,||	total tree biomass	Woodbury et al. (2007)
Eastern USA	7.5–25§	aboveground live tree biomass	Brown et al. (1999)
Russia	4.6–24§	total tree biomass	Krankina et al. (2005)
Canada	1–15†	total forest live biomass	Kurz and Apps (1999)
Latin America	13.5†	aboveground live tree biomass	Houghton (2005)
Tropical Asia	11.5†	aboveground live tree biomass	Houghton (2005)

Notes: Values reported as a range are the total estimates across different forest types or ecoregions. PNW is the Pacific Northwest.

† Includes foliage and coarse roots, but excludes fine roots.
‡ Reported as maximum levels for the study area.
§ Minimum to maximum levels across study area.
|| Mean levels across ecoregions.
¶ From small-scale ecological studies (not inventory).

For this reason we advocate the separate characterization of mean and upper bound trends in federal inventory data.

Comparison with other studies

Our estimates of live and dead biomass, NPP, and mortality compare favorably with other regional studies (Table 3). Most recent federal inventory estimates of state total live and dead tree (excluding fine roots) carbon per unit area were 9–11 kg C/m^2 (Woodbury et al. 2007) in Oregon and California. Our results produce a mean of 12 kg C/m^2 (including fine roots) for both states, but range from 3 to 24 kg C/m^2 across the ecoregions. Hicke et al. (2007) reports a range of 4–20 kg C/m^2 for mean live tree biomass (excluding fine roots) at the county level in Oregon and California. When compared with the IDB estimates of ecoregion means, aboveground woody biomass varied by 5–10%.

Smithwick et al. (2002) reported that Oregon tree (including snags) and understory biomass in very old undisturbed stands averaged 63, 58, and 12 kg C/m^2 in the Coast Range, West Cascades, and East Cascades, respectively. Our estimates of the upper bounds of tree (not including snags) and understory biomass (Fig. 2) were 55, 50, and 20 kg C/m^2 for each of these ecoregions. Our East Cascade upper bounds estimate is much higher, but is based on a much larger number of plots over a more extensive area. Our aboveground wood biomass increments averaged 0.17 kg C·m^{-2}·yr^{-1} in the East Cascades to 0.50 kg C·m^{-2}·yr^{-1} in the Coast Range. In comparison with other regions, maximum live tree biomass averaged 10 kg C/m^2 in softwood forest types and wood biomass increment averaged 0.24 kg C·m^{-2}·yr^{-1} in the mid-Atlantic region (Jenkins et al. 2001). In tropical regions, total tree live-tree biomass averaged a 15 kg C/m^2 (Sierra et al. 2007) in Columbia and ranged from 11 to 13 kg C/m^2 (aboveground biomass only) across all tropical forests (Houghton 2003).

Conclusions

The potential to store additional carbon in Pacific Northwest forests is among the highest in the world because much of the area has forests that are long-lived (e.g., Douglas-fir) and maintain relatively high productivity and biomass for decades to centuries. In Oregon and Northern California (4.4×10^7 ha), total live biomass of forests is estimated at 2.71 ± 0.28 Pg C, mean ± SD (mean of 12 kg C/ha) in the period 1991–1999. Total dead biomass (which does not include fine woody debris or litter stocks) of forests in the region was 0.51 ± 0.19 Pg C, and total NPP was 0.109 ± 0.001 Pg C/yr, mean ± SD. The majority of live and dead biomass (~65%) is on public lands (53% of forested land). Trends in NPP with age vary among ecoregions, which suggests caution in generalizing that NPP declines in late succession. Contrary to commonly accepted patterns of biomass stabilization or decline, biomass was still increasing in stands over 300 years old in the Coast Range, the Sierra Nevada and the West Cascades, and in stands over 600 years old in the Klamath Mountains. If forests were managed for maximum carbon sequestration total carbon stocks could theoretically double in the Coast Range, West Cascades, Sierra Nevada, and East Cascades and triple in the Klamath Mountains (Fig. 8). Our results indicate that Oregon and California forests are at 54% of theoretical maximum levels (3.2 ± 0.34 Pg C vs. 5.9 ± 1.34 Pg C) given the absence of stand-replacing disturbance. These theoretical levels are calculated using the mean trend of the data and account for variation in site quality, climate, and partial disturbance (i.e., thinning, insect outbreaks, non-cata-

strophic fire). An increase of 15% may be possible in just 50 years. However, these levels (if reached) may be unstable in high-frequency fire regions. A more realistic management approach to increase carbon storage on the landscape would be to increase rotation ages by 30–50 years or reduce the acreage that is harvested in areas more likely to reach the theoretical levels (Coast Range, West Cascades, Klamath Mountains). Initial conditions are important when considering management options. Maintaining mature and old forests that already store large amounts of carbon is a mitigation option, as suggested by the IPCC (2007).

Acknowledgments

This research was supported by the U.S. Department of Energy Biological and Environmental Research Terrestrial Carbon Program (Award DE-FG02-04ER63917). This study is part of a regional North American Carbon Program project. Special thanks to Catharine van Ingen for her assistance with database organization and implementation, and to Microsoft for database design funding through an E-Science grant. We thank the PNW-FIA (Pacific Northwest Forest Inventory and Analysis program) regional office for their assistance and cooperation in compiling the database and Lisa Ganio, Joe Fontaine, Brendan Rogers, and Warren Cohen for editorial comments and statistical advice. We also thank two anonymous reviewers for their extensive comments, which were very helpful for revisions.

Literature Cited

Acker, S., C. Halpern, M. Harmon, and C. Dyrness. 2002. Trends in bole biomass accumulation, net primary production and tree mortality in *Pseudotsuga menziesii* forests of contrasting age. Tree Physiology 22:213–217.

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Binkley, D., J. L. Stape, M. G. Ryan, H. R. Barnard, and J. Fownes. 2002. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. Ecosystems 5:58–67.

Bormann, F. J., and G. E. Likens. 1969. Pattern and process in forest ecosystems. Springer-Verlag, Berlin, Germany.

Brown, S. L., P. Schroeder, and J. S. Kern. 1999. Spatial distribution of biomass in forests of the eastern USA. Forest Ecology and Management 123:81–90.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Campbell, J. L., O. J. Sun, and B. E. Law. 2004. Supply-side controls on soil respiration among Oregon forests. Global Change Biology 10:1857–1869.

Canadell, J. G., C. Le Quere, M. R. Raupach, C. B. Field, E. T. Buitenhuis, P. Ciais, T. J. Conway, N. P. Gillett, R. A. Houghton, and G. Marland. 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proceedings of the National Academy of Sciences (USA) 104:18866–18870.

Cohen, W. B., T. A. Spies, R. J. Alig, D. R. Oetter, T. K. Maiersperger, and M. Fiorella. 2002. Characterizing 23 years (1972–1995) of stand replacement disturbance in western Oregon forests with Landsat imagery. Ecosystems 5:122–137.

Denman, K. L., et al. 2007. Couplings between changes in the climate system and biogeochemistry. Pages 499–587 *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [IPCC]. Cambridge University Press, Cambridge, UK.

ESRI. 2005. ArcGIS version 9.1. ESRI (Environmental Systems Research Institute), Redlands, California, USA.

Forest Products Laboratory. 1974. Wood handbook: Wood as an engineering material. Forest Products Laboratory, Madison, Wisconsin, USA.

Gough, C. M., C. S. Vogel, K. H. Harrold, K. George, and P. S. Curtis. 2007. The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. Global Change Biology 13:1935–1949.

Harcombe, P. A., M. E. Harmon, and S. Green. 1990. Changes in biomass and production over 53 years in a coastal *Picea sitchensis–Tsuga heterophylla* forest approaching maturity. Canadian Journal of Forest Research 20:1602–1610.

Harmon, M. E. 1992. Long-term experiments on log decomposition at the H. J. Andrews Experimental Forest. USDA Forest Service General Technical Report PNW-GTR 280, Pacific Northwest Forest Experiment Station, Portland, Oregon, USA.

Harmon, M., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.

Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. Science 247:699–702.

Harmon, M. E., S. L. Garman, and W. K. Ferrell. 1996. Modeling historical patterns of tree utilization in the Pacific Northwest: Carbon sequestration implications. Ecological Applications 6:641–652.

Hicke, J. A., J. C. Jenkins, D. S. Ojima, and M. Ducey. 2007. Spatial patterns of forest characteristics in the western United States derived from inventories. Ecological Applications 17: 2387–2402.

Houghton, R. A. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. Tellus B 55:378–390.

Houghton, R. A. 2005. Aboveground forest biomass and the global carbon balance. Global Change Biology 11:945–958.

IPCC. 2007. Climate change 2007: mitigation. Pages 546–548 *in* B. Metz, O. R. Davidson, P. R. Bosch, R. Dave, and L. A. Meyer, editors. Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [IPCC]. Cambridge University Press, Cambridge, UK.

Janisch, J. E., and M. E. Harmon. 2002. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. Tree Physiology 22:77–89.

Jenkins, J. C., R. A. Birdsey, and Y. Pan. 2001. Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level forest inventory data. Ecological Applications 11: 1174–1193.

Keyes, M. R., and C. C. Grier. 1981. Above- and belowground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Canadian Journal of Forest Research 11:599–605.

Krankina, O. N., R. A. Houghton, M. E. Harmon, E. H. Hogg, D. Butman, M. Yatskov, M. Huso, R. F. Treyfeld, V. N. Razuvaev, and G. Spycher. 2005. Effects of climate, disturbance, and species on forest biomass across Russia. Canadian Journal of Forest Research 35:2281–2293.

Kurz, W. A., and M. J. Apps. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecological Applications 9:526–547.

Law, B. E., P. Thornton, J. Irvine, S. Van Tuyl, and P. Anthoni. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biology 7:755–777.

Law, B. E., D. Turner, J. Campbell, O. J. Sun, S. Van Tuyl, W. D. Ritts, and W. B. Cohen. 2004. Disturbance and

climate effects on carbon stocks and fluxes across Western Oregon USA. Global Change Biology 10:1429–1444.
Law, B. E., D. Turner, M. Lefsky, J. Campbell, M. Guzy, O. Sun, S. V. Tuyl, and W. Cohen. 2006. Carbon fluxes across regions: Observational constraints at multiple scales. Pages 167–190 *in* J. Wu, B. Jones, H. Li, and O. Loucks, editors. Scaling and uncertainty analysis in ecology: methods and applications. Springer-Verlag, New York, New York, USA.
Maeglin, R. R., and H. E. Wahlgren. 1972. Western wood density survey. Report Number 2. USDA Forest Service Research Paper FPL-183, Madison, Wisconsin, USA.
McCune, B., and E. S. Menges. 1986. Quality of historical data on midwestern old-growth forests. American Midland Naturalist 116:163–172.
Means, J. H., H. A. Hansen, G. J. Koerper, P. B. Alaback, and M. W. Klopsch. 1994. Software for computing plant biomass—BioPak Users' guide. USDA Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-340, Portland, Oregon, USA.
Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Ecology and management of fire-prone forests of the western United States. Society for Conservation Biology Scientific Panel on Fire in Western U.S. Forests. Society for Conservation Biology, North American Section, Arlington, Virginia, USA.
Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.
Ohmann, J. L., M. J. Gregory, and T. A. Spies. 2007. Influence of environment, disturbance and ownership on forest vegetation of coastal Oregon. Ecological Applications 17: 18–33.
Omernik, J. M. 1987. Ecoregions of the conterminous United States. Map (scale 1:7,500,000). Annals of the Association of American Geographers 77:118–125.
Peet, R. K. 1981. Changes in biomass and production during secondary forest succession. Pages 324–338 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession: concepts and application. Springer-Verlag, New York, New York, USA.
Pienaar, L. V., and K. J. Turnbull. 1973. The Chapman-Richards generalization of Von Bertalanffy's growth model for basal area growth and yield in even-aged stands. Forest Science 19:2–22.
Ryan, M. G., D. Binkley, J. H. Fownes, C. P. Giardina, and R. S. Senock. 2004. An experimental test of the causes of forest growth decline with stand age. Ecological Monographs 74: 393–414.
Sierra, C. A., et al. 2007. Total carbon stocks in a tropical forest landscape of the Porce region, Colombia. Forest Ecology and Management 243:299–309.
Skinner, C. 2002. Influence of fire on the dynamics of dead woody material in forests of California and southwestern Oregon. USDA Forest Service General Technical Report PSW-GTR 181:445–454.
Smithwick, E. A. H., M. E. Harmon, S. M. Remillard, S. A. Acker, and J. F. Franklin. 2002. Potential upper bounds of carbon stores in the Pacific Northwest. Ecological Applications 12:1303–1317.
Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91–111 *in* L. F. Ruggerio, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service Pacific Northwest Research Station, General Technical Report PNW-GTR-285, Portland, Oregon, USA.
Spies, T. A., W. J. Ripple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4:555–568.
S-PLUS. 2005. S-PLUS version 7.02. Insightful Corporation, Seattle, Washington, USA.
Sun, O. J., J. Campbell, B. E. Law, and V. Wolf. 2004. Dynamics of carbon storage in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA. Global Change Biology 10:1470–1481.
Turner, D. P., M. Guzy, M. A. Lefsky, W. D. Ritts, S. Van Tuyl, and B. E. Law. 2004. Monitoring forest carbon sequestration with remote sensing and carbon cycle modeling. Environmental Management 33:457–466.
Turner, D. P., D. Ritts, B. E. Law, W. Cohen, Z. Yang, T. Hudiburg, J. L. Campbell, and M. Duane. 2007. Scaling net ecosystem production and net biome production over a heterogeneous region in the western United States. Biogeosciences 4:597–612.
USDA Forest Service and U.S. Geological Survey. 2002. Forest cover types: National Atlas of the United States. Earth Science Information Center, USGS, Reston, Virginia, USA. ⟨http://www-atlas.usgs.gov/metadata/foresti020l.faq.html⟩
Van Tuyl, S., B. E. Law, D. P. Turner, and A. I. Gitelman. 2005. Variability in net primary production and carbon storage in biomass across Oregon forests: An assessment integrating data from forest inventories, intensive sites, and remote sensing. Forest Ecology and Management 209:273–291.
Waddell, K. L. 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. Ecological Indicators 1:139–153.
Waddell, K. L., and B. Hiserote. 2005. The PNW-FIA integrated database [on CD]. Version 2.0. Released September 2005. Forest Inventory and Analysis Program, Pacific Northwest Research Station. Portland, Oregon, USA. ⟨http://www.fs.fed.us/pnw/fia/publications/data/data.shtml⟩
Woodbury, P. B., J. E. Smith, and L. S. Heath. 2007. Carbon sequestration in the U.S. forest sector from 1990 to 2010. Forest Ecology and Management 241:14–27.
Wright, P., M. Harmon, and F. Swanson. 2002. Assessing the effect of fire regime on coarse woody debris. USDA Forest Service General Technical Report PSW-GTR 181:621–634.

APPENDIX

Ecoregion, ownership, and forest type summary tables and statistics (*Ecological Archives* A019-008-A1).

The Condor 108:817–831
© The Cooper Ornithological Society 2006

THE EFFECTS OF POSTFIRE SALVAGE LOGGING ON CAVITY-NESTING BIRDS

RICHARD L. HUTTO[1,3] AND SUSAN M. GALLO[2]
[1]*Avian Science Center, Division of Biological Sciences, University of Montana, Missoula, MT 59812*
[2]*Maine Audubon, Falmouth, ME 04105*

Abstract. We investigated the effects of postfire salvage logging on cavity-nesting birds by comparing nest densities and patterns of nest reuse over a three-year period in seven logged and eight unlogged patches of mixed-conifer forest in the Blackfoot-Clearwater Wildlife Management Area, Montana. We found 563 active nests of 18 cavity-nesting birds; all species were found nesting in the uncut burned forest plots, but only eight nested in the salvage-logged plots. All except one species nested at a higher density in the unlogged areas, and half of the species were significantly more abundant in the unlogged plots. Every timber-drilling and timber-gleaning species was less abundant in the salvage-logged plots, including two of the most fire-dependent species in the northern Rocky Mountains—American Three-toed (*Picoides dorsalis*) and Black-backed (*P. arcticus*) Woodpeckers. Lower abundances in salvage-logged plots occurred despite the fact that there were still more potential nest snags per hectare than the minimum recommended number needed to support maximum densities of primary cavity-nesters, which suggests that reduced woodpecker densities are more related to a reduction in food (wood-boring beetle larvae) than to nest-site availability. Because cavities were present in only four of 244 randomly selected trees, and because frequency of cavity reuse by secondary cavity-nesters was higher in salvage-logged than in unlogged plots, nest-site limitation may be a more important constraint for secondary cavity-nesters in salvage-logged areas. These results suggest that typical salvage logging operations are incompatible with the maintenance of endemic levels of most cavity-nesting bird populations, especially populations of primary cavity-nesting species.

Key words: *Black-backed Woodpecker, cavity-nesting birds, fire, healthy forests, salvage logging.*

Efectos de la Extracción Forestal Post-Incendio sobre las Aves que Anidan en Cavidades

Resumen. Investigamos los efectos de la extracción forestal post-incendio sobre las aves que anidan en cavidades por medio de una comparación de la densidad de nidos y los patrones de su reutilización. El estudio se realizó durante un periodo de tres años, en fragmentos de bosque mixto de coníferas quemados con y sin extracción forestal (siete y ocho fragmentos, respectivamente) en el Área de Manejo de Fauna Silvestre Blackfoot-Clearwater, Montana. Encontramos 563 nidos activos pertenecientes a 18 especies; todas las especies se registraron anidando en los fragmentos de bosque quemado sin extracción, pero sólo ocho de ellas anidaron en los fragmentos quemados con extracción. Con sólo una excepción, la densidad de nidos de todas las especies fue mayor en los fragmentos quemados sin extracción forestal y la mitad de las especies fueron significativamente más abundantes en los fragmentos sin extracción. Todas las especies que obtienen su alimento perforando la corteza o buscando en ella fueron menos abundantes en los fragmentos con extracción, incluyendo dos de las especies más dependientes de los incendios en las Montañas Rocallosas—*Picoides dorsalis* y *P. arcticus*. Las abundancias fueron menores en los fragmentos con extracción post-incendio, a pesar de contar con un número mayor de troncos por hectárea con potencial para construir nidos, en relación con el número mínimo recomendado para mantener densidades máximas de aves que anidan en cavidades. Esto sugiere que la disminución de las densidades de los pájaros carpinteros está más relacionada con una disminución en su alimento (larvas perforadoras de escarabajos), que con la disponibilidad de sitios de anidación. Ya que se detectaron cavidades en sólo cuatro de los 244 árboles seleccionados al azar, y dado que la tasa de reutilización de cavidades por parte de las especies de anidación secundaria fue mayor en los sitios con extracción que en sitios sin extracción, la restricción de sitios de anidación puede ser un factor limitante más importante para las especies de anidación secundaria en los sitios con extracción forestal post-incendio. Estos resultados sugieren que las operaciones típicas de extracción son incompatibles con el mantenimiento de los niveles

Manuscript received 22 November 2005; accepted 15 July 2006.
[3] E-mail: hutto@mso.umt.edu

endémicos de la mayoría de las poblaciones de aves que anidan en cavidades, especialmente para poblaciones de especies de anidación primaria.

INTRODUCTION

Severe, stand-replacing fire is arguably the most ecologically important disturbance agent in conifer forests of the northern Rocky Mountains (Gruell 1983, Pierce et al. 2004). These fires generally leave a mosaic of green, unburned areas interspersed with large areas of standing dead trees, or snags (Turner and Romme 1994, Turner et al. 2003). The ecological importance of this type of forest habitat is reflected in the fact that the avian community found in forests following stand-replacing fires is comprised, in part, of species (e.g., Black-backed Woodpecker [*Picoides arcticus*], American Three-toed Woodpecker [*Picoides dorsalis*], Olive-sided Flycatcher [*Contopus cooperi*], and Mountain Bluebird [*Sialia currucoides*]) that are not only relatively abundant in, but are also relatively restricted to, severely burned forest patches (Hutto 1995, Hutto and Young 1999, Kotliar et al. 2002, Smucker et al. 2005). These species depend heavily on the abundant standing dead trees associated with severely burned forests because they provide: (1) perches from which foraging sallies are initiated, (2) food for specialized beetle larvae, which themselves serve as prey for numerous woodpecker species (Powell 2000), and (3) nesting sites (Hutto 1995).

In unburned forest, the importance of snags to cavity-nesting birds has been clearly demonstrated (Dickson et al. 1983, Marcot 1983, Scott and Oldemeyer 1983, Zarnowitz and Manuwal 1985, Schreiber and deCalesta 1992) and recommendations for snag retention during timber harvests have been incorporated into current management plans (Thomas 1979, Raphael and White 1984, Zarnowitz and Manuwal 1985, Morrison and Raphael 1993). In burned forests, however, there are still no generally accepted snag retention guidelines for postfire conditions, even though the needs of snag-dependent species in burned forests are not the same as the needs of snag-dependent species in unburned forests (Hutto 1995, 2006). The lack of snag retention guidelines for burned forests is undoubtedly a reflection of the prevailing view that forest fires are ''environmental disasters'' (Taylor 1995) and that such fires leave behind fire-damaged timber that, other than as salvaged wood, lacks value. Consequently, salvage logging is a common management practice in the western United States after high-severity, stand-replacing fires, as it is elsewhere in the world after severe disturbance events (Lindenmayer et al. 2004).

Because burned forests are valuable to snag-dependent wildlife (and other plants and animals), and because some of these species appear to be nearly restricted in their distribution to such conditions (Hutto 1995, Hobson and Schieck 1999, Nappi 2000, Kotliar et al. 2002), managers should be especially concerned about mitigating possible negative effects of salvage logging on fire-dependent plants and animals. We need information on the effects of different levels of salvage logging to be able to assess whether any level of salvage logging is compatible with wildlife needs and, if so, which kinds and minimum numbers of snags are needed to support fire-dependent species after stand-replacing fires (Hutto 1995, 2006, Nappi et al. 2004).

Unfortunately, given the inherent danger associated with severe forest fires, the prospects of obtaining information on the effects of salvage logging from multiple, independently created experimental treatment and control plots will always be limited (Hargrove and Pickering 1992, Whelan 1995, Andersen et al. 1998, van Mantgem et al. 2001). Therefore, generalizations are most likely to emerge from meta-analyses of individual studies conducted when opportunities for study after unplanned fire events presented themselves (Kotliar et al. 2002). We capitalized on one of these rare opportunities to obtain empirical data on the effects of salvage logging when a large fire burned most of the Blackfoot-Clearwater Wildlife Management Area in western Montana. By working with the State Department of Fish, Wildlife and Parks and a local timber company, we were able to design a study that included a series of otherwise similar treatment (cut) and control (uncut) plots that allowed us to: (1) assess and compare breeding, cavity-nesting bird abundance in salvage-logged vs. unlogged burned forest patches, (2) assess and compare characteristics of nest trees and randomly

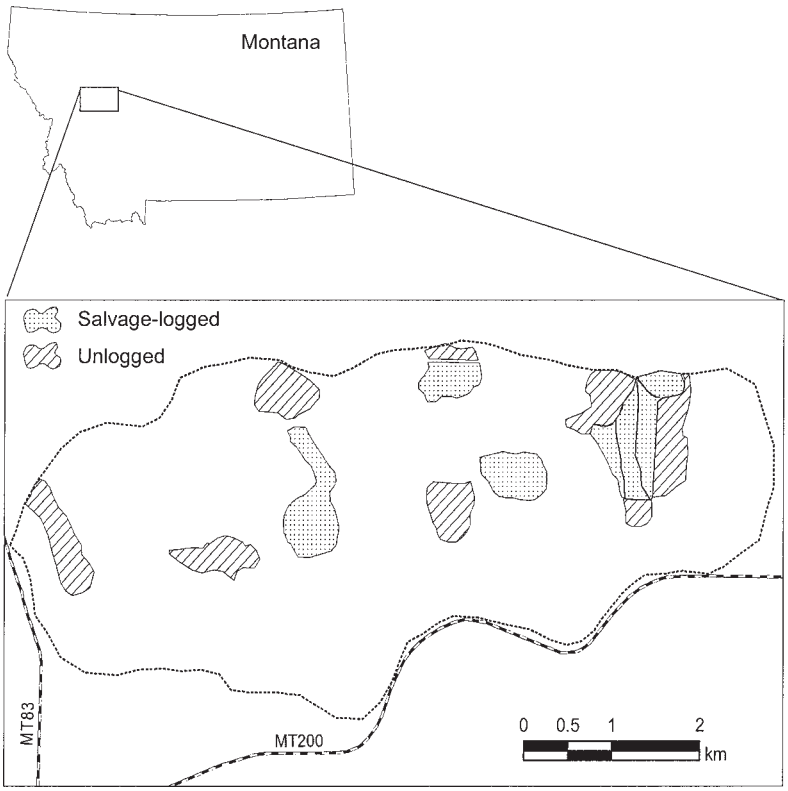


FIGURE 1. Map of the field plots used to study the effects of postfire salvage logging on cavity-nesting birds in the Blackfoot-Clearwater Wildlife Management Area, Montana. The fire boundary is indicated by the dotted line. Most of the area between plots is grassland, and MT83 and MT200 are state highways.

selected trees from salvage-logged and unlogged plots, and (3) document the reuse of cavities over a three-year period.

METHODS

STUDY AREA

This study took place on the Blackfoot-Clearwater Wildlife Management Area, which is located 80 km east of Missoula, Montana, at an elevation of approximately 1200 m. A severe fire in October of 1991 burned approximately 1600 ha of grassland and mixed-conifer forest. The burned forest areas consisted mainly of 50- to 150-year-old second-growth conifers (Douglas-fir [*Pseudotsuga menziesii*], western larch [*Larix occidentalis*], and ponderosa pine [*Pinus ponderosa*]) with occasional pockets of broad-leafed deciduous trees (*Populus* spp.). Approximately 275 ha were salvage-logged in the winter following the fire (1991–1992) in a pattern in which seven salvage-logged plots (totaling approximately 134 ha) were interspersed with eight unlogged control plots (totaling approximately 148 ha; Fig. 1). The individual plots averaged 23.9 ± 11.7 SD ha in size (range = 7–36 ha), and were delineated either on the basis of isolation of the unit or on the basis of road locations and timber harvest prescriptions provided by Champion Timber Company. The extent of salvage logging varied among plots, but in most cases all merchantable (>15 cm dbh, >4.5 m tall) fire-killed timber was removed. Most unlogged and salvage-logged forest plots were surrounded by grasslands.

NEST ABUNDANCE AND CAVITY REUSE

We located active cavity nests by searching the 15 forest plots during the breeding season from mid-May through mid-July of 1993, 1994, and 1995. We walked parallel transects (spaced at 20 m intervals) through the plots to systematically search the plots for active nests. Plots were of a size that required between one and

two days' search time to cover the entire plot. We searched plots at least twice during each breeding season, and walked transects in opposite directions from visit to visit to maximize our chances of finding all active nests. Nests were located by finding cavities directly and observing subsequent activity, following adult birds to nests, or hearing young birds in the nest. We recorded activity of adult birds at the nest (building, incubating, or feeding) at the time the nest was found and the type of cavity used (excavated or natural). The first time an active nest was found, it was considered a new nest. In subsequent years, the same nest cavities were checked for activity. Cavities active in subsequent years were considered reused nests, and cavities harboring a second pair of breeding birds of the same or a different species in a single year were classified as repeat nests.

VEGETATION AND TREE MEASUREMENTS

To characterize vegetation structure associated with the two treatments, we measured vegetation characteristics surrounding 132 randomly located trees in unlogged plots and 112 randomly located trees in salvage-logged plots. Sample trees were selected by locating random grid points on high-resolution aerial photos. If a random point fell on a tree, that tree was selected as a sample tree; otherwise the point was discarded. Random points were generated until all sample trees had been identified. Sample trees were located on the ground with the aid of aerial photos.

We recorded several characteristics associated with, and vegetation conditions surrounding, nest trees and randomly selected trees. Tree characteristics included size (diameter at breast height, measured with a dbh tape), height (measured with a clinometer), species, status (live or dead; intact or with a broken or dead top), percent bark remaining (estimated visually), and presence of a nest cavity. To assess vegetation characteristics surrounding focal trees, stakes were placed 15 m from the tree in the four cardinal directions. We made ocular estimates of the percent of bare ground (bare soil), ground cover (herbaceous plants <25 cm tall), low shrub cover (herbaceous plants >25 cm tall plus woody plants <0.5 m), and tall shrub cover (woody plants >0.5 m tall) in each quarter and then averaged the four estimates. These estimates were made from above, so the four estimates summed to 100%. Burn severity of the vegetation within 50 m of a sample tree was estimated using a subjective scale of one to five (after Hutto 1995), with 1 = 100% of the trees with green foliage or needles, 2 = most ($>60\%$) trees with green foliage or needles, and most of the rest with brown needles, 3 = 40%–60% of the trees brown-needled, and the rest either green- or black-needled, 4 = most ($>60\%$) trees black-needled, and the rest with brown needles, and 5 = all trees blackened. All vegetation measurements (including fire severity) on logged plots reflected conditions after cutting, so it was not possible to compare preharvest conditions on treatment and control plots.

STATISTICAL ANALYSES

We compared vegetation characteristics associated with the two treatments using Mann-Whitney *U*-tests for numerical data and chi-square likelihood ratios for categorical data. A Bonferonni correction for experiment-wise error was applied to adjust the *P*-value for multiple simultaneous tests. We tested for a difference in the distribution of nest abundance across species by treatment type using a chi-square likelihood ratio after combining numbers of nests across plots. Nest abundance was converted to nest density by averaging the number of nests per plot for each year of the study. We tested for differences in nest density over the three years of our study using repeated measures ANOVA. Nest densities were transformed by the inverse of the square root to achieve normality.

For each species with a minimum of nine nests, we compared characteristics of nest trees and randomly selected trees in both the unlogged and salvage-logged plots. Differences in numerical variables were tested with Mann-Whitney *U*-tests, and differences in distributions of categorical variables were tested with chi-square likelihood ratios. A Bonferonni correction for experiment-wise error was applied to all univariate tests for each species. When the same species nested in the same cavity in two or more years, the characteristics associated with that nest tree were included only once in the analysis.

For each primary cavity-nesting species, the suitability of randomly selected trees for nesting

TABLE 1. The percentage of nests found by each of three different methods and by status at the time they were found in unlogged and salvage-logged burned forest, Montana, 1993–1995. Most nests were discovered by following adult birds to the cavity, and most had either eggs or young when they were found.

	Unlogged	Salvage-logged
Method of location (n = 300)		
Following adult bird to nest	58	48
Finding cavity directly	21	23
Seeing or hearing adult or young at nest	21	29
Nest status (n = 392)		
Building, excavating, or advertising	17	18
Incubating	32	43
Feeding young	51	39

was assessed by first calculating the range of each of five characteristics associated with nest trees. If the value of a characteristic associated with a random tree fell within the range of values obtained for nest trees, that random tree was considered ''suitable'' for that characteristic. Overall suitability was then determined by combining suitability information from all the individual tree characteristics. If values of all characteristics of a random tree fell within the range of values from nest trees, that random tree was considered ''suitable'' for that species. The proportion of random trees classified as suitable for each species (all plots combined within each treatment) was then converted into an absolute number of suitable trees per hectare by multiplication with the estimated number of trees per hectare in each treatment (360 trees per ha in unlogged plots and 134 trees per ha in salvage-logged plots).

RESULTS

NEST ABUNDANCE

We found most nests between 8 and 23 June in both salvage-logged and unlogged areas. Most nests were discovered by following adult birds to the cavity, and most had either eggs or young when they were found (Table 1). Eighty-three percent of nests in unlogged plots and 77% of nests in salvage-logged plots (80% overall) were in cavities originally excavated by primary cavity-nesting birds.

We found 563 active nests distributed among 18 cavity-nesting species (Table 2). All 18 species nested in unlogged areas, whereas only eight species nested in salvage-logged areas (Table 2). The total number of active nests found in unlogged plots was almost three times higher than the total number of nests in salvage-logged plots, even though the area searched and search effort was similar between plot types (Table 2). The combined nest density was significantly higher in unlogged than in salvage-logged areas in each year of our study (treatment effect: $F_{1,13} = 8.3$, $P = 0.02$), and the mean density of all species combined increased significantly over the three years of study in both the unlogged and salvage-logged plots (year effect: $F_{2,26} = 4.2$, $P = 0.02$; Fig. 2). All cavity-nesting species except the Black-capped Chickadee (*Poecile atricapillus*) nested at a higher density in the unlogged than the salvage-logged areas, and half of all cavity-nesting species were significantly more abundant in the unlogged plots (Table 2). The most abundant species in unlogged areas (Northern Flicker [*Colaptes auratus*], House Wren [*Troglodytes aedon*], and Mountain Bluebird) were also the most abundant in salvage-logged areas, and the vast majority of nests in both salvage-logged and unlogged plots belonged to ground- and shrub-foraging species (73% and 93%, respectively) and to secondary cavity-nesting species (63% and 65%, respectively). Nevertheless, the relative abundances of all cavity-nesting species differed significantly between the two treatments ($\chi^2_{17} = 59.4$, $P < 0.001$), primarily because five timber-drilling woodpecker species and the two timber-gleaning nuthatch species nested only in the unlogged plots (Table 2).

CAVITY REUSE

Only 34% of the cavities excavated in 1993 were reused by cavity-nesting birds in 1994 (Table 3). In 1995, 36% of cavities used for nesting during either or both of the two previous years were reused. The frequency of cavity reuse in salvage-logged areas was 50% in 1994 and 44% in 1995. In contrast, the frequencies of reuse in unlogged areas were substantially lower—30% in 1994 and 33% in 1995 (Table 3). In 1995, a small percentage of cavities (2.6%) were used twice in one breeding season, and Mountain Bluebird, House Wren, and North-

TABLE 2. Total number of nests and mean nest densities (number per 40 ha ± SE) in unlogged and salvage-logged plots in burned forest in Montana. Numbers were tallied across three years from 1993 to 1995. We discovered a greater number of nests in unlogged than in salvage-logged plots for all but one species, and the mean nest densities of most cavity-nesting species were also significantly higher in the unlogged plots. Bonferonni-adjusted *P*-values are from Mann-Whitney *U*-tests for differences in mean density between the two treatments.

Species	Species code	Nesting guild[a]	Foraging guild[b]	Unlogged		Salvage-logged		*P*
				Total no. nests	Mean density	Total no. nests	Mean density	
American Kestrel (*Falco sparverius*)	AMKE	2°	GF	6	0.7 ± 0.1	5	0.4 ± 0.1	0.53
Lewis' Woodpecker (*Melanerpes lewis*)	LEWO	1°	AI	2	0.2 ± 0.1	0	0	0.35
Williamson's Sapsucker (*Sphyrapicus thyroideus*)	WISA	1°	TD	9	0.5 ± 0.1	0	0	0.07
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	RNSA	1°	TD	11	0.5 ± 0.1	0	0	0.03
Downy Woodpecker (*Picoides pubescens*)	DOWO	1°	TD	4	0.4 ± 0.1	0	0	0.03
Hairy Woodpecker (*Picoides villosus*)	HAWO	1°	TD	15	1.5 ± 0.2	5	0.6 ± 0.1	0.07
American Three-toed Woodpecker (*Picoides dorsalis*)	TTWO	1°	TD	9	0.8 ± 0.1	0	0	< 0.01
Black-backed Woodpecker (*Picoides arcticus*)	BBWO	1°	TD	10	0.9 ± 0.2	0	0	< 0.01
Northern Flicker (*Colaptes auratus*)	NOFL	1°	GF	81	7.8 ± 0.9	51	4.9 ± 0.4	0.43
Tree Swallow (*Tachycineta bicolor*)	TRSW	2°	AI	27	2.8 ± 0.5	5	0.4 ± 0.1	0.05
Black-capped Chickadee (*Poecile atricapillus*)	BCCH	1°	FS	1	0.1 ± 0.0	1	0.1 ± 0.0	0.90
Mountain Chickadee (*Poecile gambeli*)	MOCH	1°	FS	10	0.8 ± 0.2	0	0	0.01
Red-breasted Nuthatch (*Sitta canadensis*)	RBNU	1°	TG	8	0.3 ± 0.1	0	0	0.03
White-breasted Nuthatch (*Sitta carolinensis*)	WBNU	1°	TG	6	0.4 ± 0.1	0	0	0.05
House Wren (*Troglodytes aedon*)	HOWR	2°	GF	126	11.5 ± 1.4	43	4.6 ± 0.4	0.24
Western Bluebird (*Sialia mexicana*)	WEBL	2°	GF	2	0.2 ± 0.1	0	0	0.18
Mountain Bluebird (*Sialia currucoides*)	MOBL	2°	GF	70	7.1 ± 0.5	29	2.6 ± 0.3	< 0.01
European Starling (*Sturnus vulgaris*)	EUST	2°	GF	17	2.1 ± 0.4	10	0.8 ± 0.2	0.52
Combined species totals				414	38.6 ± 3.1	149	14.6 ± 1.0	< 0.01

[a] 1° = primary cavity-nesting species, 2° = secondary cavity-nesting species (Thomas 1979).
[b] GF = ground-shrub forager, TD = timber driller, AI = aerial insectivore, FS = foliage searcher, TG = timber gleaner (Bock and Lynch 1970).

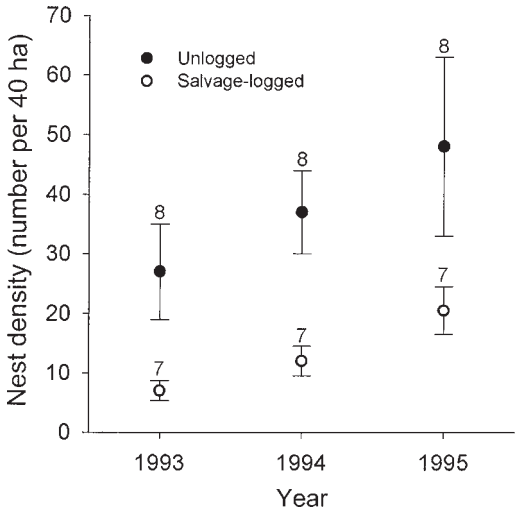


FIGURE 2. In each of the three years of study, mean nest density of all cavity-nesting species averaged over all plots was significantly higher in unlogged than in salvage-logged treatments in the Blackfoot-Clearwater Wildlife Management Area, Montana. Sample sizes appear above the error bars.

ern Flicker were the three species that most often used reused cavities for nesting. More than a quarter (27%) of Northern Flicker nests were located in previously used cavities. Although Northern Flickers may have excavated these cavities originally, it is clear they were not creating new nest cavities each breeding season.

There were 128 cavities known by observation to have been excavated by primary cavity-nesting birds. Of these, 58 were reused at least once during subsequent years, and half of those were Northern Flicker cavities being reused by flickers (Table 4). Despite the high frequency of reuse, Northern Flickers provided more cavities for other secondary cavity-nesting species than any other primary cavity-nesting species. Additionally, Northern Flicker cavities appeared to be the only cavities suitable for American Kestrels (*Falco sparverius*), possibly because flickers excavated relatively large entrance holes in relatively decayed snags. A small number of Red-naped (*Sphyrapicus nuchalis*) and Williamson's (*S. thyroideus*) Sapsuckers reused cavities excavated by Red-naped Sapsuckers (Table 4). Most of the Hairy (*Picoides villosus*), American Three-toed, and Black-backed Woodpecker cavities were reused by House Wrens and Mountain Bluebirds, which together used over a quarter of the 58 cavities originally made by primary cavity-nesting birds.

VEGETATION CHARACTERISTICS

Unlogged plots had significantly larger and taller trees, a higher density of trees, trees with more bark, higher live-tree density, and a lower proportion of intact snags than salvage-logged plots (Table 5). The burn severity surrounding randomly selected trees in unlogged plots was also slightly less than the burn severity surrounding randomly selected trees in logged plots (Table 5), although the index of severity that we used was undoubtedly affected by the removal of some green and brown-needled trees from the salvage-logged plots.

CHARACTERISTICS AND AVAILABILITY OF NEST TREES

Of the 12 species for which we found nine or more nests, all but one (Mountain Chickadee [*Poecile gambeli*]) nested in trees that were larger and taller than what was available in the salvage-logged plots; only the American Kestrel and Northern Flicker used larger trees than

TABLE 3. Numbers of new, reused (used in previous years by the same or different species), or repeat (used earlier in the same breeding season by the same or different species) nests across three years in unlogged and salvage-logged plots following fire in Montana. The proportion of cavities that were reused was higher in salvage-logged than in unlogged plots.

	Unlogged			Salvage-logged			
Year	New nests	Reused nests	Repeat nests	New nests	Reused nests	Repeat nests	Total
1993	96	N/A	N/A	26	N/A	N/A	122
1994	108	29	0	33	13	0	183
1995	108	68	5	46	26	5	258
Total	312	97	5	105	39	5	563

TABLE 4. Number of cavities first excavated by a given primary cavity-nesting bird species that were subsequently used by each of several primary and secondary cavity-nesting species in years following initial cavity excavation in Montana, 1993–1995. The cavities of seven species were reused by the same or by another species, and the Northern Flicker provided the greatest number of cavities that were reused.

Excavating species[a]	Reuse species[a]									Total reused	Total excavated	% reused	% reused by another species	No. cavities used all 3 yr
	MAKE	WISA	RNSA	NOFL	TRSW	WBNU	HOWR	MOBL	EUST					
LEWO				1						1	2	50	100	0
WISA				1	1					2	8	25	100	0
RNSA		2	2							4	11	36	50	0
HAWO				3			3	2		8	12	67	100	2
TTWO							1	4	1	6	10	60	100	2
BBWO				2		1	2	1		6	12	50	100	1
NOFL	3			22	2			2	2	31	73	42	29	7
Totals (percent)	3 (5)	2 (3)	2 (3)	29 (50)	3 (5)	1 (2)	6 (10)	9 (16)	3 (5)	58	128	48	35	12

[a] Species codes are given in Table 2.

what would be expected by chance in the unlogged plots (Fig. 3). Deciduous and broken-topped trees were also used for nesting by most species more often than would be expected due to chance (Fig. 4).

The percentage of randomly selected trees that were deemed suitable for nesting varied widely among the primary cavity-nesting species (Table 6). For some species, a single tree characteristic excluded a large number of randomly selected trees from being considered suitable. For example, Red-naped Sapsuckers nested in deciduous trees only, and because deciduous trees comprised a small percentage of random trees, the proportion of suitable nest trees for sapsuckers was close to zero in both unlogged and salvage-logged areas (Table 6). The estimated density of available nest trees ranged from zero for Red-naped Sapsuckers in salvage-logged plots, to 232 trees per ha for Hairy Woodpeckers in unlogged plots (Table 6).

Nest tree availability was not as easily assessed for secondary cavity-nesters because the presence of cavities was difficult to discern and because new cavities were undoubtedly created after we measured characteristics of randomly selected trees during the first year of our study. Nevertheless, cavities were present initially in only four of 244 randomly selected trees and only in the unlogged plots.

DISCUSSION

The densities of cavity nests in this study (14.6 and 38.6 nests per 40 hectares in salvage-logged and unlogged plots, respectively) are at the upper end of cavity nest densities that have been reported for other burned areas (Bock and Lynch 1970, Taylor and Barmore 1980, Caton 1996). Nevertheless, the higher abundance and species richness of cavity-nesting birds in unlogged compared to salvage-logged burned areas in this study is a result that is consistent with virtually all studies to date on this topic (Blake 1982, Harris 1982, Raphael and White 1984, Lyon and Marzluff 1985, Caton 1996, Saab and Dudley 1998, Haggard and Gaines 2001, Morissette et al. 2002). The single exception comes from a longer-term study in ponderosa pine-dominated communities in Idaho (V. Saab, R. Russell, and J. Dudley, USDA Forest Service, unpubl. data), where the overall density of cavity-nesting birds was observed to

TABLE 5. Vegetation characteristics associated with randomly selected trees in plots that were either unlogged (n = 132 trees) or salvage-logged (n = 112 trees) after a 1991 fire in the Blackfoot-Clearwater Wildlife Management Area, Montana. Tree sizes, tree densities, and percentage of live trees were significantly greater in unlogged than in salvage-logged plots. Means ± SE are given for numerical variables, and frequency distributions are given for categorical variables. Asterisk indicates a significant ($P < 0.05$) difference between unlogged and salvage-logged plots.

Vegetation characteristic	Unlogged	Salvage-logged
DBH (cm)*	30.7 ± 1.1	20.9 ± 0.9
Height (m)*	16.2 ± 0.4	12.7 ± 0.4
Bark (%)*	97 ± 1	94 ± 1
Tree species		
Pinus contorta	2%	0%
Pinus ponderosa	30%	19%
Larix occidentalis	10%	15%
Pseudotsuga mensiezii	53%	63%
Populus spp.	5%	3%
Tree status*		
Intact snag	74%	88%
Broken snag	5%	5%
Broken live	0%	1%
Intact live	21%	6%
Tree density (15 m radius)		
10–40 cm dbh*	23.7 ± 1.4	9.1 ± 0.8
>40 cm dbh*	1.6 ± 0.2	0.0 ± 0.0
Bare ground (%)	9 ± 1	8 ± 1
Ground cover (%)	33 ± 2	35 ± 2
Low shrub (%)	56 ± 2	55 ± 2
Tall shrub (%)	3 ± 3	2 ± 0
Burn severity*		
100% green	18%	2%
>60% green	5%	3%
40%–60% brown	25%	9%
>60% black	24%	25%
100% black	28%	62%

be slightly greater in salvage-logged plots in the first five years following fire, but not during the next five years. The combined density of all cavity-nesting birds increased over the three-year period of this study, primarily due to the creation of cavities by primary cavity-nesting species and the use of those same cavities in subsequent years by both primary and secondary cavity-nesters.

Of particular note is the fact that six of eight woodpecker species nested only in unlogged burned forest; they were entirely absent from salvage-logged areas. This is consistent with reports (Hutto 1995, Hutto and Young 1999) that, in the northern Rocky Mountains, two of these species (Black-backed and American Three-toed Woodpeckers) are not only more abundant in burned conifer forests than in any other vegetation type, but are also relatively restricted to such conditions. This result is also consistent with results from all of the previously cited studies on the effects of salvage logging on cavity-nesting birds. The number of Black-backed and American Three-toed Woodpecker nests decreased from the third to the fifth year after fire, which is similar to what Harris (1982), Caton (1996), Saab et al. (2004) and Saab et al. (V. Saab, R. Russell, and J. Dudley, USDA Forest Service, unpubl. data) found in their multiyear studies of postfire forests.

Preharvest tree density in salvage-logged areas (estimated by adding stump density to existing tree density) was 271 trees per ha, which was still well below the tree density in unlogged areas (360 trees per ha). It is therefore likely that salvage-logged and unlogged areas were somewhat different prior to the onset of fire and subsequent salvage-logging. There is always the possibility that some preharvest difference between plot types (e.g., a difference in average fire severity, slope, or aspect) might have contributed to the differences in bird densities between plot types; however, the presence of treatment replication in this study and the complete agreement between our results and the results of others who have looked at the effects of salvage logging strongly suggest that the significant reduction in abundance of cavity-nesting timber-drillers and timber-gleaners in salvage-logged areas was due primarily to the reduction in number of recently killed snags. This raises the question of whether it was a reduction in number of potential nest sites or some other aspect of habitat quality such as food availability that was affected most by the removal of standing dead trees.

Snags have traditionally been viewed as valuable for cavity-nesting birds exclusively in terms of their potential to be used as nest sites. Indeed, snag-management guidelines were originally based on meeting the nesting requirements of cavity-nesting birds (Thomas 1979). If nest trees were limiting bird densities in salvage-logged plots, then the density of suitable nest trees should have decreased to a number well below 6–8 trees per ha—the minimum number believed necessary to support maximum population densities of most cavity-nesting species

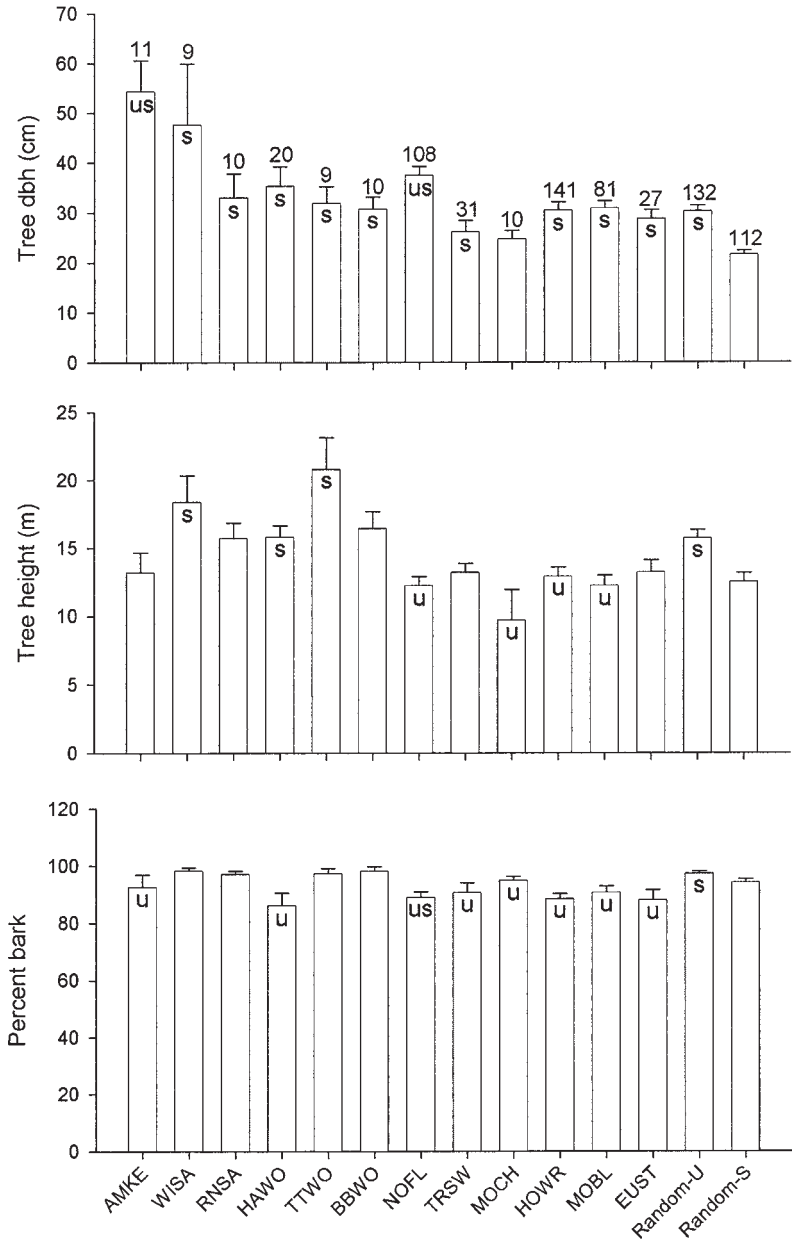


FIGURE 3. Mean nest tree characteristics (± SE) for cavity-nesting bird species (codes given in Table 2) and for randomly selected trees in unlogged (Random-U) and salvage-logged (Random-S) plots in the Blackfoot-Clearwater Wildlife Management Area, Montana. Nest trees generally differed significantly in one or more respects from randomly selected trees, especially in salvage-logged plots. Sample sizes are given above bars in the upper bar chart. Small letters indicate significant differences from randomly selected trees in salvage-logged (s) or unlogged (u) plots ($P < 0.05$, Mann-Whitney *U*-tests with Bonferonni correction for multiple comparisons).

(Thomas 1979:appendices 22, 23). We tested this hypothesis by calculating the percentage of randomly selected trees in both uncut and salvage-logged plots that could be considered suitable for nesting by each species. Most cavity-nesting species used snags rather than

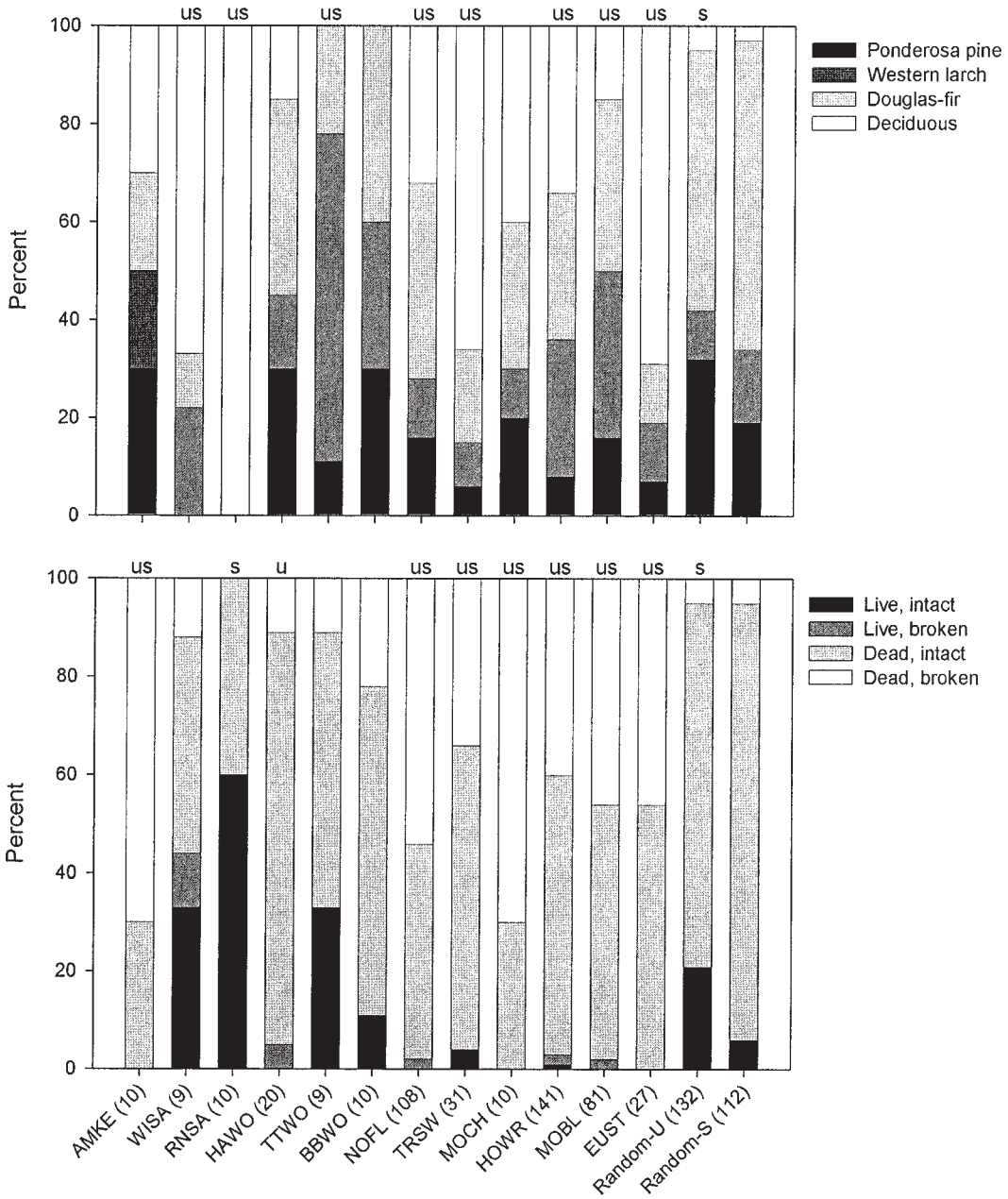


FIGURE 4. Frequency distributions of tree species and status of trees used by cavity-nesting bird species (codes given in Table 2) and of randomly selected trees in unlogged (Random-U) and salvage-logged (Random-S) plots. Most cavity-nesters used deciduous trees and broken-topped snags more than expected due to chance. Sample sizes are given at the bottom of the figure. Small letters indicate significant differences from randomly selected trees in salvage-logged (s) or unlogged (u) plots ($P < 0.05$, chi-square likelihood ratio with Bonferonni correction for multiple comparisons).

live trees for nesting, and several species used broken-topped snags more than expected based on their availability. All but one species (Mountain Chickadee) used nest trees that had significantly larger diameters than randomly selected trees in salvage-logged areas. The

TABLE 6. Percentages of randomly selected trees in unlogged (n = 132) and salvage-logged (n = 112) plots that were considered suitable for primary cavity-nesting species according to each of five different tree characteristics and all five characteristics combined in unlogged (U) and salvage-logged (S) plots in burned forest in Montana, 1993–1995. See Table 2 for Latin names of bird species. Only species with at least nine nests were included. The density of potentially suitable nest trees for each species was much greater in unlogged plots, and was greater than the minimum density needed to support maximum population densities of most cavity-nesting species in both unlogged and salvage-logged plots.

		Tree characteristic												Estimated number per ha	
		DBH		Height		Bark		Status		Species		Combined			
Species	n	U	S	U	S	U	S	U	S	U	S	U	S	U	S
Williamson's Sapsucker	9	67	21	93	94	95	92	99	99	68	81	39	10	142	14
Red-naped Sapsucker	10	60	26	67	70	95	92	95	94	5	3	3	0	11	0
American Three-toed Woodpecker	9	73	31	67	31	96	92	100	99	93	97	48	11	172	14
Black-backed Woodpecker	10	58	21	85	77	98	93	100	99	97	93	48	14	172	19
Hairy Woodpecker	20	99	87	85	77	98	96	78	93	100	100	64	63	232	84
Northern Flicker	108	91	61	99	100	79	93	99	99	100	100	62	53	224	71
Mountain Chickadee	10	52	38	80	96	95	92	99	100	78	93	36	41	128	55

selective removal of economically valuable larger-diameter trees clearly reduced the density and average size of snags in salvage-logged areas and, therefore, reduced the amount of suitable nesting habitat. Nevertheless, the decline in density of snags that might be used as nest sites by those bird species that were most negatively affected by logging still far exceeded the 6–8 snags per ha recommended as a minimum number needed to maintain maximum population densities.

These results highlight the fact that we need to appreciate snags as food resources as well as nest-site resources and that, for timber-drilling woodpecker species in particular, the number of snags needed to meet food resource needs appears to be much greater than the number needed to meet nesting requirements. Most woodpecker species in this study are relatively "tree-dependent" foragers because they forage on dead trees for beetle larvae. Burned snags are known to serve as sources of superabundant bark and wood-boring beetle larvae (Muona and Rutanen 1994, Rasmussen et al. 1996, Hart 1998), which are the primary food resource for tree-dependent foragers in burned forests (Powell et al. 2002, Nappi et al. 2003). Salvage logging undoubtedly reduces foraging opportunities for these birds, and may be the primary reason that overall habitat suitability declines for them (Caton 1996). The total disappearance of most timber-drilling and timber-gleaning birds in this study also underscores the need for a modification of current snag management guidelines (Hutto 2006) to better recognize the importance of retaining numerous snags as sources for food (beetle larvae) in burned forests.

In contrast with primary cavity-nesting birds, secondary cavity-nesters are often thought to be limited by the availability of nest sites (Brush 1983, Brawn and Balda 1988, Walankiewicz 1991). Because two-thirds of the cavities we discovered were not reused during the three years of this study, either something other than nest sites limited the density of secondary cavity-nesting birds, or many of the apparently suitable nest cavities were not really suitable at all (see also Welsh and Capen 1992). Other animals (e.g., northern flying squirrels [*Glaucomys sabrinus*] and red squirrels [*Tamiasciurus hudsonicus*]) were observed using previously active cavities, and they are known to displace secondary cavity-nesting birds or depredate their nests. The location of cavities near other nesting birds of the same or different species may also make cavities unsuitable for nesting. For example, birds may avoid nesting near American Kestrel nests because they (or their nestlings) might experience higher rates of predation. Indeed, American Kestrels were observed to prey on other secondary cavity-nesting species in this study. Other predators known to occur in the study area, and that

could have affected the suitability of cavities for secondary cavity-nesters, include striped skunks (*Mephitis mephitis*), black bears (*Ursus americana*), and weasels (*Mustela* spp.). Other factors such as a lack of foraging opportunities could also limit secondary cavity-nesting bird densities in the face of what appear to be abundant nesting opportunities.

Assuming that secondary cavity-nesters are limited by nesting opportunities, it is noteworthy that the frequency of cavity reuse was higher in salvage-logged than in unlogged plots, possibly reflecting a greater level of nest-site limitation in the salvage-logged areas. More than 80% of the nests of secondary cavity-nesters were located in cavities excavated by woodpeckers, indicating a strong reliance on primary cavity-nesting birds for cavity excavation (see also Dobkin et al. 1995). In unlogged areas, the continuous creation of roosting and nesting cavities by primary cavity-nesting species may provide abundant new cavities for secondary cavity-nesting birds to use. In contrast, fewer breeding primary cavity-nesters in salvage-logged areas create fewer new cavities, and this may force secondary cavity-nesting birds to reuse a smaller number of older cavities, which could also affect their nest success in salvage-logged forests.

In conclusion, the cavity-nesting bird community as a whole was clearly negatively affected by salvage logging in our study area in the early years following stand-replacing fire, and the main problem for primary cavity-nesting bird species does not appear to have been availability of snags as nest sites. Rather, the reduction in numbers of trees that harbored important food resources seemed to be to the detriment of the most fire-dependent cavity-nesting bird species. Especially noteworthy was the absence of several postfire specialist woodpecker species from salvage-logged areas and the general decrease in nesting densities of timber-drilling and timber-gleaning species compared to their densities in unlogged burned areas. These results are especially important in light of recent modifications to legislation and regulations by provincial governments in Canada (cited in Nappi et al. 2003) and by the U. S. government (Healthy Forests Restoration Act of 2003) to expedite and provide incentives for salvage logging on top of already documented increases in dead tree harvest in the West (Duncan 2002). Because early postfire cavity-nesting bird communities are biologically unique, and because we lose the most fire-dependent elements of that community through salvage harvests such as the ones included in this study, the merit of postfire salvage logging should be reexamined, especially when there are other, less ecologically sensitive options available for timber harvest. Although research on the effects of different levels and styles of salvage logging are urgently needed, the findings that have already emerged from this and from other studies (McIver and Starr 2000, Kotliar et al. 2002, Beschta et al. 2004, Karr et al. 2004) are entirely consistent, and they suggest that it may be difficult to retain the ecological integrity of a burned forest in the face of most kinds of postfire salvage logging.

ACKNOWLEDGMENTS

We thank two anonymous reviewers, David Dobkin, Sallie Hejl, Paul Alaback, Elaine Caton, Vita Wright, and Jock Young for comments on earlier drafts of this paper. Financial assistance for this study was provided by a McIntire-Stennis grant from the University of Montana College of Forestry and Conservation and a student research grant from the North American Bluebird Society. Generous in-kind support was provided by the Montana Department of Fish, Wildlife and Parks, Champion Timber Company, and Richard Howe. Special thanks to Mike Thompson at Montana Fish, Wildlife and Parks for his help through all phases of this project and to Ann Mull for field assistance.

LITERATURE CITED

ANDERSEN, A. N., R. W. BRAITHWAITE, G. D. COOK, L. K. CORBETT, R. J. WILLIAMS, M. M. DOUGLAS, A. M. GILL, S. A. SETTERFIELD, AND W. J. MULLER. 1998. Fire research for conservation management in tropical savannas: introducing the Kapalga fire experiment. Australian Journal of Ecology 23:95–110.

BESCHTA, R. L., J. J. RHODES, J. B. KAUFFMAN, R. E. GRESSWELL, G. W. MINSHALL, J. R. KARR, D. A. PERRY, F. R. HAUER, AND C. A. FRISSELL. 2004. Postfire management on forested public lands of the western United States. Conservation Biology 18:957–967.

BLAKE, J. G. 1982. Influence of fire and logging on nonbreeding bird communities of ponderosa pine forests. Journal of Wildlife Management 46:404–415.

BOCK, C. E., AND J. F. LYNCH. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. Condor 72:182–189.

BRAWN, J. D., AND R. P. BALDA. 1988. Population biology of cavity nesters in northern Arizona: do

nest sites limit breeding densities? Condor 90:61–71.

BRUSH, T. 1983. Cavity use by secondary cavity-nesting birds and response to manipulations. Condor 85:461–466.

CATON, E. L. 1996. Effects of fire and salvage logging on the cavity-nesting bird community in northwestern Montana. M.Sc. thesis, University of Montana, Missoula, MT.

DICKSON, J. G., R. N. CONNER, AND J. H. WILLIAMSON. 1983. Snag retention increases birds in a clearcut. Journal of Wildlife Management 47:799–809.

DOBKIN, D. S., A. C. RICH, J. A. PRETARE, AND W. H. PYLE. 1995. Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin. Condor 97:694–707.

DUNCAN, S. 2002. Postfire logging: is it beneficial to a forest? Science Findings 47:1–5.

GRUELL, G. E. 1983. Fire and vegetative trends in the northern Rockies: interpretations from 1871–1982 photographs. USDA Forest Service General Technical Report INT-158.

HAGGARD, M., AND W. L. GAINES. 2001. Effects of stand-replacement fire and salvage logging on a cavity-nesting bird community in eastern Cascades, Washington. Northwest Science 75: 387–396.

HARGROVE, W. W., AND J. PICKERING. 1992. Pseudoreplication: a *sine qua non* for regional ecology. Landscape Ecology 6:251–258.

HARRIS, M. A. 1982. Habitat use among woodpeckers in forest burns. M.Sc. thesis, University of Montana, Missoula, MT.

HART, S. 1998. Beetle mania: an attraction to fire. BioScience 48:3–5.

HOBSON, K. A., AND J. SCHIECK. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. Ecological Applications 9:849–863.

HUTTO, R. L. 1995. The composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. Conservation Biology 9:1041–1058.

HUTTO, R. L. 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. Conservation Biology 20:984–993.

HUTTO, R. L., AND J. S. YOUNG. 1999. Habitat relationships of landbirds in the Northern Region, USDA Forest Service. USDA Forest Service General Technical Report RMRS-GTR-32.

KARR, J. R., J. J. RHODES, G. W. MINSHALL, F. R. HAUER, R. L. BESCHTA, C. A. FRISSELL, AND D. A. PERRY. 2004. The effects of postfire salvage logging on aquatic ecosystems in the American West. BioScience 54:1029–1033.

KOTLIAR, N. B., S. J. HEJL, R. L. HUTTO, V. A. SAAB, C. P. MELCHER, AND M. E. MCFADZEN. 2002. Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. Studies in Avian Biology 25:49–64.

LINDENMAYER, D. B., D. R. FOSTER, J. F. FRANKLIN, M. L. HUNTER, R. F. NOSS, F. A. SCHMIEGELOW, AND D. PERRY. 2004. Salvage harvesting policies after natural disturbance. Science 303:1303.

LYON, L. J., AND J. M. MARZLUFF. 1985. Fire's effects on a small bird population, p. 16–22. *In* J. E. Lotan and J. K. Brown [EDS.], Fire's effects on wildlife habitat–symposium proceedings. USDA Forest Service General Technical Report INT-186.

MARCOT, B. G. 1983. Snag use by birds in Douglas-fir clearcuts, p. 134–139. *In* J. W. Davis, G. A. Goodwin, and R. A. Ockenfels [EDS.], Snag habitat management: proceeding of the symposium. USDA Forest Service General Technical Report RM-99.

MCIVER, J. D., AND L. STARR. 2000. Environmental effects of postfire logging: literature review and annotated bibliography. USDA Forest Service General Technical Report PNW-GTR-486.

MORISSETTE, J. L., T. P. COBB, R. M. BRIGHAM, AND P. C. JAMES. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Canadian Journal of Forest Research 32:2169–2183.

MORRISON, M. L., AND M. G. RAPHAEL. 1993. Modeling the dynamics of snags. Ecological Applications 3:322–330.

MUONA, J., AND I. RUTANEN. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. Annales Zoologici Fennici 31:109–121.

NAPPI, A. 2000. Distribution des pics et utilisation des arbres morts dans les forêts soumises aux perturbations naturelles en pessière à mousses. M.Sc. thesis, Université du Québec, Montreal, Quebec.

NAPPI, A., P. DRAPEAU, J.-F. GIROUX, AND J.-P. SAVARD. 2003. Snag use by foraging Black-backed Woodpeckers (*Picoides arcticus*) in a recently burned eastern boreal forest. Auk 120: 505–511.

NAPPI, A., P. DRAPEAU, AND J.-P. L. SAVARD. 2004. Salvage logging after wildfire in the boreal forest: is it becoming a hot issue for wildlife? Forestry Chronicle 80:67–74.

PIERCE, J. L., G. A. MEYER, AND A. J. T. JULL. 2004. Fire-induced erosion and millennial-scale climate change in northern ponderosa pine forests. Nature 432:87–90.

POWELL, H. 2000. The influence of prey density on post-fire habitat use of the Black-backed Woodpecker. M.Sc. thesis, University of Montana, Missoula, MT.

POWELL, H. D. W., S. J. HEJL, AND D. L. SIX. 2002. Measuring woodpecker food: a simple method for comparing wood-boring beetle abundance among fire-killed trees. Journal of Field Ornithology 73:130–140.

RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86.

RASMUSSEN, L. A., G. D. AMMAN, J. C. VANDYGRIFF, R. D. OAKES, A. S. MUNSON, AND K. E.

GIBSON. 1996. Bark beetle and wood borer infestation in the Greater Yellowstone area during four postfire years. USDA Forest Service Research Paper INT-RP-487.

SAAB, V. A., J. DUDLEY, AND W. L. THOMPSON. 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor 106:20–36.

SAAB, V. A., AND J. G. DUDLEY. 1998. Responses of cavity-nesting birds to stand-replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. USDA Forest Service Research Paper RMRS-RP-11.

SCHREIBER, B., AND D. S. DECALESTA. 1992. The relationship between cavity-nesting birds and snags on clearcuts in western Oregon. Forest Ecology and Management 50:299–316.

SCOTT, V. E., AND J. L. OLDEMEYER. 1983. Cavity-nesting bird requirements and responses to snag cutting, p. 19–23. *In* J. W. Davis, G. A. Goodwin, and R. A. Ockenfels [EDS.], Snag habitat management: proceeding of the symposium. USDA Forest Service General Technical Report RM-99.

SMUCKER, K. M., R. L. HUTTO, AND B. M. STEELE. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications 15:1535–1549.

TAYLOR, C. 1995. The politics of salvage timber. Journal of Forestry 93:60.

TAYLOR, D. L., AND W. J. BARMORE. 1980. Post-fire succession of avifauna in coniferous forests of Yellowstone and Grand Teton National Parks, Wyoming, p. 130–145. *In* R. M. DeGraaf [ED.], Workshop proceedings: management of western forests and grasslands for nongame birds. USDA Forest Service General Technical Report INT-86.

THOMAS, J. W. 1979. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553, USDA Forest Service, Washington, DC.

TURNER, M. G., AND W. H. ROMME. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology 9:59–77.

TURNER, M. G., W. H. ROMME, AND D. B. TINKER. 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and the Environment 1:351–358.

VAN MANTGEM, P., M. SCHWARTZ, AND M. B. KEIFER. 2001. Monitoring fire effects for managed burns and wildfires: coming to terms with pseudoreplication. Natural Areas Journal 21: 266–273.

WALANKIEWICZ, W. 1991. Do secondary cavity-nesting birds suffer more from competition for cavities or from predation in a primeval deciduous forest? Natural Areas Journal 11:203–212.

WELSH, C. J. E., AND D. E. CAPEN. 1992. Availability of nesting sites as a limit to woodpecker populations. Forest Ecology and Management 48:31–41.

WHELAN, R. J. 1995. The ecology of fire. Cambridge University Press, New York.

ZARNOWITZ, J. E., AND D. A. MANUWAL. 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. Journal of Wildlife Management 49:255–263.

View publication stats

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 121, 2019, pp. 1–17
DOI: 10.1093/condor/duz055

RESEARCH ARTICLE

Social status, forest disturbance, and Barred Owls shape long-term trends in breeding dispersal distance of Northern Spotted Owls

Julianna M. A. Jenkins,[1,*] Damon B. Lesmeister,[1,2] Eric D. Forsman,[1] Katie M. Dugger,[3] Steven H. Ackers,[2] L. Steven Andrews,[2] Chris E. McCafferty,[2] M. Shane Pruett,[2] Janice A. Reid,[1] Stan G. Sovern,[2] Rob B. Horn,[4] Scott A. Gremel,[5] J. David Wiens,[6] and Zhiqiang Yang[7]

[1] U.S. Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA
[2] Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA
[3] U.S. Geological Survey, Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA
[4] U.S. Bureau of Land Management, Roseburg District Office, Roseburg, Oregon, USA
[5] U.S. National Park Service, Olympic National Park, Port Angeles, Washington, USA
[6] U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon, USA.
[7] U.S. Forest Service, Rocky Mountain Research Station, Corvallis, Oregon, USA
*Corresponding author: julianna.jenkins@usda.gov

Submission Date: June 20, 2019; Editorial Acceptance Date: October 18, 2019; Published December 5, 2019

ABSTRACT

Dispersal among breeding sites in territorial animals (i.e. breeding dispersal) is driven by numerous selection pressures, including competition and spatiotemporal variation in habitat quality. The scale and trend of dispersal movements over time may signal changing conditions within the population or on the landscape. We examined 2,158 breeding dispersal events from 694 male and 608 female individually marked Northern Spotted Owls (*Strix occidentalis caurina*) monitored over 28 yr on 7 study areas to assess the relative importance of individual (sex, experience), reproductive (annual productivity, mate availability), and environmental (forest alteration, presence of competitor) sources of variation in breeding dispersal distance. Median breeding dispersal distance was 3.17 km, with 99% of all breeding dispersal events <37 km. Mean annual dispersal distances increased by 2.43 km in Oregon and 9.40 km in Washington between 1990 and 2017, which coincided with increases in annual detections of nonnative Barred Owl (*S. varia*). Frequency of breeding dispersal events, both among and within individuals, also increased over time. Female owls moved farther than males (median of 3.26 and 3.10 km, respectively), and birds with less experience (territory tenure) moved farther than those with more experience. Owls that were single in the year prior to dispersal moved 13–31% farther than those paired prior to dispersal. The greatest environmental change occurring over the course of our study was the expansion of Barred Owl populations. Breeding dispersal distance was positively related to Barred Owls in the study area and disturbance within the originating territory. While it appears that social factors continue to be important drivers of breeding dispersal distance in Spotted Owls, increased competition from Barred Owls and habitat alteration have a contributing effect. Increased breeding dispersal distances should be of concern for conservation efforts and considered in population monitoring because changing dispersal behavior may lead to higher rates of mortality and/or emigration from historical study areas.

Keywords: Barred Owl, breeding dispersal, forest disturbance, Northern Spotted Owl, *Strix occidentalis caurina*, *Strix varia*

El estatus social, los disturbios del bosque y la presencia de *Strix varia* determinan las tendencias de largo plazo de la distancia de dispersión reproductiva de *Strix occidentalis caurina*

RESUMEN

La dispersión entre los sitios reproductivos en los animales territoriales (i.e. dispersión reproductiva) está determinada por numerosas presiones de selección, incluyendo competencia y variación espacio-temporal en la calidad del hábitat. La escala y la tendencia de los movimientos de dispersión a lo largo del tiempo pueden indicar las condiciones cambiantes al interior de la población o en el paisaje. Examinamos 2,158 eventos de dispersión reproductiva provenientes de 694 machos y 608 hembras de *Strix occidentalis caurina* marcados individualmente, monitoreados a lo largo de 28 años en siete áreas de estudio, para evaluar la importancia relativa de las fuentes de variación individual (sexo, experiencia), reproductiva (productividad anual, disponibilidad de pareja) y ambiental (disturbio del bosque, presencia de competidores) en la distancia de dispersión reproductiva. La distancia media de dispersión reproductiva fue 3.17 km, con el 99% de todos los eventos de dispersión reproductiva menores a 37 km. Las distancias de dispersión media anual aumentaron 2.43 km en Oregón y 9.40 km en Washington entre 1990 y 2017, lo que coincidió con aumentos en las

Published by Oxford University Press for the American Ornithological Society 2019.
This work is written by (a) US Government employee(s) and is in the public domain in the US.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

detecciones anuales de la especie no nativa *S. varia*. La frecuencia de los eventos de dispersión reproductiva, tanto entre individuos como para un mismo individuo, también aumentaron a lo largo del tiempo. Las hembras de los búhos se movieron más que los machos (mediana de 3.26 y 3.10 km, respectivamente), y las aves con menos experiencia (tenencia territorial) se movieron más lejos que aquellas con más experiencia. Los búhos solteros durante el año anterior a la dispersión se movieron 13–31% más lejos que aquellos en pareja antes de la dispersión. El cambio ambiental más grande ocurrido a lo largo del tiempo de nuestro estudio fue la expansión de las poblaciones de *S. varia*. La distancia de dispersión reproductiva estuvo positivamente relacionada con *S. varia* en el área de estudio y los disturbios dentro del territorio de origen. Si bien parece que los factores sociales continúan siendo condicionantes importantes de la distancia de dispersión reproductiva en *Strix occidentalis caurina*, el aumento de la competencia por parte de *S. varia* y la alteración del hábitat tienen un efecto adicional. El aumento de las distancias de dispersión reproductiva debería ser motivo de preocupación para los esfuerzos de conservación y considerados en el monitoreo poblacional debido a que los cambios de comportamiento en la dispersión pueden llevar a mayores tasas de mortalidad y/o de emigración de las áreas de estudio históricas.

Palabras clave: dispersión reproductiva, disturbio del bosque, *Strix occidentalis caurina*, *Strix varia*

INTRODUCTION

Dispersal in territorial animals is driven by numerous selection pressures including inbreeding avoidance, competition, and spatiotemporal variation in habitat quality (Bowler and Benton 2005, Roze and Rousset 2005). There are 2 general categories of dispersal movements recognized in birds: natal dispersal, which is the movement between territories prior to the first breeding attempt, and breeding dispersal, defined as the movement of individuals between successive breeding places (Greenwood and Harvey 1982, Morrison and Wood 2009). Breeding dispersal is likely adaptive because switching breeding territories may increase access to mates or to higher-quality habitats with fewer threats or competitors. Alternatively, dispersers may also incur costs from movement to unfamiliar breeding territories, such as increased predation, resource limitation, or intra- or inter-specific aggression (Daniels and Walters 2000, Morrison and Wood 2009). Often, one sex disperses farther than the other; in mammals, male-biased dispersal is common, whereas in birds, female-biased dispersal is the norm (Greenwood 1980). Moreover, breeding dispersal movements may be short, perhaps representing a shift to an adjacent territory, or relatively far, potentially signifying emigration to another metapopulation. As a consequence, breeding dispersal involves a series of strategic decisions concerning whether or not to move, and if so, how far.

Breeding dispersal distances tend to be lower for abundant species with generalist habits, and greater for species that specialize on patchily distributed habitats (Paradis et al. 1998, Martin and Fahrig 2018). Dispersal movements may also be longer from poor-quality territories since those territories are often spatially larger (Bowman 2003). The magnitude and trend in breeding dispersal movements over time may signal population or environmental alterations. Changes within a territory such as a disturbance event (e.g., fire), the introduction of a predator (Bried and Jouventin 2007, Forero et al. 2008), or an increase in intra- or inter-specific competition may increase dispersal distances by decreasing the realized quality of a territory in terms of resource abundance, availability, and distribution (Kim et al. 2009). The abundance, availability, and distribution of resources and competitors across the landscape likely also influence the amount of time and distance required to locate a suitable territory.

The Northern Spotted Owl (*Strix occidentalis caurina*; hereafter Spotted Owl) is a long-lived territorial species with strong site and mate fidelity in both sexes (Forsman et al. 1984). Spotted Owls specialize on areas with mature coniferous forest and require old forest for nesting and roosting (Forsman et al. 2015, Davis et al. 2016, Sovern et al. 2019). The subspecies was listed as threatened under the Endangered Species Act in 1990 because of extensive loss of these forest conditions to timber harvest (USFWS 1990). Despite extensive efforts to protect old forest on federal lands under the Northwest Forest Plan (USDA and USDI 1994), Spotted Owl populations continue to decline. These declines have been linked with interspecific competition and territorial displacement by a novel invader, the Barred Owl (*S. varia*) (Dugger et al. 2016, Lesmeister et al. 2018). Forsman et al. (2002) reported a mean breeding dispersal rate of ~7% annually by color-marked Spotted Owls monitored in Oregon and Washington, USA, during 1985–1996. Investigations prior to the widespread Barred Owl expansion found that breeding dispersal in the Northern Spotted Owl and California Spotted Owl (*S. o. occidentalis*) was primarily affected by an individual's age, sex, social status (e.g., non-return of mate), and amount of habitat disturbance or alteration within their territory (Forsman et al. 2002, Blakesley et al. 2006, Gutiérrez et al. 2011).

An increased understanding of what environmental and social factors affect breeding dispersal distance in declining populations, and how these factors may change over time, can help inform conservation planning. Our primary objective was to document trends in Spotted Owl breeding dispersal distance, particularly in relation to forest disturbance and the range expansion of Barred Owls. We expected

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

dispersal distance to increase with increasing forest disturbance or the increasing occurrence of Barred Owls on historical territories of Spotted Owls. We also examined the effects of sex, prior reproductive status (productivity and pair status), and territory quality (historical productivity) on Spotted Owl breeding dispersal distances. We predicted that dispersal distance would be longer for females compared to males (Clarke et al. 1997, Forsman et al. 2002, Blakesley et al. 2006, Ganey et al. 2014), inexperienced (e.g., younger) compared to more experienced birds (Forsman et al. 2002, Kim et al. 2007), single compared to paired owls (Forsman et al. 2002, Andreu and Barba 2006), birds paired with a new mate compared to those paired with a previous mate (Forsman et al. 2002, Kim et al. 2007), and unproductive owls compared to owls that successfully fledged young prior to dispersal, or were on historically productive territories (Forsman et al. 2002, Calabuig et al. 2008, Jiménez-Franco et al. 2013).

METHODS

Spotted Owl Monitoring

We analyzed all documented breeding dispersal events of marked adult Spotted Owls from 7 study areas within 5 ecophysiographic provinces in Oregon and Washington during 1990 to 2017 (Figure 1). Study areas were the Olympic Peninsula (OLY; 2,541 km^2) and Cle Elum (CLE; 980 km^2) areas in Washington and the Oregon Coast Range (OCR; 1,810 km^2), Tyee (TYE; 810 km^2), H.J. Andrews (HJA; 1,004 km^2), South Cascades (CAS; 2,372 km^2), and Klamath (KLA; 1,074 km^2) areas in Oregon (Figure 1). Study areas and ecophysiographic provinces varied in climate, vegetation, and amount of topographic relief, but all areas were dominated by conifers or mixed conifer–hardwood forests. For more details on the environmental conditions of our study areas see Forsman et al. (2011) and Dugger et al. (2016).

We studied breeding dispersal as part of a long-term monitoring program for Spotted Owls that used a standardized survey protocol for locating and monitoring individually color-marked owls (Lint et al. 1999). Surveys were conducted during the breeding season (March through August) using night call-back methods to elicit territorial responses followed by daytime visits to locate owls, resight previously banded owls, band and determine the sex and age class of unmarked owls, and document owl social status and productivity. Specific protocols have been extensively described in prior publications (e.g., Lint et al. 1999, Dugger et al. 2016) and were consistent throughout the study period with the exception of the OLY study area where monitoring was discontinued on a portion of southern historical territories in 2006 because of budgetary limitations. We generated Thiessen polygons to represent historically occupied owl territories and to calculate territory-specific metrics (Dugger et al. 2016). Polygons were created using annual activity center locations (e.g., a used nest tree) of owls during 1990–2017. Because these polygons were generated using activity centers gathered across the study period, they are representative of historical Spotted Owl annual activity centers and do not capture annual variation in territory boundaries. Thiessen polygons extended from activity center locations to a maximum of half of the median nearest-neighbor distance, or midway between the annual activity centers of owls occupying adjacent territories, whichever distance was shorter (Dugger et al. 2016).

We defined a breeding dispersal event as the movement of a territorial owl between years to a different territory where it had the opportunity to breed, regardless of whether it actually bred previously, which included both paired or single residents (Daniels and Walters 2000, Forsman et al. 2002, Seamans and Gutierrez 2007). Spotted Owls often use different nest sites within a territory (Forsman et al. 1984), so we excluded cases where movements involved use of alternate nests in the same historical territory in different years. Movements by sub-adults (age 1–2) were only included if birds were observed as territorial with a mate prior to moving (i.e. the natal dispersal had been confirmed).

For each time interval between annual observations we recorded whether or not an individual owl dispersed to a new territory and the linear distance between activity centers. We compiled a database of breeding dispersal movements that included characteristics of the owl and territory before and after the movement. For this analysis, we only looked at dispersal events, including movements that occurred to areas outside study area boundaries. We did this to reduce potential bias toward shorter dispersal distances that can occur when study area boundaries are finite (Koenig et al. 1996). However, because our annual search effort was primarily focused within study area bounds, the frequency of long-distance breeding dispersal events are still likely underrepresented.

We considered age class and number of years at a territory prior to dispersal as measures of experience. We characterized owls into 3 age classes based on known age at banding and plumage differences between birds at year 1 (S1; rectrices with white, slightly pointed tips), year 2 (S2; rectrices with white, slightly rounded tips), and >2 years (adult; rectrices with white and brown blotches, rounded tips) (Forsman et al. 1984). We generated 3 measures of experience at a territory (i.e. territory tenure pre-dispersal): (1) number of years spent on the territory prior to moving; (2) a binary variable describing if a bird was new to a territory (n = 0 yr) or had previously occupied the territory ($n \geq$ 1 yr); and (3) a categorical variable assigned as no prior experience (n = 0 yr), low experience (0 yr < n < 3 yr), or high

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

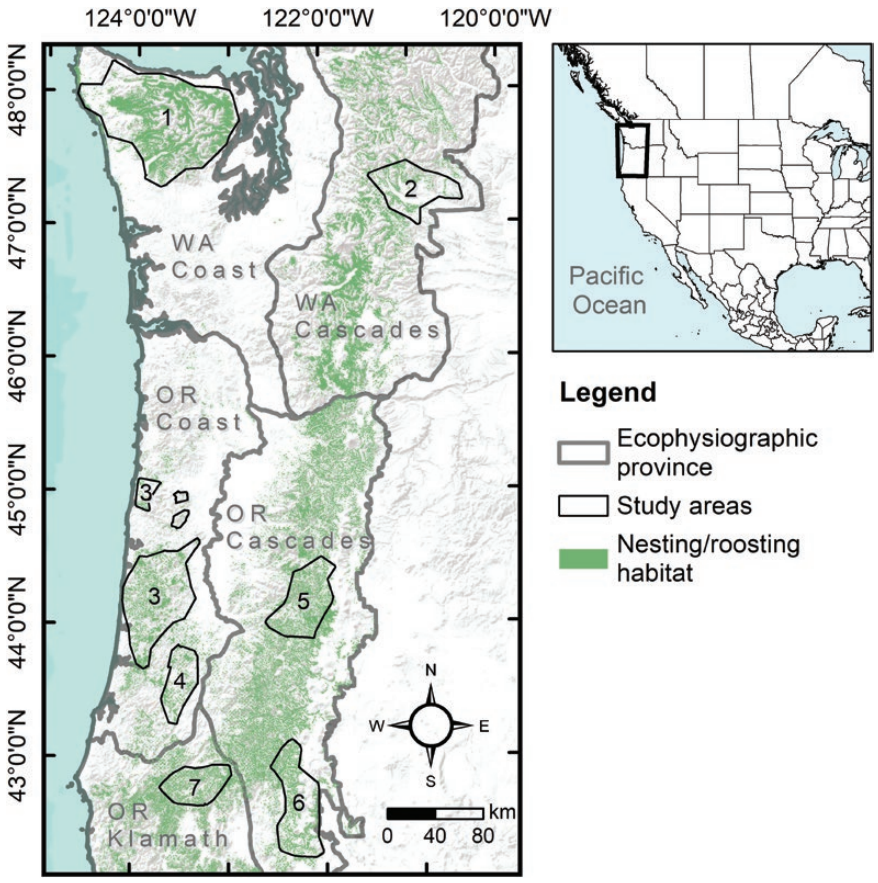


FIGURE 1. Locations of the 7 study areas (Olympic Peninsula [1], Cle Elum [2], Oregon Coast Range [3], Tyee [4], H.J. Andrews [5], South Cascades [6], and Klamath [7]) in 5 ecophysiographic provinces of Oregon and Washington used to examine trends in breeding dispersal distance in Northern Spotted Owls, 1990–2017. Also shown is the landscape distribution of suitable nesting and roosting habitat for Northern Spotted Owls as of 2012, based on a habitat suitability map developed by Glenn et al. (2017).

experience ($n \geq 3$ yr). The categorization between "low" and "high" territory experience was arbitrarily made based on category sample sizes. Because S1 and S2 birds could only have 0–1 yr of experience at a prior territory, all "experience" variables were somewhat confounded with age, thus we tested age and experience separately in models. We also generated and considered 3 potential measures of owl reproductive status prior to and after movement based on capture histories of color-marked individuals. These measures were also interrelated and considered separately in models. We recorded pair status as single, paired, or unknown, and mate status as single, paired with a new or unknown mate, paired with a mate from a previous year, or unknown. Productivity was categorized as no young fledged, successfully fledged ≥1 young, or unknown. We tested for differences in proportions of male vs. female dispersers, and in rates of productivity and pair status before and after dispersal with simple chi-square tests and report *P* values.

To address our hypothesis that dispersal distance would be shorter when individuals occupied historically productive territories, we generated an index of territory quality (TQ) based on the number of young produced from territory i within ecophysiographic province p during the study period (Blakesley et al. 2006):

$$\mathrm{TQ}_i = \frac{\sum_j (NYF_{ipj} - \overline{NYF_{pj}})}{n_i}$$

where *NYF* is the number of young fledged, j is the year with reproductive data available for each p, and n is the number of years for which reproductive data were available for a territory i. We only calculated TQ for territories for which we had at least 5 yr of productivity information available and acknowledge that this variable does not account for temporal variation in habitat quality.

Forest Disturbance

Old forest is a primary component of Spotted Owl habitat, which is susceptible to loss from timber harvest, wildfires, windstorms, insect infestations, and disease (Davis et al. 2016, Lesmeister et al. 2018). The impact of these

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

disturbance events on Spotted Owls can vary with the extent and severity of the disturbance (Comfort et al. 2016, Lesmeister et al. 2018, 2019). Following Reilly et al. (2017) we partitioned disturbances into 3 severity classifications based on estimated percent basal area removal: low (<25% removal), moderate (25–75% removal), and high (>75% removal). We predicted that low-severity disturbance (e.g., primarily timber stand thinning and insect-related loss) would have less effect on dispersal distance compared to moderate- or high-severity disturbance (e.g., clear-cut harvest, stand-replacing wildfire). Low-severity wildfires have little effect on nesting habitats of Spotted Owls, which may be more resistant to high-severity wildfire compared to younger or less–structurally complex forests (Lesmeister et al. 2019). While we acknowledge that wildfire and timber harvest are not equivalent disturbances, we combined them for our disturbance metrics because of the scarcity of fire in our dataset (Appendix Figure 6). We used Google Earth Engine (Gorelick et al. 2017) and annual Landsat disturbance data in *LandTrendr* (Kennedy et al. 2010, Cohen et al. 2017) to estimate 3 annual measures of forest disturbance for each territory (i.e. Thiessen polygon) within the prior 3 yr: (1) proportion of territory with "any severity" disturbance, (2) proportion of territory with "low severity" disturbance, and (3) proportion of territory with "moderate-to-high severity" disturbance (e.g., 1990 habitat alteration proportion was generated using the sum of disturbance in 1988, 1989, and 1990).

Occurrence of Barred Owls

Although Barred Owls were not specifically surveyed, we documented over 22,500 incidental detections of Barred Owls during surveys of Spotted Owls, and detections of Barred Owls were an effective proxy for increases in the presence of Barred Owls in each study area (Dugger et al. 2016, Yackulic et al. 2019). For each year and study area, we calculated the annual percentage of historical Spotted Owl territories (Thiessen polygons) with ≥1 detection of Barred Owls at any year previous to, and including, the current monitoring year (BO; Figure 2). A subset of territories in the OLY study area were dropped from the demography study in 2006. Thus, for consistency, the Barred Owl covariate was generated across only the OLY territories monitored throughout the study.

Dispersal Distance Modeling

We used generalized linear mixed models within an information-theoretic framework to evaluate relationships between breeding dispersal distance and individual and environmental sources of variation (Table 1; Burnham and Anderson 2002, Bolker et al. 2009). We did not include movements from non-dispersers in analyses. Prior to generating models with additive covariate effects, we ranked and selected the best performing a priori univariate model structure (linear, quadratic, pseudo-threshold vs. categorical) for related groups of covariates, using Akaike's information criterion (AIC; Table 1). Our final additive model set was generated as combinations of covariates from univariate models with $\Delta AIC \leq 2$ in each covariate group. Only univariate models that scored above the null model were considered in additive models. Covariates with a Spearman's rank correlation coefficient >0.6 were not included in the same model. We observed no linear trend in disturbance variables over time within our sampled territories (Spearman's rank correlation coefficients with year <|0.01|) but the Barred Owl covariate was considered a temporal covariate (Spearman's rank correlation with year = 0.86) because the proportions of territories with detections increased over time in all study areas (Figure 2).

We fit all models using the *lme4* package in program R using a gamma distribution with a log link (Bates et al. 2015, R Core Team 2018). We included random effects of ecophysiographic province and year on the intercept in all models, including the "intercept-only" model with no fixed effects. The random effect of ecophysiographic province was included to account for regional variation in landscape and sample sizes. Year was included as a random effect to account for temporal process variance not associated with Barred Owl occurrence. Our dataset contained multiple dispersals from some individuals; however, models failed to converge when we included a random effect of individual. When we used only the data for individuals with more than one movement, the interclass correlation coefficient for distance was 0.27 (95% CI: 0.22–0.34), indicating low measurement repeatability (Wolak et al. 2012), so we retained all movements in our analyses. We considered effects in top-ranked models to be strongly supported if the 95% confidence interval (CI) for the parameter coefficient did not include zero. We report means ± standard error unless otherwise noted. Model assumptions were verified by plotting residuals vs. fitted values. To assess model fit, we report Nakagawa's R^2 for mixed effect models for the top model (Johnson 2014, Nakagawa et al. 2017).

RESULTS

We documented 2,158 breeding dispersal events during 1990–2017 from 1,302 owls (694 male, 608 female) with median breeding dispersal distance of 3.17 km. Ninety-nine percent of all documented breeding dispersal movements were ≤37 km (range: 0.04–94.55 km; Figure 3A). Sample sizes were uneven between provinces and birds in Oregon accounted for 90% of all dispersal events (Appendix Table 4). Washington birds moved farther on average than Oregon birds; mean annual dispersal distances in Washington increased by 9.40 km between

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

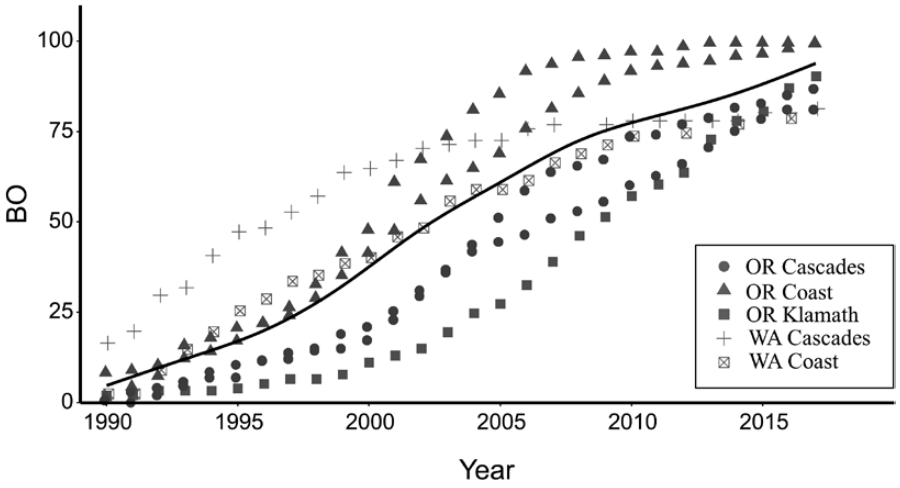


FIGURE 2. Annual trend in the percentage of cumulative Northern Spotted Owl territories with ≥1 Barred Owl (BO) detection for different ecophysiographic provinces in Oregon and Washington, USA. Spearman's rank correlation of 0.86 between year and BO (all areas combined). The solid line indicates the smoothed annual mean across provinces.

TABLE 1. Descriptions of variables and model structures considered in analyses of breeding dispersal distance for Northern Spotted Owls in Oregon and Washington, USA, 1990–2017.

Group	Variable	Structures tested against null model [a]	Used in additive model set
Sex	SEX, female or male	Categorical	SEX
Experience	EAS, experience at territory in observation prior to dispersal (years)	Linear Quadratic Pseudo-threshold [b] Categorical 2 groups Categorical 3 groups	EAS (3 groups)
	AGE, age class in observation prior to dispersal (S1, S2, Adult)	Categorical 2 groups Categorical 3 groups	
Reproductive status	PS, pair status in observation prior to dispersal (single, paired, unknown)	Categorical 3 groups	MS
	MS, mate status in observation prior to dispersal (single, paired with new mate, paired with old mate, unknown)	Categorical 4 groups	
	P, productivity in observation prior to dispersal	Categorical 3 groups	
Barred Owl	BO, annual proportion of study area territories with Barred Owl detections	Linear Pseudo-threshold	BO
Territory quality	TQ, index of territory quality of prior location (−1 to 1)	Linear	*Not used*
Habitat	D, proportion of prior territory with any severity forest disturbance in prior 3 years	Linear Quadratic Pseudo-threshold	Ln(D)
	D_MH, proportion of prior territory with moderate-to-high severity forest disturbance in prior 3 years	Linear Quadratic Pseudo-threshold	
	D_L, proportion of prior territory with low severity forest disturbance in prior 3 years	Linear Quadratic Pseudo-threshold	

[a] See Appendix Table 5 for model-selection results of initial tests of variable structures and related groups of variables.
[b] Psuedo-threshold structure was approximated using ln(x).

1990 and 2017 (Figure 3B); while in Oregon, mean annual dispersal distances increased by 2.43 km between 1990 and 2017 (Figure 3C). Sixty-one percent of owls in our dataset (n = 793) moved once. However, the proportion of repeat dispersers each year (>1 previous dispersals on record) increased over time (Figure 4), with 23% of birds (n = 300) moving 2 times, 10% (n = 131) moving 3 times, 3% (n = 40) moving 4 times, and 3% moving 5–8 times (23 moved 5 times, 10 moved 6 times, 3 moved 7 times, 2 moved 8 times).

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

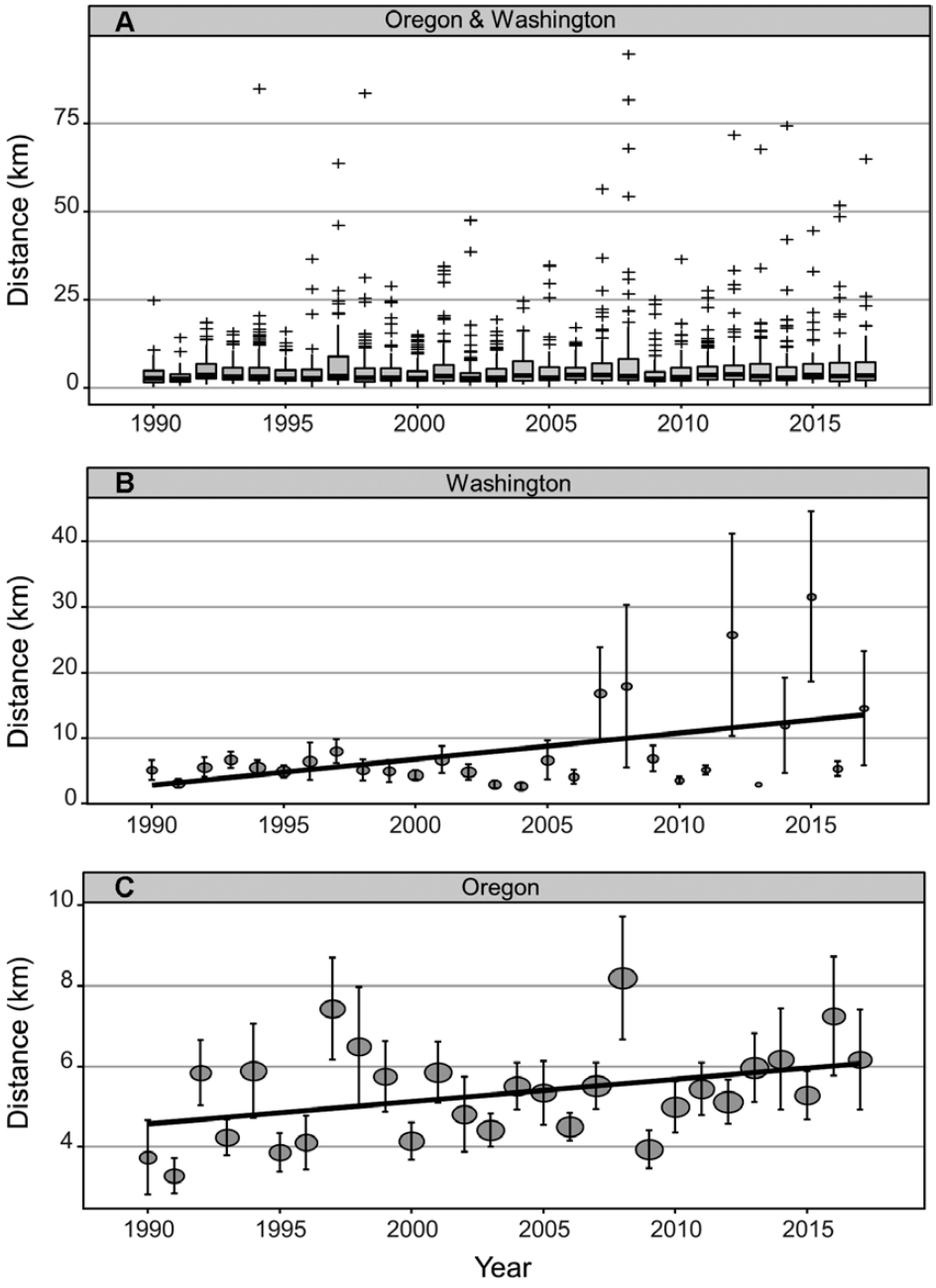


FIGURE 3. Boxplot and mean annual trend in observed breeding dispersal events in Northern Spotted Owls in Oregon and Washington from 1990 to 2017. The majority of breeding dispersal observations were <10 km from prior territories, but outliers extended as far as 95 km (**A**). Mean (± SE) breeding dispersal distances fluctuated over time with an overall positive trend, which was greater in Washington (**B**) (n = 210) compared to Oregon (**C**) (n = 1,948). The point size in panels (**B**) and (**C**) vary with annual sample size.

Ninety-two percent of all breeding dispersals were made by birds ≥3 yr old (n = 1,993; Appendix Table 4). More breeding dispersal events were observed from male Spotted Owls (54% of observed breeding dispersal events; χ^2 = 16.91, P < 0.001; Appendix Table 4). The average owl experience at the territory prior to moving was 2.06 ± 0.06 yr (range: 0–17; Appendix Figure 7). Based on the total number of territorial birds that dispersed, the percentage of birds paired and successfully producing young increased post-dispersal (χ^2 = 27.77, P < 0.001). In the year before dispersing, 18% of individuals produced young. After dispersal, 24% of dispersers produced young. The percentage of birds paired also increased post-dispersal (χ^2 = 18.45, P < 0.001). Prior to dispersal, 77% of dispersers were paired (18% single, 36% paired with prior mate, 41% paired with new/unknown mate, 5% pair status unknown).

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

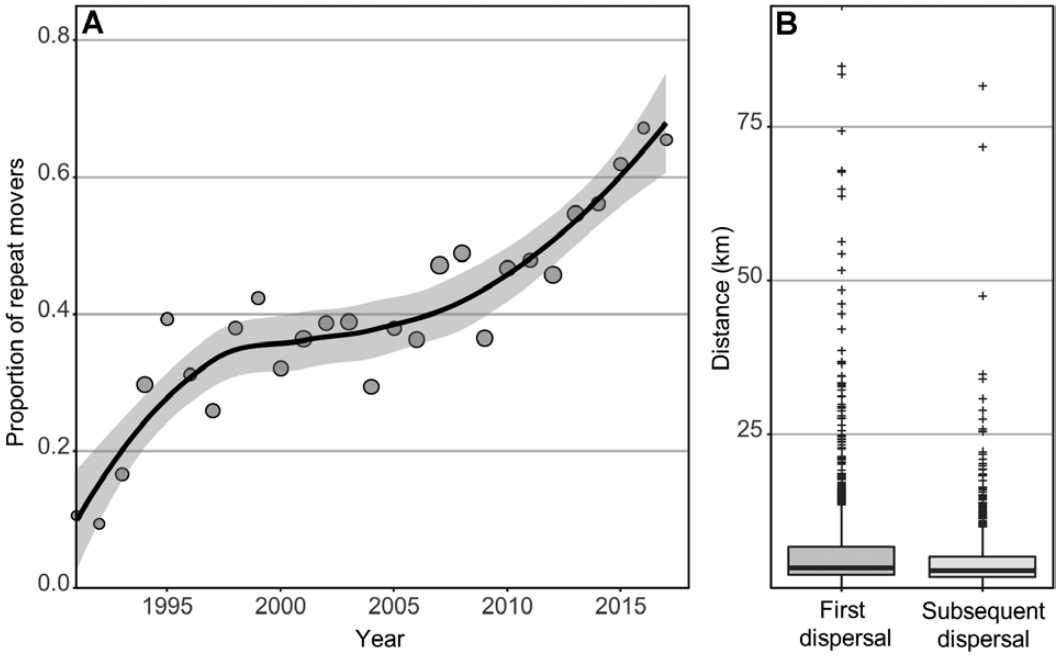


FIGURE 4. The annual proportion of individual Northern Spotted Owls dispersing more than once increased over time in our sample of 1,258 breeding dispersal events (**A**). Subsequent dispersal distances were indistinguishable from initial dispersal events (**B**). In panel (**A**), point size reflects annual sample size with the smoothed mean and standard error shown.

After dispersal, 83% of dispersers were paired (13% single, 20% paired with prior mate, 62% paired with new/unknown mate, 4% unknown paired status). Of the owls that were paired prior to dispersing, the mean experience with that mate was 1.37 ± 0.08 yr (range: 0–15 yr; Appendix Figure 7). Overall, forest disturbance was low across territories within our dispersal dataset; 75% of breeding dispersal movements originated from territories with <2% of their area disturbed at any severity in the prior 3 yr and 99% of movements originated from territories with <23% of their area disturbed at any severity in the prior 3 yr (Appendix Figure 6). Eleven movements originated from territories with >30% of the area disturbed within the prior 3 yr (max = 96.4%).

The best-supported model of breeding dispersal distance included the additive effects of sex, experience at a site prior to dispersal, the pseudo-threshold effect of disturbance at a site, Barred Owl occurrence, and mate status (SEX + EAS + ln[D] + BO + MS) with random effects of ecophysiographic province and year on the intercept (Table 2; Appendix Figure 8). Ecophysiographic province accounted for 1.2% of the overall variance and year accounted for 3.3% of the overall variance. The 95% CIs of coefficients of all covariates in the top model did not overlap zero, except for mate status "unknown" (Table 3), which was not different from mate status "single." Holding other covariates constant at their median or mode, male breeding dispersals were 20% shorter than females (exp[β] = 0.80, 95% CI: 0.75–0.86; Table 3, Figure 5). Similarly, breeding dispersals were 31% shorter when experience at territory prior to dispersal was high (exp[β] = 0.69, 95% CI: 0.62–0.76; Figure 5) compared to no prior experience at a territory, and 14% shorter when experience at territory prior to dispersal was low (exp[β] = 0.86, 95% CI: 0.77–0.95; Figure 5) compared to no prior experience at a territory. Dispersal distance was positively associated with Barred Owl occurrence (exp[β] = 1.50, 95% CI: 1.20–1.86; Figure 5) and with proportion of disturbance on the originating territory (exp[β] = 1.04, 95% CI: 1.02–1.06; Figure 5). Models with additive effects of disturbance and Barred Owl occurrence outperformed models that considered these effects independently (Table 2). We tested for an interaction between forest disturbance and our Barred Owl covariate within the top model; however, the interaction term was not supported based on AIC ranking.

DISCUSSION

We found that sex, territory tenure, pair status prior to moving, Barred Owl occurrence, and the degree of territory disturbance were all predictors of breeding dispersal distance in Spotted Owls. Our data fit the general pattern observed in birds of females dispersing farther than males, often attributed to intrasexual competition and inbreeding avoidance (Greenwood and Harvey 1982, Pusey 1987, Forsman et al. 2002). We also found that younger birds or those with less experience with mates or territories dispersed farther than older or more

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

TABLE 2. Model-selection results used to characterize sources of variation in breeding dispersal distances of Northern Spotted Owls in Oregon and Washington, USA, 1990–2017. Model covariates include sex, experience at prior territory (EAS), mate status prior to move (MS), Barred Owl (BO), and territory disturbance prior to move (D). All models also included random effects of ecophysiographic province and time on the intercept. *k* is number of parameters. w_i is Akaike's weight. Dev is the residual deviance.

Model	ΔAIC [a]	*k*	w_i	Dev
EAS + SEX + ln(D) + BO + MS [b]	0	12	0.9936	1698.6
EAS + SEX + ln(D) + BO	10.1	9	0.0063	1708.6
EAS + SEX + ln(D)	19.2	8	<0.001	1706.5
EAS + SEX + MS	25.9	10	<0.001	1711.3
EAS + SEX + BO	29.8	8	<0.001	1724.3
EAS + SEX	37.3	7	<0.001	1721.9
EAS + ln(D)	42	7	<0.001	1725.2
EAS + BO	49.5	7	<0.001	1740.9
EAS + MS	55.4	9	<0.001	1734.2
EAS	57.3	6	<0.001	1738.6
MS	99.5	7	<0.001	1770.2
Ln(D)	124.8	5	<0.001	1791.3
SEX	125.5	5	<0.001	1791.8
BO	137.8	5	<0.001	1807.9
Intercept only	141.8	4	<0.001	1806.1
EAS + SEX + ln(D) + MS [c]	.	11	.	.

[a] Akaike's information criterion (AIC) of top model was 41266.2.
[b] Nakagawa's marginal R^2 value was 0.48; see Appendix Figure 8 for residual plot.
[c] Model did not converge.

TABLE 3. Estimated coefficients (β), standard error (SE), and confidence intervals (CI) from the top candidate model of breeding dispersal distance for Northern Spotted Owls in Oregon and Washington, USA, 1990–2017.

			95% CI	
Variable	β[a]	SE	lower	upper
Intercept[b]	8.984	0.109	8.770	9.197
MALE	−0.220	0.038	−0.294	−0.146
EAS, 1–2 years	−0.147	0.054	−0.252	−0.042
EAS, ≥ 3 years	−0.373	0.053	−0.477	−0.269
MS, paired new mate	−0.131	0.055	−0.238	−0.024
MS, paired previous mate	−0.213	0.059	−0.329	−0.097
MS, unknown	0.019	0.093	−0.164	0.202
ln(D)	0.043	0.009	0.025	0.062
BO	0.402	0.111	0.184	0.621

[a] All coefficient statistics are presented untransformed on log-link scale.
[b] Intercept: adult female, single prior to dispersing, first year at prior territory.
Abbreviations: EAS = experience at prior territory; MS = mate status in prior year; D = proportion of prior territory disturbed (any severity) within 3 years; BO = cumulative proportion of study area with Barred Owl detection.

experienced individuals, which may reflect a competitive advantage of strong site and mate fidelity (Andreu and Barba 2006, Calabuig et al. 2008, Forero et al. 2008). In contrast to our findings, Blakesley et al. (2006) did not find differences in dispersal distance between sexes or age classes in California Spotted Owls. However, they utilized a much smaller sample size (n = 54). Generally, in territorial animals, adults (or territory holders) are able to displace younger individuals (or nonresidents) from established areas (Murray 1967). Spotted Owls do not vacate territories annually (nonmigratory). Thus, the ability of a nonresident to displace a resident individual is likely further reduced. Furthermore, since dispersal comes with inherent risk, we expected dispersing individuals to settle on the first uncontested suitable site they found (Murray 1967). Collectively, dispersal distances were negatively skewed toward short-distance dispersal events and the median dispersal distance (3.17 km) was similar to what was observed in our region previously (3.5 km; Forsman et al. 2002), which is shorter than observations of California Spotted Owls (7 km; Blakesley et al. 2006).

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

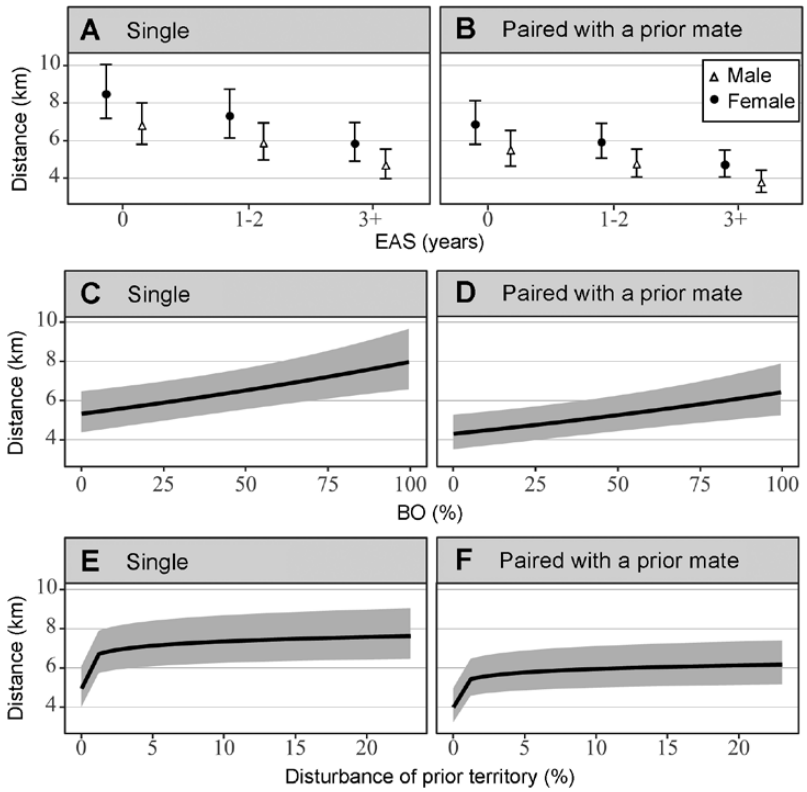


FIGURE 5. Predicted dispersal distance of Northern Spotted Owls with 95% confidence intervals for sex, prior territory experience (EAS) (**A** and **B**), Barred Owl coverage within study areas (BO) (**C** and **D**), and disturbance (**E** and **F**). Predictions were generated for Spotted Owls that were single or paired with a previous mate before dispersing, while holding other covariates at the covariate median or mode.

Animals occupying habitats with stable conditions typically show site fidelity or restricted movements between alternate breeding sites (Greenwood and Harvey 1982). Historically, this was true of Spotted Owls (Forsman et al. 2002). We found some support for increased breeding dispersal distances over time as well as an increase in the number of dispersal events by individual Spotted Owls, which could indicate a potential reduction in stability of habitat conditions for Spotted Owls in the last 20 yr. Early increases in frequency of repeat movers (1990–1995) were likely representative of study initiation effects (i.e. our ability to detect a second dispersal improved as the length of the study increased), rather than true biological increase. However, this was also a period of consistent old-forest harvest on federal lands, which may have contributed to greater dispersal movements during this time. We did not detect time trends in forest disturbance within our sampled territories, but since 1990 there was a positive trend in the proportion of Spotted Owl territories with Barred Owl detections and a correspondingly negative trend in survival and recruitment of Spotted Owl populations in our study areas (Dugger et al. 2016). Our data and analyses suggested that additive effects of habitat disturbance and competition with Barred Owls increased distances moved by Spotted Owls. We also observed higher rates of long-distance dispersal and an increased frequency of repeat dispersal events in the later years of our study, which coincided with increasing occurrence of Barred Owls.

Interspecific interactions have important implications for spatial ecology of sympatric predator communities. Interspecies competition with brown bears (*Ursus arctos*), for example, affects movement patterns of American black bears (*U. americanus*) but only when high-quality resources are spatially restricted (Belant et al. 2010). Similarly, interference competition among gray wolves (*Canus lupus*) can influence the distribution of coyotes (Berger and Gese 2007). Because of antagonistic interactions and high overlap in resource selection, Barred Owls may increase Spotted Owl breeding dispersal distance directly through conspecific territorial displacement and resource competition (Jenkins et al. 2019b, Wiens et al. 2014). Hybridization (direct competition for mates) occurs but is uncommon in our study areas (Kelly and Forsman 2004). Competition with Barred Owls has been linked to reductions in territory occupancy (Kelly et al. 2003, Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011, 2016; Yackulic et al. 2012,

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

Sovern et al. 2014, Forsman et al. 2015) and apparent survival (Anthony et al. 2003, Forsman et al. 2011, Glenn et al. 2011, Diller et al. 2016, Dugger et al. 2016), both of which represent a combination of increased emigration (dispersal outside of a study area) and/or increased mortality of territory-holding adults. Barred Owls have also been associated with reduced reproduction by Spotted Owls (Olson et al. 2005, Wiens et al. 2014, Dugger et al. 2016). In contrast, Barred Owl presence was not supported as affecting natal dispersal distance in the same study populations of Spotted Owls during 1985–2013 (Hollenbeck et al. 2018). However, Hollenbeck et al. (2018) modeled annual Barred Owl presence at the individual-territory scale, which includes temporal and spatial variability associated with the lack of focused Barred Owl surveys (i.e. Barred Owl detection rates <1.0). In contrast, for this study we developed an annual index of cumulative Barred Owl presence across each study area. This cumulative index is likely a better representation of overall increases in density of Barred Owls at the study area scale, but precludes direct comparisons between these 2 studies. Elsewhere, experimentally augmented nest predation risk increased the likelihood and distance of breeding dispersal in Boreal Owls (*Aegolius funereus*; Hakkarainen et al. 2001). We do not consider Barred Owls a primary nest predator of Spotted Owls, but interspecific territoriality may disrupt Spotted Owl pair bonding and limit the availability of breeding territories for Spotted Owls, thereby leading to reductions in breeding propensity (Mangan et al. 2019), mate retention, and nesting success, and subsequent increases in breeding dispersal distances. Barred Owls may also reduce prey availability for Spotted Owls, either indirectly through changes to predator avoidance strategies used by prey (e.g., Schmidt 2006), or directly by excluding Spotted Owls from productive foraging habitats or via reductions in prey populations (Hamer et al. 2001, Wiens et al. 2014).

The decline in populations of Spotted Owls throughout the region (Dugger et al. 2016) is also likely a factor contributing to increased breeding dispersal patterns in recent years. In a review of 75 bird species, Paradis et al. (1998) found that breeding dispersal distances were longer for less abundant species than among abundant species, and dispersal distances of male Merlin (*Falco columbarius*) decreased with increased population density (Wiklund 1996). Spotted owl populations have declined on all of our study areas, and Washington study areas experienced declines earlier in the study period and more precipitously than study areas in Oregon provinces (Dugger et al. 2016), which may help explain the greater increase in mean dispersal distances in those areas. Spotted Owls occur at low densities because of their large home ranges and small populations. Spotted Owl territory size also increases with latitude (Dugger et al. 2016), which likely contributes to the reduced density and correspondingly higher mean breeding dispersal distances observed in Washington birds. Concomitant with declines in population density, it stands to reason that mate availability also declined across our study, thus increasing the distances that single birds must travel to find an available mate. As in previous studies of Spotted Owls (Forsman et al. 2002, Gutiérrez et al. 2011), the greatest proportion of dispersal movements were made by birds that failed to successfully produce young in the year prior (Appendix Table 4). However, our model with mate status was more supported than the model of productivity for predictions of dispersal distance (Appendix Table 5). Our model predicted that single Spotted Owls moved farther than formerly paired individuals, which indicates that mate availability is a primary social driver of breeding dispersal distance. Spotted Owls are a K-selected species that do not often breed every year (Stoelting et al. 2015). Thus one unsuccessful year with a mate may have less importance to a long-lived animal than the loss or lack of a mate.

We found that dispersal distance increased with increasing proportions of forest disturbance within the original territory prior to dispersal. We predicted that moderate- to high-severity disturbances would have a greater effect on distance than low-severity disturbances. However, our tests of disturbance variables, ranked "any" disturbance severity higher than "low" or "moderate-to-high" severity in predicting dispersal distances. This lack of distinction could have been because the extent of disturbances within occupied territories was small as the majority (90%) of dispersing birds had ≤7% of their territory disturbed in the 3 yr prior to movement (Appendix Figures 6 and 7). Our study areas were mostly within the late-successional reserve network under the Northwest Forest Plan (Lint et al. 1999), which has been largely successful in protecting late-successional forest on federal lands (Davis et al. 2016). When considering broadly all federal lands, most losses of Spotted Owl nesting habitat have been due to wildfire (Davis et al. 2016), but we observed relatively little loss of forest due to wildfire within our 28-yr sample of breeding dispersals. Further targeted study of breeding owl movements and survival following fire in our region are needed. Timber harvest or wildfire is unlikely to be contained within a single territory, thus it makes sense that birds that lost a proportion of their territory may need to travel farther to find an unoccupied or unaffected territory. Additionally, given dispersal distances are increasing due to Barred Owls, dispersing Spotted Owls may increasingly encounter non-habitat on lands managed outside the standards and guidelines of the Northwest Forest Plan. These areas include non-forest and intensively managed industrial forests that commonly surround late-successional reserves.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

There are multiple factors influencing Spotted Owl breeding dispersal, and while it appears that social factors such as mate availability continue to be the important drivers in movement decisions, increased competition from Barred Owls and forest disturbance also have an effect. Increases in dispersal distance, when paired with increased rates of adult dispersal observed in recent years (D. B. Lesmeister and K. M. Dugger personal observations), may have important implications for studies estimating apparent survival from long-term Spotted Owl demographic data. Given Spotted Owls are moving farther and more frequently, permanent emigration from study areas is likely also increasing over time. Apparent survival models cannot differentiate between emigration and mortality, so dispersal movements that result in permanent emigration from study area boundaries can lead to underestimates of apparent survival (Zimmerman et al. 2007). Conversely, if increased dispersal distances are leading to increased movement through young industrial forests or other nonsuitable roosting cover, higher rates of mortality are also possible. Given the changing dispersal patterns we have observed, it is increasingly important to consider the impact of these behavioral changes on conservation efforts as well as long-term monitoring programs designed to detect trends in Spotted Owl populations.

ACKNOWLEDGMENTS

This study would not have been possible without the help of a small army of dedicated field biologists who collected the data on the Spotted Owl demographic study areas in Washington and Oregon. We would also like to thank R. Davis, U.S. Forest Service Spotted Owl monitoring lead, for assistance with forest disturbance parameters. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The full data used for this analysis are available from Dryad.

Conflict of Interest Statement: The authors declare no conflicts of interest.

Funding statement: Funding for this project was provided by the U.S. Department of Agriculture Forest Service Pacific Northwest Research Station, and the U.S. Department of Interior Bureau of Land Management.

Ethics statement: All handling and marking of Spotted Owls was authorized and in compliance with regulations of the U.S. Fish and Wildlife Service, Oregon Department of Fish and Wildlife, Washington Department of Fish and Wildlife, and the Federal Bird Banding Lab. All protocols were approved by the Oregon State University Institutional Animal Care and Use Committee.

Author contributions: D.B.L., E.D.F., K.M.D., and J.D.W. conceived the research, design, sourced funding, and substantially edited the manuscript. J.M.J. developed and preformed analysis and wrote the manuscript. J.M.J., D.B.L., E.D.F., K.M.D., S.H.A., L.S.A., C.E.M., M.S.P., J.A.R., S.G.S., R.B.H., and S.A.G. conducted the research. Z.Y. developed environmental metrics and reviewed the manuscript.

Data depository: Analyses reported in this article can be reproduced using the data provided by Jenkins et al. (2019a).

LITERATURE CITED

Andreu, J., and E. Barba (2006). Breeding dispersal of Great Tits *Parus major* in a homogeneous habitat: Effects of sex, age, and mating status. Ardea 94:45–58.

Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, et al. (2003). Status and trends in demography of Northern Spotted Owls, 1985–2003. Wildlife Monographs 163:1–48.

Bates, D., M. Maechler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Belant, J. L., B. Griffith, Y. Zhang, E. H. Follmann, and L. G. Adams (2010). Population-level resource selection by sympatric brown and American black bears in Alaska. Polar Biology 33:31–40.

Berger, K. M., and E. M. Gese (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? The Journal of Animal Ecology 76:1075–1085.

Blakesley, J. A., D. R. Anderson, and B. R. Noon (2006). Breeding dispersal in the California Spotted Owl. The Condor 108:71–81.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. Stevens, and J. S. White (2009). Generalized linear mixed models: A practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Bowler, D. E., and T. G. Benton (2005). Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. Biological Reviews of the Cambridge Philosophical Society 80:205–225.

Bowman, J. (2003). Is dispersal distance of birds proportional to territory size? Canadian Journal of Zoology 81:195–202.

Bried, J., and P. Jouventin (2007). Influence of breeding success on fidelity in long-lived birds: An experimental study. Journal of Avian Biology 30:392–398.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer-Verlag, New York, NY, USA.

Calabuig, G., J. Ortego, P. J. Cordero, and J. M. Aparicio (2008). Causes, consequences and mechanisms of breeding dispersal in the colonial Lesser Kestrel, *Falco naumanni*. Animal Behaviour 76:1989–1996.

Clarke, A. L., B.-E. Sæther, and E. Røskaft (1997). Sex biases in avian dispersal: A reappraisal. Oikos 79:429–438.

Cohen, W. B., Z. Yang, S. P. Healey, R. E. Kennedy, and N. Gorelick (2017). A LandTrendr multispectral ensemble for forest disturbance detection. Remote Sensing of Environment 205:131–140.

Comfort, E. J., D. A. Clark, R. G. Anthony, J. Bailey, and M. G. Betts (2016). Quantifying edges as gradients at multiple scales improves habitat selection models for Northern Spotted Owl. Landscape Ecology 31:1227–1240.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

Daniels, S. J., and J. R. Walters (2000). Between-year breeding dispersal in Red-cockaded Woodpeckers: Multiple causes and estimated cost. Ecology 81:2473–2484.

Davis, R. J., B. Hollen, J. Hobson, J. E. Gower, and D. Keenum (2016). Status and trends of Northern Spotted Owl habitats. USDA Forest Service General Technical Report PNW-GTR-929. Pacific Northwest Research Station, Portland, OR, USA.

Diller, L. V., K. A. Hamm, D. A. Early, D. W. Lamphear, K. M. Dugger, C. B. Yackulic, C. J. Schwarz, P. C. Carlson, and T. L. McDonald (2016). Demographic response of Northern Spotted Owls to Barred Owl removal. Journal of Wildlife Management 80:691–707.

Dugger, K. M., R. G. Anthony, and L. S. Andrews (2011). Transient dynamics of invasive competition: Barred Owls, Spotted Owls, habitat, and the demons of competition present. Ecological Applications 21:2459–2468.

Dugger, K. M., E. D. Forsman, A. B. Franklin, R. J. Davis, G. C. White, C. J. Schwarz, K. P. Burnham, J. D. Nichols, J. E. Hines, C. B. Yackulic, et al. (2016). The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls. The Condor: Ornithological Applications 118:57–116.

Forero, M. G., J. A. Donazar, J. Blas, and F. Hiraldo (2008). Causes and consequences of territory change and breeding dispersal distance in the Black Kite. Ecology 80:1298–1310.

Forsman, E. D., R. G. Anthony, K. M. Dugger, E. M. Glenn, A. B. Franklin, G. C. White, C. J. Schwarz, K. P. Burnham, D. R. Anderson, J. D. Nichols, et al. (2011). Population demography of Northern Spotted Owls. Studies in Avian Biology, no. 40.

Forsman, E. D., R. G. Anthony, J. A. Reid, P. J. Loschl, S. G. Sovern, M. Taylor, B. L. Biswell, E. A. Ellingson, C. Meslow, G. S. Miller, et al. (2002). Natal and breeding dispersal of Northern Spotted Owls. Wildlife Monographs 149:1–35.

Forsman, E. D., E. C. Meslow, and H. M. Wight (1984). Distribution and biology of the Spotted Owl in Oregon. Wildlife Monographs 122:1–64.

Forsman, E. D., S. G. Sovern, M. Taylor, and B. L. Biswell (2015). Home range and habitat selection by Northern Spotted Owls on the eastern slope of the Cascade Mountains, Washington. Journal of Raptor Research 49:109–128.

Ganey, J. L., D. L. Apprill, T. A. Rawlinson, S. C. Kyle, R. S. Jonnes, and J. P. Ward (2014). Breeding dispersal of Mexican Spotted Owls in the Sacramento Mountains, New Mexico. The Wilson Journal of Ornithology 126:516–524.

Glenn, E. M., R. G. Anthony, E. D. Forsman, and G. S. Olson (2011). Local weather, regional climate, and annual survival of the Northern Spotted Owl. The Condor 113:150–158.

Glenn, E. M., D. B. Lesmeister, R. J. Davis, B. Hollen, and A. Poopatanapong (2017). Estimating density of a territorial species in a dynamic landscape. Landscape Ecology 32:563–579.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment 202:18–27.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Greenwood, P. J., and P. H. Harvey (1982). The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1–21.

Gutiérrez, R. J., W. S. LaHaye, and G. S. Zimmerman (2011). Breeding dispersal in an isolated population of Spotted Owls *Strix occidentalis*: Evidence for improved reproductive output. Ibis 153:592–600.

Hakkarainen, H., P. Ilmonen, V. Koivunen, and E. Korpimäki (2001). Experimental increase of predation risk induces breeding dispersal of Tengmalm's Owl. Oecologia 126:355–359.

Hamer, T. E., D. W. Hays, C. M. Senger, and E. D. Forsman (2001). Diets of Northern Barred Owls and Northern Spotted Owls in an area of sympatry. Journal of Raptor Research 35:221–227.

Hollenbeck, J. P., S. M. Haig, E. D. Forsman, and J. D. Wiens (2018). Geographic variation in natal dispersal of Northern Spotted Owls over 28 years. The Condor: Ornithological Applications 120:530–542.

Jenkins, J. M. A., D. B. Lesmeister, E. D. Forsman, K. M. Dugger, S. H. Ackers, L. S. Andrews, C. E. McCafferty, M. S. Pruett, J. A. Reid, S. G. Sovern, et al. (2019a). Data from: Social status, forest disturbance, and Barred Owls shape long-term trends in breeding dispersal distance of Northern Spotted Owls. The Condor: Ornithological Applications 121:1–17. doi:10.5061/dryad.931zcrjfr.

Jenkins, J. M. A., D. B. Lesmeister, J. D. Wiens, J. T. Kane, V. R. Kane, and J. Verschuyl (2019b). Three-dimensional partitioning of resources by congeneric forest predators with recent sympatry. Scientific Reports 9:6036.

Jiménez-Franco, M. V., J. E. Martínez, I. Pagán, and J. F. Calvo (2013). Factors determining territory fidelity in a migratory forest raptor, the Booted Eagle *Hieraaetus pennatus*. Journal of Ornithology 154:311–318.

Johnson, P. C. (2014). Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. Methods in Ecology and Evolution 5:944–946.

Kelly, E. G., and E. D. Forsman (2004). Recent records of hybridization between Barred Owls (*Strix varia*) and Northern Spotted Owls (*S. occidentalis caurina*). The Auk 121:806–810.

Kelly, E. G., E. D. Forsman, and R. G. Anthony (2003). Are Barred Owls displacing Spotted Owls? The Condor 105:45–53.

Kennedy, R. E., Z. Yang, and W. B. Cohen (2010). Detecting trends in forest disturbance and recovery using yearly Landsat time series: 1. LandTrendr – Temporal segmentation algorithms. Remote Sensing of Environment 114:2897–2910.

Kim, S. Y., R. Torres, and H. Drummond (2009). Simultaneous positive and negative density-dependent dispersal in a colonial bird species. Ecology 90:230–239.

Kim, S. Y., R. Torres, C. Rodríguez, and H. Drummond (2007). Effects of breeding success, mate fidelity and senescence on breeding dispersal of male and female Blue-footed Boobies. The Journal of Animal Ecology 76:471–479.

Koenig, W. D., D. Van Vuren, and P. N. Hooge (1996). Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology & Evolution 11:514–517.

Kroll, A. J., T. L. Fleming, and L. L. Irwin (2010). Site occupancy dynamics of Northern Spotted Owls in the Eastern Cascades, Washington, USA, 1990–2003. Journal of Wildlife Management 74:1264–1274.

Lesmeister, D. B., R. J. Davis, P. H. Singleton, and J. D. Wiens (2018). Northern Spotted Owl habitat and populations: Status and threats. In Synthesis of science to inform land management within the Northwest Forest Plan area (T. A. Spies, P. A. Stine, R. A. Gravenmier, J. W. Long, and M. J. Reilly, Editors). USDA

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

Forest Service General Technical Report PNW-GTR-966. Pacific Northwest Research Station, Portland, OR, USA. pp. 245–299.

Lesmeister, D. B., S. G. Sovern, R. J. Davis, D. M. Bell, M. J. Gregory, and J. C. Vogeler (2019). Mixed-severity wildfire and habitat of an old-forest obligate. Ecosphere 10:e02696.

Lint, J., B. Noon, R. Anthony, E. Forsman, M. Raphael, M. Collopy, and E. Starkey (1999). Northern Spotted Owl effectiveness monitoring plan for the Northwest Forest Plan. USDA Forest Service General Technical Report PNW-GTR-440:43. Pacific Northwest Research Station, Portland, OR, USA.

Mangan A. O., T. Chestnut, J. C. Vogeler, I. K. Breckheimer, W. M. King, K. E. Bagnall, and K. M. Dugger (2019). Barred Owls reduce occupancy and breeding propensity of Northern Spotted Owl in a Washington old-growth forest. The Condor: Ornithological Applications 121:1–20.

Martin, A. E., and L. Fahrig (2018). Habitat specialist birds disperse farther and are more migratory than habitat generalist birds. Ecology 99:2058–2066.

Morrison, J. L., and P. B. Wood (2009). Broadening our approaches to studying dispersal in raptors. Journal of Raptor Research 43:81–89.

Murray, B. G. (1967). Dispersal in vertebrates. Ecology 48:975–978.

Nakagawa, S., P. C. D. Johnson, and H. Schielzeth (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. Journal of the Royal Society Interface 14:20170213.

Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, and W. J. Ripple (2005). Modeling of site occupancy dynamics for Northern Spotted Owls, with emphasis on the effects of Barred Owls. Journal of Wildlife Management 69:918–932.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory (1998). Patterns of natal and breeding dispersal in birds. Journal of Animal Ecology 67:518–536.

Pusey, A. E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology & Evolution 2:295–299.

R Core Team (2018). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs (2017). Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). Ecosphere 8:e01695.

Roze, D., and F. Rousset (2005). Inbreeding depression and the evolution of dispersal rates: A multilocus model. The American Naturalist 166:708–721.

Schmidt, K. A. (2006). Non-additivity among multiple cues of predation risk: A behaviorally-driven trophic cascade between owls and songbirds. Oikos 133:82–90.

Seamans, M. E., and R. J. Gutierrez (2007). Habitat selection in a changing environment: The relationship between habitat alteration and Spotted Owl territory occupancy and breeding dispersal. The Condor 109:566–576.

Sovern, S. G., E. D. Forsman, G. S. Olson, B. L. Biswell, M. Taylor, and R. G. Anthony (2014). Barred Owls and landscape attributes influence territory occupancy of Northern Spotted Owls. The Journal of Wildlife Management 78:1436–1443.

Sovern, S. G., D. B. Lesmeister, K. M. Dugger, M. S. Pruett, R. J. Davis, and J. M. Jenkins (2019). Activity center selection by Northern Spotted Owls. Journal of Wildlife Management 83:714–727.

Stoelting, R. E., R. J. Gutiérrez, W. L. Kendall, and M. Z. Peery (2015). Life-history tradeoffs and reproductive cycles in Spotted Owls. The Auk: Ornithological Advances 132:46–64.

USDA and USDI (1994). Final Supplemental Environmental Impact Statement on Management of Habitat for Late-Successional and Old-Growth Forest Related Species within the Range of the Northern Spotted Owl. USDA Forest Service and USDI Bureau of Land Management, Portland, OR, USA.

USFWS (1990). Endangered and threatened wildlife and plants: Determination of threatened status for the Northern Spotted Owl. Federal Register 55:26114–26194.

Wiens, J. D., R. G. Anthony, and E. D. Forsman (2014). Competitive interactions and resource partitioning between Northern Spotted Owls and Barred Owls in western Oregon. Wildlife Monographs 185:1–50.

Wiklund, C. G. (1996). Determinants of dispersal in breeding Merlins (*Falco columbarius*). Ecology 77:1920–1927.

Wolak, M. E., D. J. Fairbairn, and Y. R. Paulsen (2012). Guidelines for estimating repeatability. Methods in Ecology and Evolution 3:129–137.

Yackulic, C. B., L. L. Bailey, K. M. Dugger, R. J. Davis, A. B. Franklin, E. D. Forsman, S. H. Ackers, L. S. Andrews, L. V. Diller, S. A. Gremel, et al. (2019). The past and future roles of competition and habitat in the range-wide occupancy dynamics of Northern Spotted Owls. Ecological Applications 29:e01861.

Yackulic, C. B., J. Reid, R. Davis, J. E. Hines, J. D. Nichols, and E. Forsman (2012). Neighborhood and habitat effects on vital rates: Expansion of the Barred Owl in the Oregon coast ranges. Ecology 93:1953–1966.

Zimmerman, G. S., R. J. Gutiérrez, and W. S. Lahaye (2007). Finite study areas and vital rates: Sampling effects on estimates of Spotted Owl survival and population trends. Journal of Applied Ecology 44:963–971.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

APPENDIX TABLE 4. Summary statistics for breeding dispersal distance moved by different groups of Northern Spotted Owls, 1990–2017.

		Breeding dispersal distance (km)			
	n	Mean	SE	min	max
Sex, female	983	5.98	0.27	0.04	94.55
Sex, male	1,175	5.17	0.20	0.09	84.86
Oregon Cascades	520	5.48	0.33	0.51	84.86
Oregon Coast Range	1,086	5.57	0.24	0.04	94.55
Oregon Klamath	342	4.84	0.33	0.24	67.66
Washington Cascades	99	6.75	0.83	0.88	56.37
Washington Coast	111	6.61	0.90	0.18	71.69
P0, unproductive	1,540	5.65	0.20	0.04	94.55
P1, fledged young	382	4.82	0.34	0.25	64.89
P2, unknown productivity	236	6.02	0.51	0.28	67.66
MS1, single	376	6.30	0.43	0.39	94.55
MS2, paired with new mate	895	5.84	0.28	0.04	84.86
MS3, paired with previous mate	773	4.64	0.21	0.17	67.66
MS4, unknown status	114	6.86	0.86	0.55	63.70
Age, adult (age 3+)	1,993	5.43	0.17	0.04	94.55
Age, sub-adult (age 1)	50	6.25	0.74	0.09	22.79
Age, sub-adult (age 2)	115	7.18	0.74	0.91	67.92
EAS, 0 years	971	6.47	0.30	0.04	94.55
EAS, 1–2 years	544	5.31	0.28	0.23	54.34
EAS, 3–17 years	643	4.33	0.20	0.24	67.66

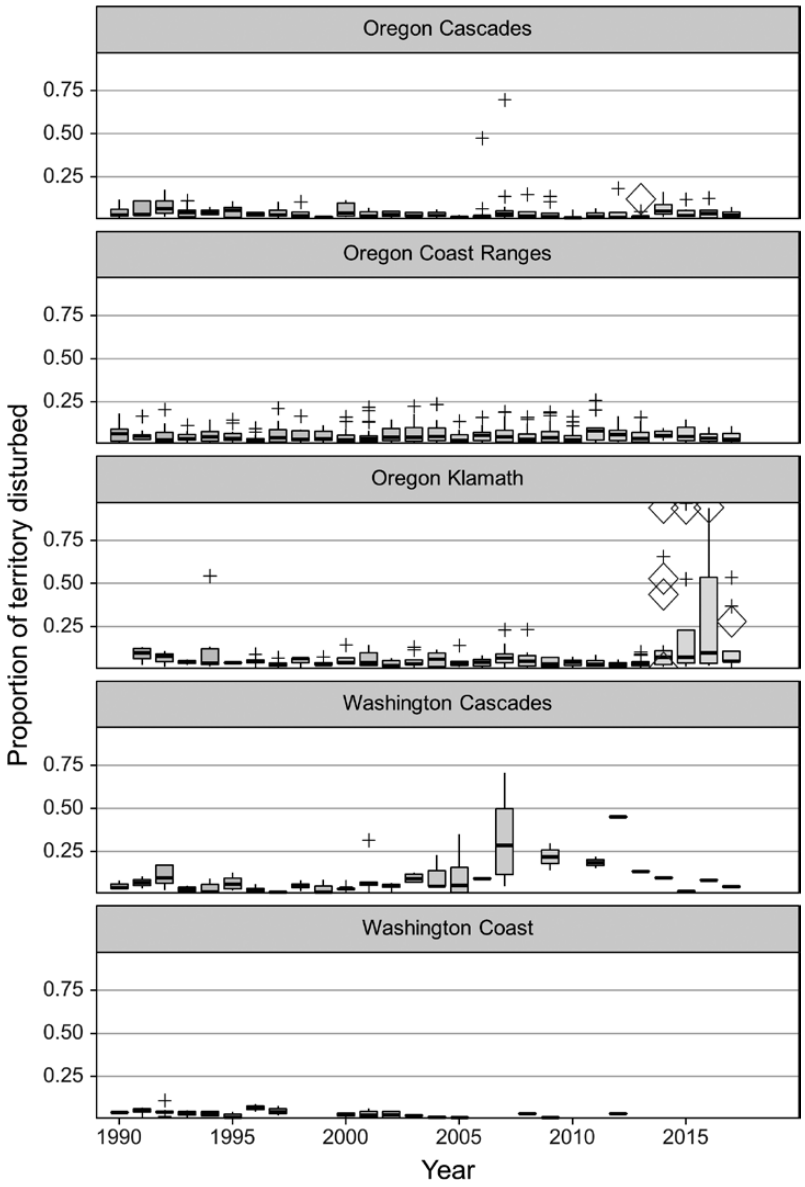
Abbreviations: P = prior productivity, MS = prior mate status, EAS = experience at prior territory, *n* = number of breeding dispersals.

APPENDIX TABLE 5. Summary of model-selection results for initial tests of variable structures within related groups used to characterize sources of variation in breeding dispersal distances of Northern Spotted Owls in Oregon and Washington, USA, 1990–2017. Structures with asterisks were considered in additive models. All models also included random effects of ecophysiographic province and time on the intercept. Abbreviations given in Table 1. *k* is number of parameters. w_i is Akaike's weight. Dev is the residual deviance.

Variable group	Model	ΔAIC [a]	*k*	w_i	Dev
Experience	EAS_3groups*	0.0	6	0.644	1738.6
Experience	EAS + EAS^2	1.7	6	0.270	1740.3
Experience	ln(EAS)	4.4	5	0.072	1743.4
Experience	EAS	7.9	5	0.013	1746.6
Experience	EAS_2groups	14.8	5	<0.001	1751.2
Reproductive	MS*	42.2	7	<0.001	1770.2
Experience	ADULT	62.8	5	<0.001	1785.3
Experience	AGECLASS	64.4	6	<0.001	1785.1
Environment	ln(D)*	67.5	5	<0.001	1791.3
Sex	sex*	68.2	5	<0.001	1791.8
Environment	ln(D_LO)	71.5	5	<0.001	1794.4
Reproductive	P	71.7	6	<0.001	1792.5
Environment	ln(D_HI)	72.1	5	<0.001	1794.6
Reproductive	PS	75.0	6	<0.001	1798.1
Environment	D_HI + D_HI^2	78.6	6	<0.001	1799.2
Environment	D_HI	78.8	5	<0.001	1800.8
Environment	D	79.7	5	<0.001	1801.5
Environment	D + D^2	80.1	6	<0.001	1800.2
Barred Owl	BO*	80.5	5	<0.001	1807.9
Barred Owl	ln(BO)	81.4	5	<0.001	1808.8
NULL	intercept-only	84.5	4	<0.001	1806.1
Environment	D_LO	85.6	5	<0.001	1805.7
Environment	D_LO + D_LO^2	86.2	6	<0.001	1804.2
Territory Quality	TQ	86.4	5	<0.001	1806.2

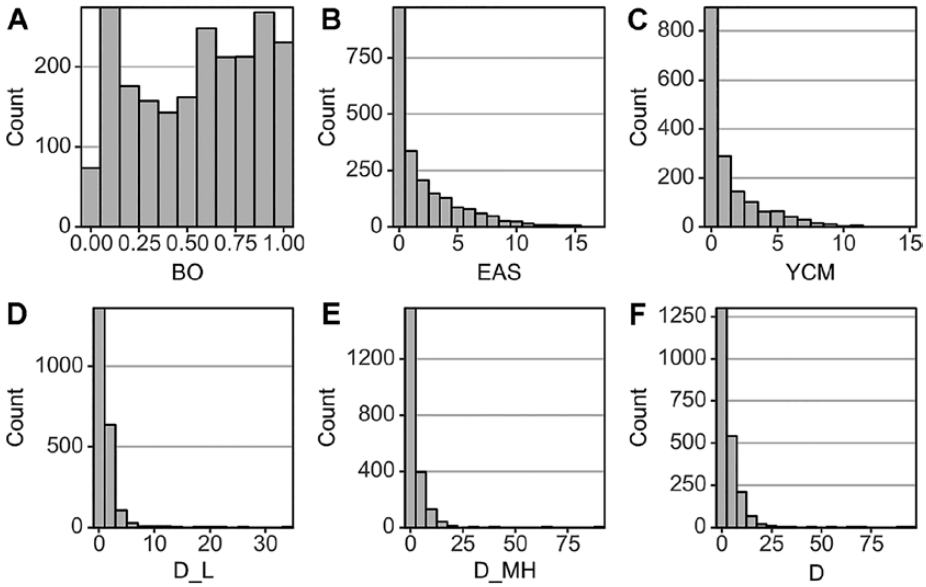
[a] Akaike's information criterion (AIC) of top model was 42420.2.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

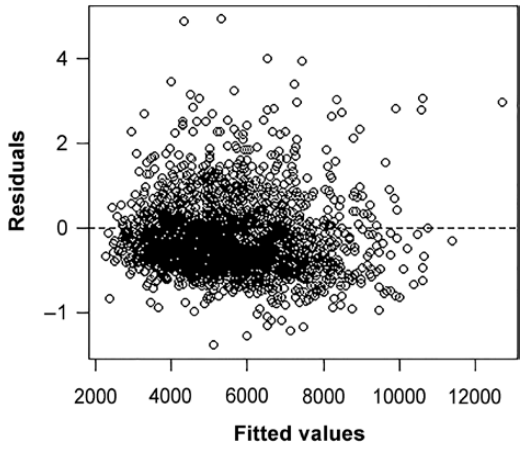


Appendix Figure 6. Boxplots showing proportion of disturbance in sampled pre-dispersal (occupied) territories for Northern Spotted Owls in each ecophysiographic province with outliers shown and disturbances from fire overlaid as diamonds. The sample presented here is not representative of disturbance trends within entire study areas or ecophysiographic provinces over time.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019



Appendix Figure 7. Histograms of continuous variables used in analysis of Northern Spotted Owl breeding dispersal distance. Abbreviations: Barred Owl = BO, experience at territory prior to dispersal = EAS, years with mate prior to move = YCM, low-severity disturbance on prior territory = D_L, moderate- to high-severity disturbance on prior territory = D_MH, total disturbance on prior territory = D.



Appendix Figure 8. Residuals plot from top model of breeding dispersal distance in Northern Spotted Owls.

Downloaded from https://academic.oup.com/condor/advance-article-abstract/doi/10.1093/condor/duz055/5658470 by U S Dept of Agriculture user on 11 December 2019

ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/230788091

Impact of postfire logging on soil bacterial and fungal communities and soil biogeochemistry in a mixed-conifer forest in central Oregon

Article *in* Plant and Soil · July 2012

DOI: 10.1007/s11104-011-0925-5

CITATIONS
39

READS
250

7 authors, including:



Tara Nicolle Jennings
US Forest Service
5 PUBLICATIONS **116** CITATIONS
SEE PROFILE



Jane E Smith
US Forest Service
83 PUBLICATIONS **2,618** CITATIONS
SEE PROFILE



K. Cromack
Oregon State University
157 PUBLICATIONS **10,374** CITATIONS
SEE PROFILE



Bruce Caldwell
Oregon State University
34 PUBLICATIONS **4,605** CITATIONS
SEE PROFILE

All content following this page was uploaded by Jane E Smith on 15 May 2014.

The user has requested enhancement of the downloaded file.

Plant Soil (2012) 350:393–411
DOI 10.1007/s11104-011-0925-5

REGULAR ARTICLE

Impact of postfire logging on soil bacterial and fungal communities and soil biogeochemistry in a mixed-conifer forest in central Oregon

Tara N. Jennings · Jane E. Smith · Kermit Cromack Jr. · Elizabeth W. Sulzman · Donaraye McKay · Bruce A. Caldwell · Sarah I. Beldin

Received: 30 November 2010 / Accepted: 15 July 2011 / Published online: 30 July 2011
© Springer Science+Business Media B.V. (outside the USA) 2011

Abstract
Aims Postfire logging recoups the economic value of timber killed by wildfire, but whether such forest management activity supports or impedes forest recovery in stands differing in structure from historic conditions remains unclear. The aim of this study was to determine the impact of mechanical logging after wildfire on soil bacterial and fungal communities and other measures influencing soil productivity.
Methods We compared soil bacterial and fungal communities and biogeochemical responses of 1) soils compacted, and 2) soils compacted and then subsoiled, to 3) soils receiving no mechanical disturbance, across seven stands, 1–3 years after postfire logging.
Results Compaction decreased plant-available N on average by 27% compared to no mechanical disturbance, while subsoiling decreased plant-available P (Bray) on average by 26% compared to the compacted and non-mechanically disturbed treatments. Neither bacterial nor fungal richness significantly differed among treatments, yet distinct separation by year in both bacterial and fungal community composition corresponded with significant increases in available N and available P between the first and second postharvest year.
Conclusions Results suggest that nutrients critical to soil productivity were reduced by mechanical applications used in timber harvesting, yet soil bacteria and fungi, essential to mediating decomposition and nutrient cycling, appeared resilient to mechanical disturbance. Results of this study contribute to the understanding about impacts of harvesting fire-killed trees and bear consideration along with the recovery potential of a site and the impending risk of future fire in stands with high densities of fire-killed trees.

Keywords Postfire salvage logging · Wildfire · T-RFLP · Soil bacterial and fungal communities · Soil chemical and physical properties · Community level physiological profiles

Responsible Editor: Hans Lambers.

Elizabeth W. Sulzman, deceased.

T. N. Jennings · K. Cromack Jr.
Department of Forest Ecosystems and Society,
Oregon State University,
Corvallis, OR 97331, USA

T. N. Jennings · J. E. Smith (✉) · D. McKay · S. I. Beldin
U.S. Department of Agriculture, Forest Service,
Pacific Northwest Research Station,
Forestry Sciences Laboratory, 3200 Jefferson Way,
Corvallis, OR 97331, USA
e-mail: jsmith01@fs.fed.us

E. W. Sulzman
Department of Crop and Soil Science,
Oregon State University,
Corvallis, OR 97331, USA

B. A. Caldwell
Department of Botany and Plant Pathology,
Oregon State University,
Corvallis, OR 97331, USA

Introduction

The effects of mechanical disturbance that occur with logging operations, such as compaction and subsoiling, on soil productivity and forest recovery are of concern worldwide, and depend upon severity, time since disturbance, and site factors (Grigal 2000; Marshall 2000; Rab 2004; Bassett et al. 2005; Yildiz et al. 2007, 2010; Hartmann et al. 2009). Successful forest regeneration following logging operations may rely upon natural forest regeneration or upon successful reforestation from nursery stock (Bassett et al. 2005; Yildiz et al. 2007, 2010; Lindenmayer et al. 2008; Perry et al. 2008). Similarly, disturbance from fire, whether prescribed or natural, varies within forest ecosystems, depending on intensity and length of time since fire (Bárcenas-Moreno and Bååth 2009; Keeley 2009; Yildiz et al. 2010). Re-establishment of understory plant diversity and ecosystem functions of natural forest communities with herbs, shrubs, and tree species mixtures may be important in sustaining long-term productivity (Fisher and Binkley 2000; Fox 2000; Rothe and Binkley 2001; Rothe et al. 2002; Talkner et al. 2009).

Fire effects upon forest ecosystems have long been of interest in understanding forest recovery and subsequent management and sustainability of forests worldwide (Kauffman and Uhl 1990; Attiwill and Adams 1993; Fox 2000; Fisher and Binkley 2000; Cochrane and Laurance 2002; Boerner et al. 2008, 2009; Perry et al. 2008). Forest wildfires have been a universal concern, including in the western United States. This has prompted the need to evaluate the effect of postfire treatments on forest ecosystem recovery (Cochrane et al. 1999; McIver and Starr 2000; Beschta et al. 2004; Sessions et al. 2004; Lindenmayer et al. 2008; Perry et al. 2008). It is well established that severe wildfire negatively impacts soil nutrient pools (Neary et al. 1999; Knicker 2007; Bormann et al. 2008; Hebel et al. 2009); however, the effect of postfire timber removal on soil productivity is not well understood and its application remains highly controversial among land managers, scientists, and the interested public (Lindenmayer et al. 2008). Postfire logging, currently underway in forests to salvage the economic value of timber killed by wildfire, may reduce burn severity to soils in the event of reburning by removing large, dead wood (Poff 1989); may increase the risk of fire (Donato et al. 2006) or fire severity (Thompson et al. 2007); or may decrease the amount of carbon (C) for long-term storage (DeLuca and Aplet 2008; Mitchell et al. 2009).

Forest harvesting equipment, including that used in postfire logging, frequently results in soil compaction, reducing soil pore size and decreasing oxygen availability and water and nutrient movement to tree roots (Dick et al. 1988; Page-Dumroese et al. 2006; Craigg and Howes 2007; Hartmann et al. 2009). To alleviate compaction, the practice of subsoiling or deep tillage is used to fracture the lower soil strata. Based on results from agricultural soils, tillage may degrade soil structure, adversely affecting microbial biomass and diversity by loss of macro-aggregates (Lupwayi et al. 2001). In forest soils, as a remedial treatment for soil compaction, subsoiling may actually ameliorate the more severe soil structure degradation from compaction. Disruption of the belowground component has immediate and potentially long-lasting effects on the below- and aboveground ecosystem (Froehlich et al. 1985; Perry et al. 1989; Neary et al. 1999; Beschta et al. 2004). However, in the case of soil compaction, subsoiling as a remedial treatment has been found to increase rooting volume, decrease bulk density, and increase aeration porosity, potentially having a positive effect on soil productivity (Otrosina et al. 1996; Carlson et al. 2006).

Soil microbes can indirectly influence soil productivity by enhancing nutrient availability for plant uptake, or reducing plant productivity through competition for nutrients with plant roots by promoting nutrient loss via leaching (Wardle et al. 2004; van der Heijden et al. 2008). For example, beneficial rhizosphere microorganisms, including mycorrhizal fungi and plant growth-promoting rhizobacteria (PGPR), such as *Rhizobium* and certain *Pseudomonas* species, can increase the availability of nutrients or plant growth substances to plants or suppress parasitic and nonparasitic pathogens (Schippers et al. 1987; Smith and Read 2008; Courty et al. 2010). Disturbances such as fire and harvesting can impact the abundance, activity, and composition of soil microbial communities (Smith et al. 2005; Smith et al. 2008; Kennedy and Egger 2010), thereby contributing to changes in nutrient cycling, organic matter decomposition rates, and ecosystem C accrual (Pietikäinen and Fritze 1995; Neary et al. 1999). While some studies in pine and mixed-conifer forests have reported minimal or

no modification of the mineral soil microbial community size or activity (Dick et al. 1988; Chow et al. 2002; Shestak and Busse 2005; Busse et al. 2006), another has shown deep and long-lasting effects of organic matter removal and soil compaction on microbial community structures (Hartmann et al. 2009). Understanding soil microbial tolerance to levels and thresholds of disturbance severity is critical to long-term forest productivity (Marshall 2000).

Our objective was to compare microbial communities in soils compacted and decompacted (subsoiled) by mechanical equipment to soils receiving no mechanical disturbance after a wildfire in a mixed conifer forest in central Oregon. In this forest, we investigated the structure, metabolism, and function of soil bacterial and fungal communities in relation to physicochemical properties. Studies incorporating approaches for assessing both structural and functional diversity in examining microbial response to wildfire (Yeager et al. 2005), soil compaction (Axelrood et al. 2002a, b; Shestak and Busse 2005; Busse et al. 2006; Hartmann et al. 2009), or both (Kennedy and Egger 2010) are varied in their approaches and responses. We hypothesized that post-fire mechanized salvage logging would compact surface soils resulting in restricted microbial- and invertebrate-habitable pore space. This would reduce organic matter turnover and nutrient (N,P) mineralization. Restricted microbial grazing by soil invertebrates would stabilize microbial populations and increase diversity in compacted soils. Subsoiling would ameliorate these effects by increasing microbial access to nutrients, but result in a loss of microbial diversity due to an increase in predation from microbivores.

Materials and methods

Study area

This study was conducted within the Booth and Bear Butte (B&B) Fire Complex, located on the east side of the Cascade Mountains of Oregon in the Deschutes National Forest. The B&B Fire burned 36,733 ha in the summer of 2003. Timber sales approved prior to the B&B Fire and subsequently harvested 1 year after the fire provided a unique and timely opportunity to study the impacts of postfire logging without the uncertainty surrounding the approval of proposed postfire-logged stands. Timber harvest and subsoiling of portions of the compacted areas occurred in summer 2004. Subsoiling (on approximately 17% of a stand) was completed on all stands within a 3-day period. Compacted areas occupied approximately 2% to 5% of a stand. Stands, ranging in size from 5 to 12 ha (Table 1), were thinned from below with a feller buncher operation that consists of a shear machine used to cut and place trees into a trail, and a rubber tire skidder machine that pulls the trees to a landing.

Stands within the study are characterized by a dominant overstory of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) and Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) with white fir (*Abies concolor* Gord. & Glend., Lindl. ex Hildebr.) or grand fir (*Abies grandis* Dougl. ex D. Don, Lindl.) occurring as co-dominants (Simpson 2007). Before logging, stands were comprised mainly of second-growth trees. Nearly all stands contain a few large, 100 to 200-year-old trees, and dense shrubs typifying early successional stages after fire and subsequent logging. Stands contain an understory of snowbrush ceanothus *(Ceanothus velutinus* Dougl.), dwarf rose *(Rosa gymnocarpa* Nutt.), common snowberry *(Symphoricarpos albus* [L.] Blake), dwarf Oregon-grape (*Mahonia nervosa* [Pursh] Nutt.), trailing blackberry (*Rubus ursinus* Cham. and Schlecht) and red huckleberry (*Vaccinium parvifolium* Sm.). Soils are Vitricryands and Vitrixerands with sandy loam texture (Table 1). Elevations of all stands are about 1,000 m (Table 1). Average air temperatures range from −1°C in the winter months to 20°C in the summer months. Average annual precipitation ranges from 50 to 150 cm. About 70% of the precipitation falls during November through April. During the driest months (July, August, and September), the average monthly precipitation is less than 2.5 cm.

Study design

The study was a randomized genuine replicate block design (GRBD) (Hinkelmann and Kempthorne 2008) consisting of seven stands representing a mix of burn severities, including one stand that occurred within the perimeter of the B&B Fire, but was spared from fire. Since most fires are spatially heterogeneous, leaving unburned or low severity burned areas as well as more severely burned areas, all seven stands were included in the study. The study was designed to

Table 1 Stand locations and characteristics

Stand	Unit #	Unit size (ha)	Elevation (m)	Slope %	Aspect	Soil family	Location
TD	37	10.1	1030	4	SSE	Ashy-skeletal, frigid Typic Vitricryands	N 44°31′46, W 21°42′29
UN	54	6.9	955	6	NNE	Ashy over medial-skeletal, frigid Alfic Vitrixerands	N 44°29′25, W 21°42′15
MS	83	6.7	1000	6	E	Ashy over medial-skeletal, frigid Alfic Vitrixerands	N 44°29′46, W 21°43′48
Big	85	11.7	970	21	NNE	Ashy, frigid Typic Vitricryands	N 44°29′26, W 21°42′38
SP	118	7.3	970	3	E	Ashy over medial-skeletal, frigid Alfic Vitrixerands	N 44°00′00, W 21°42′45
AKA	140	7.1	955	4	SE	Ashy over medial-skeletal, frigid Alfic Vitrixerands	N 44°32′05, W 21°40′56
FT	143	5.3	1030	12	SE	Ashy-skeletal, frigid Typic Vitricryands	N 44°31′35, W 21°42′39

compare the effects on soil of mechanical harvesting to non-mechanically disturbed areas. Within each replicate stand, several areas representing each of the three treatments were identified: 1) compacted (compaction from heavy ground-based equipment), 2) subsoiled (compaction followed by subsoiling), and 3) no mechanical disturbance (Fig. 1).

A sampling grid with grid points every 4–6 m was established within each stand (Fig. 1). Grid points were marked with a wooden stake and all stake locations were recorded with the Global Positioning System (GPS). A 10 m buffer zone within the perimeter of each stand was not sampled to avoid potential edge effects. Compacted and subsoiled treatments were based on visual indications of soil disturbance with heavy equipment using a classification system similar to those of Craigg and Howes (2007) and Frey et al. (2009) in which the compacted treatment was identified by topsoil displaced in lateral berms, and the subsoiled treatment as areas where fracturing of the compacted soil was evident. Visual classification systems of soil disturbance have been successfully used by the British Columbia Ministry of Forests and are currently under developmental use in the U.S. Forest Service Region 6 (Pacific Northwest) (Curran et al. 2005). Treatment designations were further assessed by the ease or difficulty of pounding stakes into the ground and validated with a combination of soil strength and bulk density measurements (described below). Within each stand, plots were established at 3 grid points randomly selected from each treatment type for sampling soil physical, chemical, and biological properties (Table 2). Grid point plots were treated as genuine replicates because of their random placement on multiple discontinuous treatment areas within a stand (Hinkelmann and Kempthorne 2008) (Fig. 1). When measurements were made through time (more than one season and year), these data were treated as repeated measures and analyzed using the appropriate split-plot design. For the responses for which we did not composite the replicates we fit a mixed linear model that included fixed effects for treatment (df=2) and season (df=5). We included random effects for site (df=6) and for replicates within treatment areas within sites (df=54) and the residual error (df=300). For responses for which we composited the material from the 3 replicates for each treatment within each site we also fit a mixed linear model with fixed effects for treatment and season. The random effects included site (df=6), variation among site by treatment combinations (df=12) and the residual error (df=90). All models were fit using SAS's PROC MIXED (SAS Institute 2003). There were seven stands with

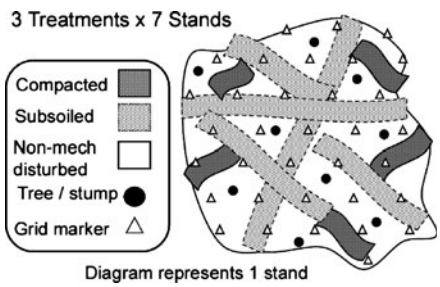


Fig. 1 Genuine replicate block study design with three discontinuous treatments within a stand 1) compacted (compaction from heavy ground-based equipment), 2) subsoiled (compaction followed by subsoiling), and 3) no mechanical disturbance. Three plots from each treatment were randomly selected for soil analyses (7 stands × 3 treatments × 3 plots = 63 plots)

Table 2 Soil physical, chemical, biochemical, biological, and biodiversity response variables measured for each stand

Soil response variable	2005		2006			2007	
	Summer	Fall	Spring	Summer	Fall	Spring	Summer
Texture	1[a]						
Soil resistance (MPa)	1[b]						
Bulk density (g cm^{-3})		1[b]	1[b]			1[b]	
Moisture (%)	3[c]	3[c]	3[c]	3[c]	3[c]	3[c]	
CEC (c mol_c kg^{-1})	3[c]			3[c]			3[c]
C:N	3[c]			3[c]			3[c]
pH	3[c]			3[c]			3[c]
Total C (g kg^{-1})	3[c]			3[c]			3[c]
Total P (mg kg^{-1})							3[c]
Available P (P-Bray) (mg kg^{-1})	3[c]			3[c]			3[c]
Total N (g kg^{-1})	3[c]			3[c]			3[c]
Anaerobic net N mineralization NH_4–N (mg kg^{-1})							3[c]
Anaerobic incubation NH_4–N (mg kg^{-1})							3[c]
Bacterial richness	3[a]	3[a]	3[a]	3[a]	3[a]	3[a]	
Fungal richness	3[a]	3[a]	3[a]	3[a]	3[a]	3[a]	
Bacterial functional diversity						3[c]	
Respiration (μmol m^{-2} s^{-1})	3[a]	3[a]	3[a]	3[a]	3[a]	3[a]	
Phosphatase activity (μmol g^{-1} h^{-1})						3[c]	

Numerals indicate the number of times a variable was measured per treatment per stand for season(s) indicated

[a] Treatments × $stand^{-1}$

[b] Selected stake × $treatment^{-1}$ × $stand^{-1}$

[c] Combined samples within treatment × $stand^{-1}$

three treatments each and three plots of each treatment, for a total of 63 plots; each plot was sampled over seven seasons: summer and fall 2005; spring, summer, and fall 2006; and spring and summer 2007. The response variables were selected based on their ability to influence and measure soil microbes and their processes.

Soil physical properties

Soil physical properties were measured at various times and replications, as shown in Table 2. Differences in soil strength were measured at each stand in one plot per treatment in the fall of 2005 (Table 2) using the Rimik 4011 recording soil penetrometer (Rimik International Pty Ltd, Queensland, Australia) at 2.5 cm increments. Five measurements at each sampling point were taken to a maximum depth of 60 cm. Bulk density was assessed in the fall of 2005 (0–5 cm) and the springs of 2006 (5–10 cm) and 2007 (0–5 cm, 5–10 cm). Gravimetric water content (% moisture) was measured in each plot during each sampling period to calculate water-filled pore space, an attribute critical to mass flow of nutrients, as well as to limits to biological activity.

Soil chemistry, N mineralization, and incubation N

Mineral soils for chemical analysis, N mineralization, and incubation N were collected to a 10 cm depth, using a garden trowel on each plot during each summer sampling period (Table 2). Soil samples were combined by treatment per stand and then sieved (2.0 mm) and air-dried before being analyzed. Total C and N were analyzed by the dry combustion technique (Bremner 1996; Nelson and Sommers 1996) using a Flash EA112 NC soil analyzer (Thermo Electron Corporation, Milan, Italy). Cation exchange capacity (CEC) was estimated using the sum of exchangeable cations (Robertson et al. 1999) for the

summer 2005 and 2006 samplings, and the ammonium acetate method (Rhoades 1982) for the summer 2007 soils. Soil pH was measured employing the 1:2 (soil:water) dilution method using deionized water (Robertson et al. 1999). Plant available P was analyzed using the dilute acid-fluoride method (P-Bray) (Kuo 1996) at the Oregon State University Central Analytical Lab (OSU CAL). Total P was measured at the OSU CAL using a Kjeldahl digestion (Bremner 1996; Taylor 2000), followed by P determination on an ALPKEM autoanalyzer (Technicon Instruments, Saskatoon, Canada).

Nitrogen mineralization potential, the conversion of organic N in microbial biomass to inorganic N under laboratory conditions, is considered a potential estimate of biologically available N (Myrold 1987; Perry et al. 2008). Anaerobic incubation N and net minerlizable N were measured in summer 2007 at the OSU CAL using the procedure of Bundy and Meisinger (1994). After incubation at 40°C for 7 days, 50 ml of 2 M KCl was added to extract NH_4–N for 1 h. The extracted NH_4 was determined on an ALPKEM autoanalyzer (Technicon Instruments, Saskatoon, Canada).

Genetic analysis of samples

Bacterial and fungal richness was measured at each plot within each stand for the first 6 sampling periods (Table 2). At each plot, a sparse litter layer of pine needles was removed and the mineral soil sampled to a depth of 10 cm and put in a 50 ml tube. Samples were placed in a cooler, transported to the lab and stored in a −80°C freezer until further processing. Small pebbles and vegetation (not including roots) were removed from the sample prior to DNA extraction. A MoBio Power Soil™ DNA isolation kit was used to extract total genomic DNA from approximately 0.5 g of each soil sample (MoBio Laboratories, Carlsbad, CA, USA).

Soil bacteria DNA was amplified using 16S rDNA gene primers 8F (FAM) and 907R (Edwards et al. 1989; Muyzer et al. 1995) in a 50 μl reaction mix containing: 1x PCR buffer, 2 mM $MgCl_2$, 0.2 mM dNTPs, 0.2 μM Primer, 0.064% BSA. Each soil DNA extract was run twice under the following conditions: 95°C for 3 min, followed by 30 cycles at 95°C for 30 s, 55°C for 1 min, 72°C for 45 s, and ending with an extension step of 72°C for 7 min. Once amplified, the two products were pooled to capture the diversity more fully. These pooled products were then purified using a MoBio Ultra Clean DNA Clean Up kit (MoBio Laboratories, Carlsbad, CA). Restriction enzyme *Msp*I was selected over *Alu*I for terminal restriction fragment length polymorphism (T-RFLP) community analysis after comparison trials on replicate samples revealed its ability to identify the greatest amount of variation. *Msp*I consistently is considered a top performing restriction enzyme for T-RFLP of bacterial samples (Liu et al. 1997; Engebretson and Moyer 2003). Digests were run according to the manufacturer's specifications by incubating the restriction digest for 3 h at 37°C. Restricted samples were submitted to Oregon State University Center for Gene Research and Biotechnology for analysis using an ABI Prism 3100 Genetic Analyzer (Applied Biosystems Inc., Foster City, CA, USA) to run capillary gel electrophoresis. Approximately 1 ng of amplified DNA was submitted for analysis for each sample. The analysis produced one community profile for each sample, where a profile consists of peaks of varying height and base pair length. The peaks (operational taxonomic units or OTUs) can be used to determine the richness of a given sample (Liu et al. 1997). Length and fluorescence of the terminal restriction fragments (TRF) were determined using GeneScan version 2.5 and Genotyper version 3.7 software (Applied Biosystems Inc., Foster City, CA). OTUs were binned to 1 bp in width.

Methods for identifying soil fungi were followed as stated above with the following exceptions. The fungal ITS spacer region was amplified using ITS-1f (Gardes and Bruns 1993) and ITS-4 (FAM) (White et al. 1990) and the reaction mixture and thermocycling program of Dickie et al. (2002). Restriction enzyme *Hinf*I was selected over *Hae*III for T-RFLP community analysis after comparison trials on replicate samples revealed its ability to identify the greatest amount of variation. Both *Hinf*I and *Hae*III are widely used in fungal T-RFLP profiling (Avis et al. 2006; Dickie and FitzJohn 2007; Alvarado and Manjon 2009). GeneMapper software 4.0 (Applied Biosystems Inc., Foster City, CA) was used to determine fragment fluorescence, OTUs were binned to 1 bp in width, and a binary analysis of presence or absence was performed following the methods of Rinehart (2004).

Community level physiological profiles

Soils for CLPPs were collected and processed in spring 2006 to a 10 cm depth at each plot. Soil samples were combined by treatment per stand, sieved (2.0 mm) and approximately 10 g was placed in small envelopes, and stored at 4°C until processing. The physiological potential, an estimate of functional diversity of the bacterial community, can be determined through the utilization patterns of various C sources (Garland 1996; Garland et al. 1997) but obviously is biased towards culturable, aerobic and fast-growing bacteria. The CLPPs were qualitatively assessed using Biolog EcoPlates™ (Biolog Inc., Hayward, CA, USA) following the method described in Sinsabaugh et al. (1999). Plates were incubated at room temperature and color development was determined using a BioTek PowerWave X 340 spectrophotometer (BioTek Instruments, Winoski, VT, USA) at a wavelength of 596 nm. Absorbance values were recorded at 24 h intervals for 5 consecutive days (Sinsabaugh et al. 1999). The data used in this analysis are from the day 3 readings and have been standardized to the water control. The water column values (all zeros) were removed and all resulting negative values were changed to zero.

Soil respiration

Soil respiration was measured at 3 plots per treatment in each stand for the first six sampling periods (Table 2). Soil respiration data were obtained following the methods in Law et al. (2001) using a LI6200 infrared gas analyzer (LiCor, Lincoln, NE, USA). Soil respiration rates were expressed as μmol m^{-2} s^{-1} of CO_2, using the same convention and quantification as Sulzman et al. (2005).

Phosphatase enzyme activity

Phosphatase enzyme activity was assayed from soil samples collected in spring 2007 using the *p*-nitrophenyl-phosphate (*p*-NPP) assay of Tabatabai (1994) as modified by Caldwell et al. (1999). After soils were sieved (<2 mm), slurries were prepared with deionized water, and 1 ml of slurry was incubated with 1 ml of 50 mM *p*-NPP at 30°C. These assays were run without conventional buffers to measure enzyme activity under actual soil matrix conditions (pH, cation concentrations), rather than to estimate potential enzyme activities present at optimum pH with increased ionic strength. After 1 h, 0.5 ml of 0.5 M $CaCl_2$ was added and reactions were terminated by adding 2 ml of 0.5 M NaOH to the assay. Controls consisted of slurry without substrate and substrate without slurry. After centrifugation, supernatant *p*-nitrophenol (*p*-NP) concentrations were measured at 410 nm, and enzyme activities were calculated on a dry weight basis (Caldwell et al. 1999).

Statistical analyses

The mean responses for soil properties (Table 3) were compared among treatments, and when appropriate, among seasons and years. No significant treatment by season interactions were detected for any of the measured response variables; therefore, only main effects are presented. Results were considered significant at $P=0.05$ and were considered a statistical trend at $P=0.1$. The variability inherent in field studies with smaller sample numbers, such as when soil samples were composited in this study, affords practical value for using statistical trends at $P=0.1$ (Steel et al. 1997). The F statistic and α level of significance are presented in the text when not included in a table.

Multivariate statistical analyses were performed using PC-ORD version 5.0 (McCune and Grace 2002). Sample community profiles were examined using nonmetric multidimensional scaling (NMS) with the Sørensen distance measure. The medium NMS autopilot mode was selected, with 200 maximum iterations, 0.0001 instability criterion, 15 real runs, and 30 randomized runs. The final model dimensions were chosen by comparing the NMS runs with real data to Monte Carlo simulations with random numbers. The proportion of variation represented by each axis was assessed by calculating the coefficient of determination (R^2) between distances in the ordination space and Sørensen distances in the original distance matrix. The relationships between plots in ordination space and their corresponding environmental variables were assessed by over laying the variables as a joint plot. Preliminary ordinations were examined and the data set further modified, first by excluding peaks occurring in fewer than five samples and then by an arcsine square root transformation of each response in order to normalize the data

Table 3 Effects of management treatments on soil physical, biochemical, chemical, biological and biodiversity response variables, with means and ANOVA results

Soil response variable	Treatment				
	Compacted	Subsoiled	Non-mechanically Disturbed	$F_{[df,df]}$	P
Bulk density at 5 cm depth (g cm^{-3})	0.98 (0.04)	0.95 (0.04)	0.90 (0.04)	$2.71_{[2,12]}$	0.08
Bulk density at 10 cm depth (g cm^{-3})	1.02 (0.04) a	0.85 (0.04) b	1.00 (0.04) a	$5.17_{[2,12]}$	**0.02**
Moisture (%)	17.61 (1.37)	18.44 (1.37)	20.60 (1.37)	$2.02_{[2,12]}$	0.18
CEC (c mol_c kg^{-1})	18.61 (1.01)	19.06 (1.01)	19.64 (1.01)	$0.62_{[2,12]}$	0.56
C:N	20.61 (0.55)	19.82 (0.55)	20.53 (0.55)	$0.87_{[2,12]}$	0.44
pH	6.76 (0.08)	6.69 (0.08)	6.86 (0.08)	$2.13_{[2,12]}$	0.16
Total C (g kg^{-1})	31.4 (2.8)	30.2 (2.8)	31.5 (2.8)	$0.14_{[2,12]}$	0.87
Total P (mg kg^{-1})	1189.54 (73.89) a,b	1152.09 (73.89) a	1296.24 (73.89) b	$2.86_{[2,12]}$	0.10
Available P (P-Bray) (mg kg^{-1})	9.57 (0.66) a	7.29 (0.66) b	9.80 (0.66) a	$13.69_{[2,12]}$	**<0.01**
Total N (g kg^{-1})	1.6 (0.1)	1.6 (0.1)	1.6 (0.1)	$0.10_{[2,12]}$	0.90
Anaerobic net N mineralization NH_4–N (mg kg^{-1})	28.11 (4.22) a	32.73 (4.22) a,b	38.03 (4.22) b	$6.53_{[2,12]}$	**0.01**
Anaerobic incubation NH_4–N (mg kg^{-1})	29.51 (4.41) a	35.19 (4.41) a,b	40.47 (4.41) b	$6.65_{[2,12]}$	**0.01**
Mean # bacterial OTUs (*Msp*I)	24.43 (0.99) a	21.00 (0.99) b	22.36 (0.99) b	$3.00_{[2,12]}$	0.09
Mean # fungal OTUs (*Hinf*I)	20.29 (1.38)	17.67 (1.38)	18.38 (1.38)	$1.38_{[2,12]}$	0.29
Cumulative # bacterial OTUs (*Msp*I)	52.17 (3.98)	43.83 (3.98)	47.31 (3.98)	$1.11_{[2,12]}$	0.36
Cumulative # fungal OTUs (*Hinf*I)	38.17 (2.61)	32.40 (2.61)	36.12 (2.61)	$1.25_{[2,12]}$	0.32
Respiration (μmol m^{-2} s^{-1})	2.45 (0.19) a	2.36 (0.19) a	2.93 (0.19) b	$2.55_{[2,54]}$	0.09
Phosphatase (μmol g^{-1} h^{-1})	28.08 (3.32) a,b	22.74 (3.32) a	32.63 (3.32) b	$2.77_{[2,54]}$	0.07

Means are listed with standard errors in parentheses. The F statistic is testing the null hypothesis of no difference among treatment means. Within a column, means with a common lowercase letter are not different at α=0.1. Means differing at α=0.05 are shown in bold

set. Using the blocked multiresponse permutation (MRBP, Euclidean distance, treatments or year/season as groups) and unblocked multiresponse permutation (MRPP, Sørenson distance, treatments or year/season as groups) procedures, the strength and statistical significance of group membership was tested. If data contained repeated measures, MRBP was used, otherwise MRPP was used. The *P*-value and *A* statistic (*A*) describing within-group heterogeneity compared to the random expectation, were recorded for each MRBP and MRPP analysis. Similarities of each of the bacterial and fungal communities among treatments were assessed using a nested PerMANOVA with Sørenson distance where samples were nested within site. Soil biogeochemical properties were correlated with community compositional ordinations to investigate links between community composition and functional capability for the six seasons.

NMS, where samples were ordinated in C-substrate space, was used to analyze the Biolog™ spectrophotometer data for bacteria. The data needed no further transformation after looking at initial ordinations for normalization. For outlier analysis, MRPP and PerMANOVA Sørensen distance was used.

Diversity was estimated using the Shannon-Wiener index (*H*): $H = -\sum p_i (\ln p_i)$, where p_i is the ratio of the number of OTUs for bacteria or fungi found in each sample to the total number of peaks for bacteria or fungi found in all samples for the OTU data (Magurran 1988). Biolog™ substrate diversity was similarly calculated, except that p_i was the ratio of average well color development (AWCD) on each substrate to the sum of all AWCD on all substrates. Evenness was calculated for the OTU data using: $E = H'/H_{max} = H'/\ln S$, where H is the Shannon-Wiener diversity index, S is the total number of peaks found

in all samples, and E is a number between 0 and 1 (Magurran 1988).

Results

Soil physical properties

Overall, soil strength was greatest in the compacted treatment and least in the subsoiled treatment (Fig. 2). Soil strength measurements revealed distinct differences among all treatments at most 2.5 cm increments between 7.5 and 17.5 cm and distinct differences between compacted and other treatments at all increments to a depth of 17.5 cm (Fig. 2). At levels deeper than 17.5 cm, compacted and non-mechanically treated soils did not differ in soil strength; however, the subsoiled treatment showed distinctly less resistance compared to those treatments at depths of 25–35 cm (Fig. 2). Bulk density at 10 cm taken more than 1 year after harvesting was 15% lower, on average, in the subsoiled treatment (95% (Confidence Interval (CI)=6–24%)) (Table 3).

Percent moisture was up to 85% lower in summer compared with fall and spring (95% CI=70–93%, 95% CI=74–94%, respectively) ($F_{[2,\ 111]}$=119.69, P<0.0001), but differences among treatments were not observed (P=0.18) (Table 3).

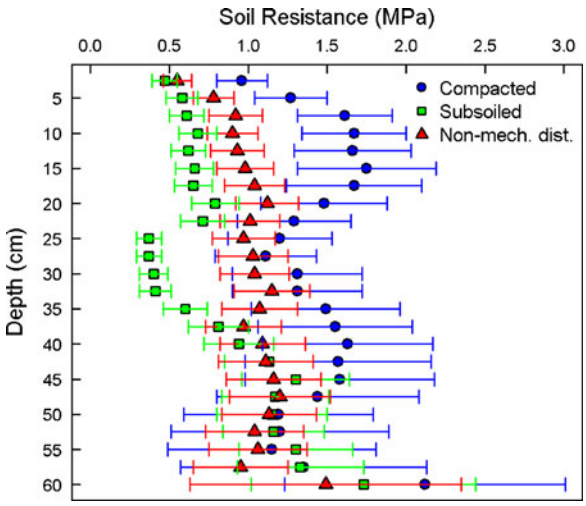


Fig. 2 Soil strength measurements by treatment. Measurements were taken at 2.5 cm increments to a maximum depth of 60 cm. Differences in soil strength were seen to a depth of 17.5 cm for most measurements. *Error bars* represent 1 SE

Soil chemistry, N mineralization, and incubation N

Differences were not observed among treatments for soil CEC, C:N, pH, total C, total N (P>0.1) (Table 3). Soil CEC was higher in summer 2005 compared to summers 2006 or 2007 ($F_{[2,\ 36]}$=16.63, P<0.0001). Plant-available P (Bray) was up to 26% lower in the subsoiled treatment compared to the compacted or non-mechanically disturbed treatments (95% CI=9–39%, 95% CI=11–41%), respectively (P<0.001) with a similar tendency for total P (P=0.1, 95% CI=−1.2–24%) (Table 3). Plant-available P (Bray) was higher in summer 2006 than in summers 2005 or 2007 ($F_{[2,\ 36]}$=18.76, P<0.0001). Compaction decreased anaerobic incubation NH_4-N by 26% (95% CI=3.5–51%) and net mineralizable (anaerobic) NH_4 by 27% (95% CI=2–50%) compared to the non-mechanically disturbed treatment (P=0.01 for both) (Table 3). Total N ($F_{[2,\ 36]}$=27.58, P<0.001) was higher in summer 2006 than in summer 2005. Increased N in the second summer led to lower C:N ($F_{[2,\ 36]}$=47.78, P<0.0001) in summer 2006 compared to summers 2005 and 2007.

Soil microbial communities

A total of 275 OTUs for soil bacteria were detected. Compaction tended to increase the mean number of bacteria OTUs, on average, by 9% and 14% when compared to both the non-mechanically disturbed and subsoiled treatments (95% CI=−0.5–19%, 95% CI=5–25%), respectively (P=0.09, Table 3). Shannon-Wiener indices for bacteria OTUs among treatments (4.0 to 4.1) suggest that bacteria OTUs in our samples were equally distributed and showed high community complexity, and evenness values of 0.70 to 0.73 suggest that OTUs were equally abundant. The average number of soil bacteria OTUs differed with respect to sampling period ($F_{[5,\ 90]}$=11.53, P<0.0001) (Fig. 3). Similarly, Shannon-Wiener indices were higher in year 1 (summer 2005, fall 2005, spring 2006) (4.0 to 4.1, with evenness values of 0.71 to 0.73) compared to year 2 (summer 2006, fall 2006, spring 2007) (3.6, with evenness values of 0.63 to 0.65).

A total of 160 OTUs for soil fungi were detected. There were no detected differences in the average number of fungi OTUs among treatments ($F_{[2,\ 12]}$=1.38, P=0.29) but differences were detected among sampling periods ($F_{[5,\ 90]}$=51.39, P<0.0001) (Fig. 3).

Fungal richness in all treatments declined after the first sampling season (summer 2005) and increased in the last sampling season (spring 2007) (Fig. 3). Similarly, Shannon-Wiener indices were higher in the first and last sampling seasons (4.0 and 4.2, evenness 0.81 and 0.83, respectively) compared to the other sampling seasons (3.4 to 3.6, evenness 0.67 to 0.72).

There were no observed differences in the cumulative number of bacteria and fungi OTUs among treatments (P=0.3 for both) (Table 3). All treatments showed a gradual increase in the cumulative mean number of bacteria and fungi OTUs over time (Fig. 4).

Variation in bacterial community composition was not detected among treatments (PerMANOVA $F_{[2,\ 105]}$= 0.61, P=0.76). NMS ordinations of the average number of OTUs showed differences in the bacterial community composition between year 1 (summer 2005, fall 2005, spring 2006) and year 2 (summer 2006, fall 2006, spring 2007) (MRPP P<0.0001, A= 0.13) and among seasons (PerMANOVA $F_{[2,123]}$=4.91, P=0.0002). Responses of CEC and percent moisture helped explain the variation in the soil sample community from summer 2005, spring 2006, and spring 2007 (Table 4). In addition to these variables, available P explained separation of the bacterial community in summer 2006 soil samples. No environmental measures explained variation in either of the fall measurement periods (Table 4).

Variation in fungal community composition was also not detected among treatments (PerMANOVA $F_{[2,105]}$=1.27, P=0.23). NMS ordinations showed differences in the fungal community composition between year 1 (summer 2005, fall 2005, spring 2006) and year 2 (summer 2006, fall 2006, spring 2007) (MRPP P<0.0001, A=0.12), and among seasons (PerMANOVA $F_{[2,123]}$=5.41, P=0.0002). Responses of CEC, total C, and percent moisture (Table 3) helped explain the variation in the soil sample community from fall 2005 and summer 2006 (Table 4). No environmental measures explained variation in summer 2005, fall 2006, or either spring measurement periods (Table 4).

Community level physiological profiles

Variation in functional diversity, as measured by absorbance values, was not detected among treatments (MRBP P=0.11, A=0.022) (Table 4). Differentiation in Shannon-Wiener indices for CLPPs for bacteria was not observed among treatments (3.0 in compacted, 2.9 in both the subsoiled and non-mechanically disturbed treatments). Ordinations of the CLPP data in species space showed that C substrate groups, amines/amides, amino acids, and carbohydrates significantly correlated with the variation in species composition in spring 2007 (Table 4); amines/amides were more correlated with axis 3 (R^2= 0.460), amino acids with axis 1 (R^2=0.634), which explains more variation than axis 3, and carbohydrates with axis 2 (R^2=−0.456). Proportion of variation (R^2) explained by each axis was 0.63, 0.16, and 0.21, respectively.

Soil respiration and phosphatase activity

Soil respiration rates tended to be higher in the non-mechanically disturbed treatment compared to both

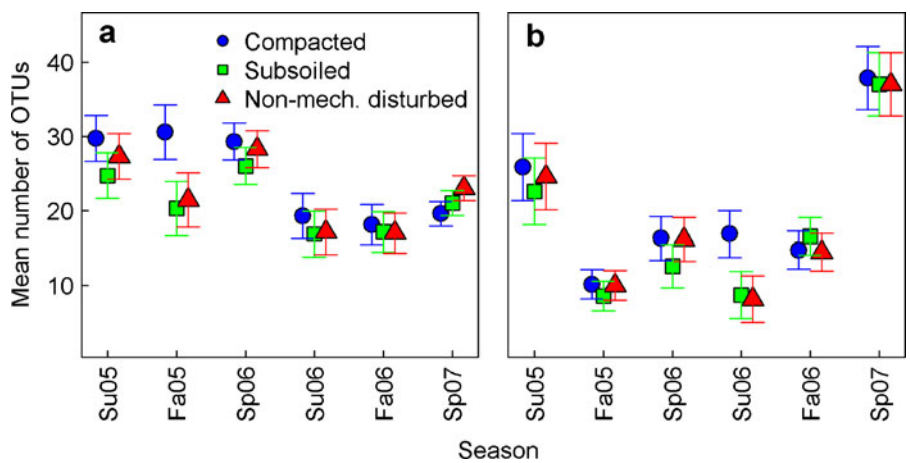


Fig. 3 Mean number of **a** bacterial (*Msp*I) and **b** fungal (*Hinf*I) OTUs differed among seasons. Bacterial OTUs tended to be higher in the compacted treatment; however there were no differences among treatments in the mean number of fungal OTUs

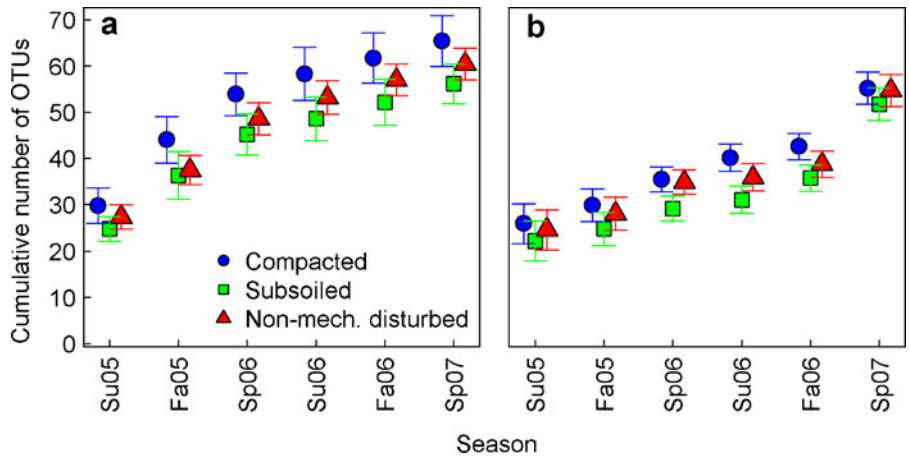


Fig. 4 Cumulative mean number of **a** bacterial (*Msp*I) and **b** fungal (*Hinf*I) OTUs by season and treatment. All treatments showed a gradual increase in the cumulative mean number of bacteria and fungi OTUs over time

the compacted and subsoiled treatments (P=0.09) (Table 3). Soil respiration rates were, on average, more than 20% lower in fall compared to summer or spring (95% CI=26–42%, 95% CI=14–33%, respectively, P<0.01 for both). Evidence suggested that phosphatase activity was, on average, 30% lower in the subsoiled treatment compared to the non-mechanically disturbed treatment (P=0.07, 95% CI= 10–51%) (Table 3).

Discussion

Following forest ecosystem disturbances, such as wildfires and logging, soil microorganisms, including fungi, bacteria, and protozoans, facilitate decomposition processes for both aboveground forest floor and wood residues, and for belowground components, such as fine and coarse roots (Stark 1972; Richards 1987; Perry et al. 2008). These important soil biota help to sustain forests by re-establishing nutrient cycling processes following forest disturbance, while also facilitating establishment of trees and understory vegetation components, which depend upon both free-living and symbiotic microbes for nutrient uptake (Paul and Clark 1996; Dighton 2003; Perry et al. 2008; Smith and Read 2008; Simard 2009; Courty et al. 2010).

The net mineralizable N mean values for all of our treatments (Table 3) shows that most of the available mineral soil N pool is being maintained in microbial tissues, based upon research used to develop the anaerobic N mineralization method employed in our study (Myrold 1987; Bundy and Meisinger 1994; Perry et al. 2008). The soil microbial biota, such as bacteria and fungi, also are important in taking up other key nutrient elements, including P and base cations from soil mineral and organic matter sources (Stark 1972; Cromack et al. 1975; Entry et al. 1992; Tiessen et al. 1994; Smith and Read 2008).

Soil organic matter is a primary source of soil N required for the decomposition of residual forest floor and woody components aboveground and fine and coarse roots belowground (Richards 1987; Tiessen et al. 1994; Dighton 2003). Fungi, due to their ability to create hyphal networks through long-lived fungal rhizomorphs and mycelial strands (Treseder et al. 2005), facilitate translocation of important nutrients such as N and P from soil sources into the residual forest floor aboveground woody components. Similar fungal networks are created by ectomycorrhizal fungi of trees, including Douglas-fir and ponderosa pine (Simard 2009; Courty et al. 2010), enabling N to be mobilized from a variety of soil organic matter sources (Lilleskov et al. 2010), soil P from organic and inorganic soil sources (Entry et al. 1992; Perry et al. 2008; Smith and Read 2008), and soil water from transport by ectomycorrhizal fungi to tree seedlings (Warren et al. 2008).

Soil N availability studies have provided a useful comparative basis in forest productivity studies (Fisher and Binkley 2000) and for evaluating forest management activities, such as thinning, fertilization or prescribed burning (Waring et al. 1992; Monleon et

Table 4 Statistical outcomes for NMS ordinations for each season, and MRBP and PerMANOVA results showing no community differences for bacteria (*Msp*I) and fungi (*Hae*III) by treatment (TRT)

Season	Microbe	NMS	MRBP-TRT	PerMANOVA-TRT	Vectors
Summer 2005	Bacteria	[a]Stress=10.80 Instability=0.000001	A=−0.004 P=0.60	P=0.46	CEC
	Fungi	[b]Stress=38.74 Instability=0.001070	A=−0.011 P=0.80	P=0.88	None
Fall 2005	Bacteria	[a]Stress=9.77 Instability=0.000001	A=−0.005 P=0.56	P=0.53	None
	Fungi	[c]Stress=9.54 Instability=0.000001	A=−0.005 P=0.58	P=0.15	% Moisture
Spring 2006	Bacteria	[c]Stress=10.75 Instability=0.000001	A=0.023 P=0.09	P=0.29	None
	Fungi	[c]Stress=9.08 Instability=0.000001	A=0.047 P=0.05	P=0.02	None
Summer 2006	Bacteria	[c]Stress=9.34 Instability=0.000001	A=0.005 P=0.36	P=0.29	P-Bray, CEC, % Moisture
	Fungi	[c]Stress=4.21 Instability=0.000001	A=0.005 P=0.39	P=0.31	CEC, Total C
Fall 2006	Bacteria	[c]Stress=10.07 Instability=0.000001	A=0.012 P=0.22	P=0.43	None
	Fungi	[a]Stress=13.56 Instability=0.000090	A=−0.033 P=0.93	P=0.52	None
Spring 2007	Bacteria	[c]Stress=8.304 Instability=0.000001	A=−0.0104 P=0.70	P=0.57	% Moisture
	Fungi	[b]Stress=32.24 Instability=0.000010	A=0.018 P=0.20	P=0.11	None
	CLPP	[c]Stress=8.30 Instability=0.000001	A=0.022 P=0.11	P=0.41	Amines/Amides, Amino Acids, Carbohydrates

The "Vectors" column contains variables that showed a significant correlation (R^2) with the bacterial, fungal, and functional community structure

[a] Denotes 2-D solution

[b] Denotes 1-D solution

[c] Denotes 3-D solution

al. 1997; Velazquez-Martinez and Perry 1997; Jones et al. 2010). In support of our hypothesis, compaction decreased plant-available N by 27%, on average, and NH_4–N and N mineralization by 26%, on average, compared to the non-mechanically disturbed treatment. Similarly, Lindo and Visser (2003) found decreased NH_4–N after clearcut harvesting, whereas DeLuca and Zouhar (2000) reported an increase in the levels of NH_4–N and potentially mineralizable N immediately following harvesting and prescribed fire. The anaerobic N availability index values in our study were similar to values reported by Myrold (1987) and Hebel et al. (2009) for other central Oregon forest sites (Table 3). Myrold (1987) also found a highly significant correlation (R^2=0.731) between anaerobic mineralizable N and microbial biomass N, using data from seven sites across Oregon. Based upon results of that research (Myrold 1987), the significantly higher net mineralizable anaerobic N on the non-mechanically disturbed treatment in our study (Table 3) may indicate that there was a greater microbial biomass N pool present under that treatment. Breland and Hansen (1996) postulated that N mineralization in compacted soil was reduced by increased physical protection of organic materials and microbial biomass against attack by microbivores. Busse et al. (2006) suggested that a decrease in pore size that benefits microbial community

stability may reduce plant nutrient availability. These observations are in agreement with several other studies on how soil structure affects habitable pore space for microorganisms and the turnover of soil organic matter and nutrients, such as N (Elliott et al. 1980; Battigelli et al. 2004; Li et al. 2004; Coleman 2008).

In support of our hypothesis, soils subjected to mechanical harvesting equipment after wildfire, and measured 1 year after harvesting, exhibited increased soil resistance compared to soils receiving no mechanical disturbance (Fig. 2). However, there were no observed differences in bulk density at 10 cm between the compacted and non-mechanically disturbed treatments 1 and 3 years after harvesting. Page-Dumroese et al. (2006) reported that in coarse-textured soils, bulk density measurements change relatively quickly with time and at the 10 cm depth may indicate recovery not reflected in soil strength measurements after 1 and 5 years. Frey et al. (2009) found no difference in bulk density at 10 cm between their lightly compacted and undisturbed treatments or between their moderately compacted and undisturbed treatments in two of three study sites, even though moderate compaction was characterized as topsoil displaced in lateral or side berms. Furthermore, Frey et al. (2009) reported that the physical effects of different levels of compaction from heavy logging machinery significantly changed the bacterial community structure in their severely compacted soil (approximately 32% increase in bulk density relative to undisturbed soil) and resulted in only minimal changes in bacterial OTU abundance in moderately (18% increase in bulk density) and lightly (3% increase in bulk density) compacted soils. In contrast, we did not observe variation in bacterial community composition among treatments.

In contrast to our hypothesis that subsoiling may alleviate nutrient loss due to compaction, we observed that plant-available P (Bray) was up to 26% lower in the subsoiled treatment compared to the non-mechanically disturbed and compacted treatments. This decrease would be expected to lead to decreased plant growth; however, subsoiling improved tree seedling growth compared to the compacted and non-mechanically disturbed treatments (JE Smith, unpublished data). Subsoiling also tended to decrease total P by 11%, on average, compared to the non-mechanically disturbed treatment. The decrease in plant-available and total P in the subsoiled treatment in this study may be linked to fractions of the organic matter that were not measured. Some P stored in plant residues becomes associated with the active and passive fractions of soil organic matter, where it can be stored for future release and very slowly converted to soluble inorganic forms that plants can use (Brady and Weil 2002).

The decrease in plant-available P (Bray) could be related to the 30% reduction in phosphatase activity that we detected in the subsoiling treatment, which mineralizes this P from organic forms. Dick et al. (1988) found that compaction in skid trails lowered phosphatase by 41% (and all enzyme activities assayed by 41–75%) in the 10–20 cm depth. However, there was a consistent trend that enzyme activities in the top 10 cm were lower in the compacted treatment compared to the control, but differences were small and not significant. Dick et al. (1988) did not detect differences in phosphatase between subsoiled treatments and the control. Boerner et al. (2008) found that fire and the combination of fire and mechanical treatment from harvesting lowered phosphatase activity compared to the mechanical treatment alone in a dry mixed conifer forest in Oregon. They further noted that phosphatase activity was reduced by treatments that included fire in the majority of fire and fire surrogate sites in the western United States. In contrast, phosphatase activity in our study did not differ between the one stand that escaped fire and the others that burned.

Contrary to our hypothesis, salvage logging soil disturbance did not appear to have an effect on microbial diversity; however, compaction tended to increase the mean number of bacterial OTUs by 9% and 14% when compared to the non-mechanically disturbed and subsoiled treatments, respectively. Variation in fungal richness was not detected between mechanically disturbed treatments and the non-mechanically disturbed treatment. However, the ordination approach we used revealed distinct separation in both the bacterial and fungal community composition between the first and second postharvest year that corresponded with significant increases in total and available N and available P. Tree mortality from fire and the removal of trees in our study may have led to a shift from root and rhizosphere associated bacteria and fungi to saprotrophic dominated communities. Studies suggest that overstory harvesting and the presence of living trees more greatly

influences soil microbial communities than an intact forest floor (Busse et al. 2006; Kennedy and Egger 2010). Disruption of root C transport after tree girdling or root severing leads to changes in both fungal and bacterial communities (Högberg and Högberg 2002; Brant et al. 2006; Yarwood et al. 2009) and induces the rapid growth of opportunistic saprophytic fungi that utilize dying mycorrhizal mycelia (Lindahl et al. 2010).

A trend over six sampling seasons suggested that the compacted soil contained a slightly greater cumulative mean number of bacterial OTUs (Fig. 4). A decrease in pore size may have led to less predation on the bacterial community, as suggested for compacted conditions in similar forest types (Shestak and Busse 2005; Busse et al. 2006). Soil compaction alters pore size distribution and may benefit the bacterial community by increasing the volume of habitable pores and decreasing the pore space available to larger microbivores such as nematodes and protozoa (van der Linden et al. 1989; Hassink et al. 1993; Breland and Hansen 1996). Moldenke et al. (2000) found that compaction caused by skid trails in the Deschutes National Forest in central Oregon contributed to a shift in the food web to one that utilized primarily bacteria.

Soil respiration is a direct measure of both microbial and root activity. In our study, compaction tended to reduce respiration rates and this effect was not alleviated by subsoiling. Lindo and Visser (2003) found that clearcutting significantly reduced soil respiration in the forest floor. In contrast, Concilio et al. (2005) reported increased soil respiration with selective harvesting. Ma et al. (2004) found that thinning resulted in nominal impact on soil respiration, but that burning significantly reduced soil respiration. These varied responses may be attributed to the influence of understory vegetation on soil moisture and temperature. For example, Ma et al. (2004) reported that soil respiration was reduced significantly in burned ceanothus patches, but increased in unburned but thinned ceanothus patches. Law et al. (2001) showed that soil surface CO_2 effluxes were lowest for bare soil, and highest near shrubs, some of which were N_2 fixers with higher photosynthetic rates. The increased activities shown by respiration and by phosphatase in the non-mechanically disturbed treatment, for example, may indicate the effects of increased ceanothus and other understory plant recovery and colonization. Thus, there may be greater microbial activity with more plants, such as ceanothus, but not necessarily greater bacterial diversity than is being shown in the compacted treatment. The more compacted soil may have shown greater bacterial genetic diversity, yet less activity for respiration and phosphatase.

Varied responses of microbial communities and soil physicochemical properties to compaction and other soil disturbances may be explained by the complexity of soil disturbances that occur during mechanized harvesting and to levels of soil disturbance (Shestak and Busse 2005; Busse et al. 2006; Boerner et al. 2009; Frey et al. 2009). Busse et al. (2006) suggested that soil microbial response to compaction is typically more pronounced in studies with additional impacts of soil displacement and mixing such as that which occurs with the creation of skid trails. Recent studies in 100-year-old mixed-conifer forests (Shestak and Busse 2005) and in younger pine and mixed-conifer plantations (Li et al. 2003, 2004; Busse et al. 2006) reported little or no effect of compaction on microbial community size, activity, or function. Nevertheless, negative responses by microbial communities to compaction in forest ecosystems abound (Dick et al. 1988; van der Linden et al. 1989; Torbert and Wood 1992; Li et al. 2003; Tan et al. 2005, 2008) and can be long-lasting (Hartmann et al. 2009), emphasizing the need for scrutiny and thoughtful interpretation when investigating soil microorganism response to disturbance and its relation to soil processes.

Conclusions

Postfire logging in a dry, mixed conifer forest with sandy loam volcanic soils appeared to have minimal effects on soil microbial richness. However, this short-term study revealed decreased plant-available N and P in the soil after postfire logging disturbances that could have long-lasting effects in a system that already is nutrient limited. A shift in bacterial communities corresponding with an increase in plant available N and P suggests that soil microbes in these postfire landscapes are resilient to mechanical disturbance. Clearly, effects of postfire timber harvesting on soil microbes, nutrients, and processes warrant longer term investigation. Management decisions about whether or not to harvest fire-killed trees should be balanced with

the recovery potential of a site, and the potential for high densities of fire-killed trees to increase the area of severely burned soil in the event of future fire.

Acknowledgements This research was made possible with funding received from the Joint Fire Science Program; Oregon State University Department of Forest Science; the USDA Forest Service, Pacific Northwest Research Station; and the National Science Foundation Microbial Observatory (Grant No. 0348689). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation. Mention of trade or firm names does not constitute an endorsement by the U.S. Department of Agriculture. We thank Drs. Bernard Bormann, Peter Bottomley, Jim Kennedy, and Jonathan Martin for helpful comments on the manuscript. We thank Nicole Kurhanewicz, Zach Sutton, and William Austin for lab and field assistance. Special thanks to Liz Schwartz and Drs. Nicole DeCrappeo, Stephanie Boyle and Laurel Kluber for assistance with Biolog™ and T-RFLP results interpretation; Drs. Lisa Ganio (Quantitative Sciences Group), Greg Brenner (Pacific Analytics), Bruce McCune, and Dan Luoma for assistance with the study design and statistical analysis; Drs. George Weaver and Brian Knaus for assistance with graphics; Dr. Angeline Cromack for editing; and Brian Tandy, Terry Craigg, and others at the Deschutes National Forest for site information. Lastly, we dedicate this publication to the memory of Dr. Elizabeth Sulzman, an extraordinary scientist, educator, and mentor.

References

Alvarado P, Manjon JL (2009) Selection of enzymes for terminal restriction fragment length polymorphism analysis of fungal internally transcribed spacer sequences. Appl Environ Microbiol 75:4747–4752. doi:10.1128/AEM.00568-09

Attiwill PM, Adams MA (1993) Nutrient cycling in forests. New Phytol 124:561–582

Avis PG, Dickie IA, Mueller GM (2006) A 'dirty' business: testing the limitations of terminal restriction fragment length polymorphism (TRFLP) analysis of soil fungi. Mol Ecol 15:873–882. doi:10.1111/j.1365-294X.2005.02842.x

Axelrood PE, Chow ML, Arnold CS, Lu K, McDermott JM, Davies J (2002a) Cultivation-dependent characterization of bacterial diversity from British Columbia forest soils subjected to disturbance. Can J Microbiol 48:643–654. doi:10.1139/W02-058

Axelrood PE, Chow ML, Radomski CC, McDermott JM, Davies J (2002b) Molecular characterization of bacterial diversity from British Columbia forest soils subjected to disturbance. Can J Microbiol 48:655–674. doi:10.1139/W02-059

Bárcenas-Moreno G, Bååth E (2009) Bacterial and fungal growth in soil heated at different temperatures to simulate a range of fire intensities. Soil Biol Biochem 41:2517–2526. doi:10.1016/j.soilbio.2009.09.010

Bassett IE, Simcock RC, Mitchell ND (2005) Consequences of soil compaction for seedling establishment: implications for natural regeneration and restoration. Aust Ecol 30:827–833

Battigelli JP, Spence JR, Langor DW, Berch SM (2004) Short-term impact of forest soil compaction and organic matter removal on soil mesofauna density and oribatid mite diversity. Can J For Res 34:1136–1149

Beschta RL, Rhodes JJ, Kauffman JB, Gresswell RE, Minshall GW, Karr JR, Perry DA, Hauer FR, Frissell CA (2004) Postfire management on forested public lands of the western United States. Conserv Biol 18:957–967. doi:10.1111/j.1523-1739.2004.00495.x

Boerner REJ, Giai C, Huang J, Miesel JR (2008) Initial effects of fire and mechanical thinning on soil enzyme activity and nitrogen transformations in eight North American forest ecosystems. Soil Biol Biochem 40:3076–3085. doi:10.1016/j.soilbio.2008.09.008

Boerner REJ, Huang J, Hart SC (2009) Impacts of Fire and Fire Surrogate treatments on forest soil properties: a meta-analytical approach. Ecol Appl 19:338–358. doi:10.1890/07-1767.1

Bormann BT, Homann PS, Darbyshire RL, Morrissette BA (2008) Intense forest wildfire sharply reduces mineral soil C and N: the first direct evidence. Can J For Res 38:2771–2783. doi:10.1139/X08-136

Brady NC, Weil RR (2002) The nature and property of soils, 13th edn. Prentice-Hall, Upper Saddle River

Brant JB, Sulzman EW, Myrold DD (2006) Microbial community utilization of added carbon substrates in response to long-term carbon input manipulation. Soil Biol Biochem 38:2219–2232. doi:10.1016/j.soilbio.2006.01.022

Breland TA, Hansen S (1996) Nitrogen mineralization and microbial biomass as affected by soil compaction. Soil Biol Biochem 28:655–663. doi:10.1016/0038-0717(95)00154-9

Bremner JM (1996) Nitrogen-total. In: Sparks DL, Page AL, Helmke PA, Loeppert RH, Soltanpour PN, Tabatabai MA, Johnston CT, Sumner ME (eds) Methods of soil analysis. Part 3. Chemical methods—SSSA Book Series No. 5. Soil Science Society of America and American Society of Agronomy, Madison, pp 1085–1121

Bundy LG, Meisinger JJ (1994) Nitrogen availability indices. In: Weaver RW, Angle JS, Bottomley PS (eds) Methods of soil analysis. Soil Science Society of America, Madison, pp 951–984

Busse MD, Beattie SE, Powers RF, Sanchez FG, Tiarks AE (2006) Microbial community responses in forest mineral soil to compaction, organic matter removal, and vegetation control. Can J For Res 36:577–588. doi:10.1139/X05-294

Caldwell BA, Griffiths RP, Sollins P (1999) Soil enzyme response to vegetation disturbance in two lowland Costa Rican soils. Soil Biol Biochem 31:1603–1608. doi:10.1016/S0038-0717(99)00067-X

Carlson CA, Fox TR, Colbert SR, Kelting DL, Allen HL, Albaugh TJ (2006) Growth and survival of *Pinus taeda* in response to surface and subsurface tillage in the southeastern United States. For Ecol Manage 234:209–217. doi:10.1016/j.foreco.2006.07.002

Chow ML, Radomski CC, McDermott JM, Davies J, Axelrood PE (2002) Molecular characterization of bacterial diversity

in Lodgepole pine (*Pinus contorta*) rhizosphere soils from British Columbia forest soils differing in disturbance and geographic source. FEMS Microbiol Ecol 42:347–357. doi:10.1111/j.1574-6941.2002.tb01024.x

Cochrane MA, Laurance WF (2002) Fire as a large scale edge effect in Amazonian forests. J Trop Ecol 8:311–325

Cochrane MA, Alencar A, Schulze MD, Souza CM Jr, Nepstad DC, Lefebvre P, Davidson EA (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science 284:1832–1835

Coleman DC (2008) From peds to paradoxes: linkages between soil biota and their influences on ecological processes. Soil Biol Biochem 40:271–289. doi:10.1016/j.soilbio.2007.08.005

Concilio A, Ma S, Li Q, LeMoine J, Chen J, North M, Moorhead D, Jensen R (2005) Soil respiration response to prescribed burning and thinning in mixed-conifer and hardwood forests. Can J For Res 35:1581–1591. doi:10.1139/X05-091

Courty P-E, Buée M, Diedhiou AG, Frey-Klett P, Le Tacon F, Rineau F, Turpault M-P, Uroz S, Garbaye J (2010) The role of ectomycorrhizal communities in forest ecosystem processes: new perspectives and emerging concepts. Soil Biol Biochem 42:679–698. doi:10.1016/j.soilbio.2009.12.006

Craigg TL, Howes SW (2007) Assessing quality in volcanic ash soils. In: Page-Dumroese D, Miller R, Mital J, McDaniel P, Miller D (tech eds) Volcanic-ash-derived forest soils of the inland northwest: properties and implications for management and restoration. 9–10 November 2005, Coeur d'Alene, ID. Proceedings RMRS-P-44; Fort Collins, Colorado, USDA Forest Service, Rocky Mountain Research Station, pp 44–66

Cromack K Jr, Todd RL, Monk CD (1975) Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. Soil Biol Biochem 7:265–268

Curran MP, Miller RE, Howes SW, Maynard DG, Terry TA, Heninger RL, Niemann T, van Rees K, Powers RF, Schoenholts SH (2005) Progress towards more uniform assessment and reporting of soil disturbance for operations, research, and sustainability protocols. For Ecol Manage 220:17–30. doi:10.1016/j.foreco.2005.08.002

DeLuca TH, Aplet GH (2008) Charcoal and carbon storage in forest soils of the Rocky Mountain West. Front Ecol Environ 6(1):18–24. doi:10.1890/070070

DeLuca TH, Zouhar KL (2000) Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests. For Ecol Manage 138:263–271. doi:10.1016/S0378-1127(00)00401-1

Dick RP, Myrold DD, Kerle EA (1988) Microbial biomass and soil enzyme activities in compacted and rehabilitated skid trail soils. Soil Sci Soc Am J 52:512–516. doi:10.2136/sssaj1988.522512x

Dickie IA, FitzJohn RG (2007) Using terminal restriction fragment length polymorphism (T-RFLP) to identify mycorrhizal fungi: a methods review. Mycorrhiza 17:259–270. doi:10.1007/s00572-007-0129-2

Dickie IA, Xu B, Koide RT (2002) Vertical niche differentiation of ectomycorrhizal hyphae in soil as shown by T-RFLP analysis. New Phytol 156:527–535. doi:10.1046/j.1469-8137.2002.00535.x

Dighton J (2003) Fungi in ecosystem processes. Marcel Dekker, New York

Donato DC, Fontaine JB, Campbell JL, Robinson WD, Kauffman JB, Law BE (2006) Post-wildfire logging hinders regeneration and increases fire risk. Science 311:352. doi:10.1126/science.1122855

Edwards U, Rogall T, Blöcker H, Emde M, Böttger EC (1989) Isolation and direct complete nucleotide determination of entire genes. Characterization of a gene coding for 16S ribosomal RNA. Nucleic Acids Res 17(19):7843–7853. doi:10.1093/nar/17.19.7843

Elliott ET, Anderson RV, Coleman DC, Cole CV (1980) Habitable pore space and microbial trophic interactions. Oikos 35:327–335

Engebretson JJ, Moyer CL (2003) Fidelity of select restriction endonucleases in determining microbial diversity by terminal-restriction fragment length polymorphism. Appl Environ Microbiol 69(8):4823–4829. doi:10.1128/AEM.69.8.4823-4829.2003

Entry JA, Rose C, Cromack K Jr (1992) Microbial biomass and nutrient concentrations in hyphal mats of the ectomycorrhizal fungus *Hysterangium setchellii* in a coniferous forest soil. Soil Biol Biochem 24:447–453

Fisher RF, Binkley D (2000) Ecology and management of forest soils, 3rd edn. Wiley, New York

Fox RT (2000) Sustained productivity in intensively managed forest plantations. For Ecol Manage 138:187–202

Frey B, Kremer J, Rüdt A, Sciacca S, Matthies D, Lüscher P (2009) Compaction of forest soils with heavy logging machinery affects soil bacterial community structure. Eur J Soil Biol 45:312–320. doi:10.1016/j.ejsobi.2009.05.006

Froehlich HA, Miles DWR, Robbins RW (1985) Soil bulk density recovery on compacted skid trails in central Idaho. Soil Sci Soc Am J 49:1015–1017

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118. doi:10.1111/j.1365-294X.1993.tb00005.x

Garland JL (1996) Patterns of potential C source utilization by rhizosphere communities. Soil Biol Biochem 28:223–230. doi:10.1016/0038-0717(95)00113-1

Garland JL, Cook KL, Loader CA, Hungate BA (1997) The influence of microbial community structure and function on community level physiological profiles. In: Insam H, Rangger A (eds) Microbial communities. Springer, Heidelberg, pp 171–183

Grigal DF (2000) Effects of extensive forest management on soil productivity. For Ecol Manage 138:167–185. doi:10.1016/S0378-1127(00)00395-9

Hartmann M, Lee S, Hallam SJ, Mohn WW (2009) Bacterial, archaeal and eukaryal community structures throughout soil horizons of harvested and naturally disturbed forest stands. Environ Microbiol 11:3045–3062. doi:10.1111/j.1462-2920.2009.02008.x

Hassink J, Bouwman LA, Zwart KB, Brussaard L (1993) Relationships between habitable pore space, soil biota and mineralization rates in grassland soils. Soil Biol Biochem 25:47–55. doi:10.1016/0038-0717(93)90240-C

Hebel CL, Smith JE, Cromack K Jr (2009) Invasive plant species and soil microbial response to wildfire burn severity in the Cascade Range of Oregon. Appl Soil Ecol 42:150–159. doi:10.1016/j.apsoil.2009.03.004

Hinkelmann K, Kempthorne O (2008) Design and analysis of experiments, volume I: introduction to experimental design, 2nd edn. Wiley-Interscience, New York

Högberg MN, Högberg P (2002) Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. New Phytol 154:791–795. doi:10.1046/j.1469-8137.2002.00417.x

Institute SAS (2003) SAS system for Windows (computer software). SAS Institute, Cary, North Carolina

Jones MD, Twieg BD, Ward V, Barker J, Durall DM, Simard SW (2010) Functional complementarity of Douglas-fir ectomycorrhizas for extracellular enzyme activity after wildfire or clearcut logging. Funct Ecol 24:1139–1151. doi:10.1111/j.1365-2435.2010.01699.x

Kauffman JB, Uhl C (1990) Interactions of anthropogenic activities, fire, and rain forests in the Amazon Basin. In: Goldammer J (ed) Fire in the tropical biota. Springer, New York, pp 117–134

Keeley JE (2009) Fire intensity, fire severity and burn severity: a brief review and suggested usage. Int J Wildland Fire 18:116–126. doi:10.1071/WF07049

Kennedy N, Egger KN (2010) Impact of wildfire intensity and logging on fungal and nitrogen-cycling bacterial communities in British Columbia forest soils. For Ecol Manage 260:787–794. doi:10.1016/j.foreco.2010.05.037

Knicker H (2007) How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. Biogeochemistry 85:91–118. doi:10.1007/s10533-007-9104-4

Kuo S (1996) Phosphorus. In: Sparks DL, Page AL, Helmke PA, Loeppert RH, Soltanpour PN, Tabatabai MA, Johnston CT, Sumner ME (eds) Methods of soil analysis. Part 3. Chemical methods—SSSA Book Series No. 5. Soil Science Society of America and American Society of Agronomy, Madison, pp 869–919

Law BE, Kelliher FM, Baldocchi DD, Anthoni PM, Irvine J, Moore D, van Tuyl S (2001) Spatial and temporal variation in respiration in a young ponderosa pine forest during a summer drought. Agric For Meteorol 110:27–43. doi:10.1016/S0168-1923(01)00279-9

Li Q, Allen HL, Wilson CA (2003) Nitrogen mineralization dynamics following the establishment of a loblolly pine plantation. Can J For Res 33:364–374. doi:10.1139/X02-184

Li Q, Allen HL, Wollum AG II (2004) Microbial biomass and bacterial functional diversity in forest soils: effects of organic matter removal, compaction, and vegetation control. Soil Biol Biochem 36:571–579

Lilleskov EA, Hobbie EA, Horton TR (2010) Conservation of ectomycorrhizal fungi: exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. Fungal Ecol. doi:10.1016/j.funeco.2010.09.008

Lindahl BD, de Boer W, Finlay RD (2010) Disruption of root carbon transport into forest humus stimulates fungal opportunists at the expense of mycorrhizal fungi. ISME J 4:872–881. doi:10.1038/ismej.2010.19

Lindenmayer D, Burton P, Franklin J (2008) Salvage logging and its ecological consequences. Island, Washington

Lindo Z, Visser S (2003) Microbial biomass, nitrogen and phosphorus mineralization, and mesofauna in boreal conifer and deciduous forest floors following partial and clear-cut harvesting. Can J For Res 33:1610–1620. doi:10.1139/X03-080

Liu W-T, Marsh TL, Cheng H, Forney LJ (1997) Characterization of microbial diversity by determining terminal restriction fragment length polymorphisms of genes encoding 16S rRNA. Appl Environ Microbiol 63(11):4516–4522

Lupwayi NZ, Arshad MA, Rice WA, Clayton GW (2001) Bacterial diversity in water-stable aggregates of soils under conventional and zero tillage management. Appl Soil Ecol 16:251–261

Ma S, Chen J, North M, Erickson HE, Bresee M, Le Moine J (2004) Short-term effects of experimental burning and thinning on soil respiration in an old-growth, mixed-conifer forest. Environ Manage 33(Suppl 1):S148–S159. doi:10.1007/s00267-003-9125-2

Magurran A (1988) Ecological diversity and its management. Princeton University Press, Princeton

Marshall VG (2000) Impacts of forest harvesting on biological processes in northern forest soils. For Ecol Manage 133:43–60. doi:10.1016/S0378-1127(99)00297-2

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software, Gleneden Beach

McIver JD, Starr L (2000) Environmental effects of postfire logging: Literature review and annotated bibliography. USDA Forest Service, Pacific Northwest Research Station, Gen Tech Rep PNW-GTR-486. Portland, Oregon, 72 p

Mitchell SR, Harmon ME, O'Connell KEB (2009) Forest fuel reduction alters fire severity and long-term carbon storage in three Pacific Northwest ecosystems. Ecol Appl 19 (3):643–655. doi:10.1890/08-0501.1

Moldenke AR, Pajutee M, Ingham E (2000) The functional roles of forest soil arthropods: the soil is a lively place. In: Powers RF, Hauxwell DL, Nakamura GM (eds) Proceedings of the California Forest Soils Council Conference on Forest Soils Biology and Forest Management. USDA Forest Service, Pacific Southwest Research Station, Gen Tech Rep PSW-GTR-178, Berkeley, California, pp 7–22

Monleon VJ, Cromack K Jr, Landsberg JD (1997) Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. Can J For Res 27:369–378

Muyzer G, Teske A, Wirsen CO, Jannasch HW (1995) Phylogenetic relationships of *Thiomicrospira* species and their identification in deep-sea hydrothermal vent samples by denaturing gradient gel electrophoresis of 16S rDNA fragments. Arch Microbiol 164:165–172. doi:10.1007/BF02529967

Myrold DD (1987) Relationship between microbial biomass nitrogen and a nitrogen availability index. Soil Sci Soc Am J 51:1047–1049. doi:10.2136/sssaj1987.5141047x

Neary DG, Klopatek CC, DeBano LF, Ffolliott PF (1999) Fire effects on belowground sustainability: a review and synthesis. For Ecol Manage 122:51–71. doi:10.1016/S0378-1127(99)00032-8

Nelson DW, Sommers LE (1996) Total carbon, organic carbon and organic matter. In: Sparks DL, Page AL, Helmke PA, Loeppert RH, Soltanpour PN, Tabatabai MA, Johnston CT, Sumner ME (eds) Methods of soil analysis. Part 3. Chemical methods—SSSA Book Series No. 5. Soil Science Society of America and American Society of Agronomy, Madison, pp 961–1010

Otrosina WJ, Sung S-J, White LM (1996) Effects of subsoiling on lateral roots, sucrose metabolizing enzymes, and soil

ergosterol in two Jeffrey pine stands. Tree Physiol 16:1009–1013. doi:10.1093/treephys/16.11-12.1009

Page-Dumroese DS, Jurgensen MF, Tiarks AE, Ponder F Jr, Sanchez FG, Fleming RL, Kranabetter JM, Powers RF, Stone DM, Elioff JD, Scott DA (2006) Soil physical property changes at the North American long-term soil productivity study sites: 1 and 5 years after compaction. Can J For Res 36:551–564. doi:10.1139/X05-273

Paul EA, Clark FE (1996) Soil microbiology and biochemistry, 2nd edn. Academic, San Diego

Perry DA, Amaranthus MP, Borchers JG, Borchers SL, Brainerd RE (1989) Bootstrapping in ecosystems. BioScience 39(4):230–237

Perry DA, Oren R, Hart SC (2008) Forest ecosystems, 2nd edn. Johns Hopkins University Press, Baltimore

Pietikäinen J, Fritze H (1995) Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. Soil Biol Biochem 27(1):101–109. doi:10.1016/0038-0717(94)00125-K

Poff R (1989) Compatibility of timber salvage operations with watershed values. In: Berg NH (Tech coord) Proceedings of the symposium on fire and watershed management: October 26–28, 1988, Sacramento, California. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, pp 137–140

Rab MA (2004) Recovery of soil physical properties from compaction and soil profile disturbance caused by logging of native forest in Victorian Central Highlands, Australia. For Ecol Manage 191:329–340

Rhoades JD (1982) Cation exchange capacity. In: Page AL, Miller RH, Keeney DR (eds) Methods of soil analysis, part 2. Agron Monogr 9, Am Soc Agron, Madison, Wisconsin pp 149–157

Richards BN (1987) The microbiology of terrestrial ecosystems. Longman Scientific and Technical, Burnt Mill

Rinehart TA (2004) AFLP analysis using GeneMapper® software and an Excel® macro that aligns and converts output to binary. Biotechniques 37:186–187

Robertson GP, Sollins P, Ellis BG, Lajtha K (1999) Exchangeable ions, pH, and cation exchange capacity. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P (eds) Standard soil methods for long-term ecological research. Oxford University Press, New York, pp 106–114

Rothe A, Binkley D (2001) Nutritional interactions in mixed species forests: a synthesis. Can J For Res 31:1855–1870

Rothe A, Cromack K Jr, Resh SC, Makineci E, Son Y (2002) Soil carbon and nitrogen changes under Douglas-fir with and without red alder. Soil Sci Soc Am J 66:1988–1995

Schippers B, Bakker AW, Bakker PAHM (1987) Interactions of deleterious and beneficial rhizosphere microorganisms and the effect of cropping practices. Annu Rev Phytopathol 25:339–358. doi:10.1146/annurev.py.25.090187.002011

Sessions J, Bettinger P, Buckman R, Newton M, Hamann J (2004) Hastening the return of complex forests following fire: the consequences of delay. J For 102:38–45

Shestak CJ, Busse MD (2005) Compaction alters physical but not biological indices of soil health. Soil Sci Soc Am J 69:236–246

Simard SW (2009) The foundational role of mycorrhizal networks in self-organization of interior Douglas-fir forests. For Ecol Manage 158:S95–S107

Simpson M (2007) Forested plant associations of the Oregon East Cascades. In: USDA Forest Service, Pacific Northwest Region Tech Pap R6-NR-ECOL-TP-03-2007

Sinsabaugh RL, Klug MJ, Collins HP, Yeager PE, Petersen SO (1999) Characterizing soil microbial communities. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P (eds) Standard soil methods for long term ecological research. Oxford University Press, New York, pp 318–348

Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic, New York

Smith JE, McKay D, Brenner G, McIver J, Spatafora JW (2005) Early impacts of forest restoration treatments on the ectomycorrhizal fungal community and fine root biomass in a mixed conifer forest. J Appl Ecol 42:526–535. doi:10.1111/j.1365-2664.2005.01047.x

Smith NR, Kishchuk BE, Mohn WW (2008) Effects of wildfire and harvest disturbances on forest soil bacterial communities. Appl Environ Microbiol 74(1):216–224. doi:10.1128/aem.01355-07

Stark N (1972) Nutrient cycling pathways and litter fungi. BioScience 22:355–360

Steel RGD, Torrie JH, Dickey DA (1997) Principles and procedures of statistics: a biometrical approach, 3rd edn. WCB McGraw-Hill, Boston

Sulzman EW, Brant JB, Bowden RD, Lajtha K (2005) Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO_2 efflux in an old growth coniferous forest. Biogeochemistry 73:231–256. doi:10.1007/s10533-004-7314-6

Tabatabai MA (1994) Soil enzymes. In: Weaver RW, Angle S, Bottomley P, Bezdicek D, Smith S, Tabatabai A, Wollum A (eds) Methods of soil analysis, Part 2. Microbiological and biochemical properties—SSSA Book Series No. 5. Soil Science Society of America, Madison, pp 775–833

Talkner U, Jansen M, Beese FO (2009) Soil phosphorus status and turnover in central-European beech forest ecosystems with differing tree species diversity. Eur J Soil Sci 60:338–346

Tan X, Chang SX, Kabzems R (2005) Effects of soil compaction and forest floor removal on soil microbial properties and N transformations in a boreal forest long-term soil productivity study. For Ecol Manage 217:158–170. doi:10.1016/j.foreco.2005.05.061

Tan X, Chang SX, Kabzems R (2008) Soil compaction and forest floor removal reduced microbial biomass and enzyme activities in a boreal aspen forest soil. Biol Fert Soils 44:471–479. doi:10.1007/s00374-007-0229-3

Taylor MD (2000) Determination of total phosphorus in soil using simple Kjeldahl digestion. Commun Soil Sci Plant Anal 31:2665–2670. doi:10.1080/00103620009370616

Thompson JR, Spies TA, Ganio LM (2007) Reburn severity in managed and unmanaged vegetation in a large wildfire. Proc Natl Acad Sci USA 104(25):10743–10748. doi:10.1073/p

Tiessen H, Cueva E, Chacon P (1994) The role of soil organic matter in soil fertility. Nature 371:783–785

Torbert HA, Wood CW (1992) Effects of soil compaction and water-filled pore space on soil microbial activity and N losses. Commun Soil Sci Plan 23:1321–1331. doi:10.1080/00103629209368668

Treseder KK, Allen MF, Ruess RW, Pregitzer KS, Hendrick RL (2005) Lifespans of fungal rhizomorphs under nitrogen

fertilization in a Pinyon-Juniper woodland. Plant Soil 270:249–255

van der Heijden MGA, Bardgett RD, van Straalen NM (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett 11 (3):296–310. doi:10.1111/j.1461-0248.2007.01139.x

van der Linden AMA, Jeurissen LJJ, van Veen JA, Schippers B (1989) Turnover of soil microbial biomass as influenced by soil compaction. In: Hansen J, Henriksen K (eds) Nitrogen in organic wastes applied to soil. Academic, London, pp 25–36

Velazquez-Martinez A, Perry DA (1997) Factors influencing the availability of nitrogen in thinned and unthinned Douglas-fir stands in the central Oregon Cascades. For Ecol Manage 93:195–203. doi:10.1016/S0378-1127(96)03953-9

Wardle DA, Bardgett RD, Klironomos JN, Setala H, van der Putten WH, Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304:1629–1633. doi:10.1126/science.1094875

Waring RH, Savage T, Cromack K Jr, Rose C (1992) Thinning and nitrogen fertilization in a grand fir stand infested with western spruce budworm. Part IV: an ecosystem perspective. For Sci 38:275–286

Warren JM, Brooks JR, Meinzer FC, Eberhart JL (2008) Hydraulic redistribution of water from *Pinus ponderosa* trees to seedlings: evidence for an ectomycorrhizal pathway. New Phytol 178:382–394

White T, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic, London, pp 315–322

Yarwood SA, Myrold DD, Högberg MN (2009) Termination of belowground C allocation by trees alters soil fungal and bacterial communities in a boreal forest. FEMS Microbiol Ecol 70:151–162. doi:10.1111/j.1574-6941.2009.00733.x

Yeager CM, Northup DE, Grow CC, Barns SM, Kuske CR (2005) Changes in nitrogen-fixing and ammonia-oxidizing bacterial communities in soil of a mixed conifer forest after wildfire. Appl Environ Microbiol 71(5):2713–2722. doi:10.1128/aem.71.5.2713-2722.2005

Yildiz O, Sarginci M, Eşen D, Cromack K Jr (2007) Effects of vegetation control on nutrient removal and *Fagus orientalis*, Lipsky regeneration in the western Black Sea Region of Turkey. For Ecol Manage 240:186–194

Yildiz O, Eşen D, Karaoz OM, Sarginci M, Toprak B, Soysal Y (2010) Effects of different site preparation methods on soil carbon and nutrient removal from Eastern beech regeneration sites in Turkey's Black Sea Region. Appl Soil Ecol 45:49–55

View publication stats

Forest Ecology and Management 497 (2021) 119523

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Tamm reviews

Managing nonperennial headwater streams in temperate forests of the United States

Stephanie K. Kampf [a,*], Kathleen A. Dwire [b], Mathew P. Fairchild [c], Jason Dunham [d], Craig D. Snyder [e], Kristin L. Jaeger [f], Charles H. Luce [g], John C. Hammond [h], Codie Wilson [i], Margaret A. Zimmer [j], Marielle Sidell [a]

[a] Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO 80523, USA
[b] USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO 80526, USA
[c] USDA Forest Service, Arapaho & Roosevelt National Forests and Pawnee National Grassland, Fort Collins, CO 80526, USA
[d] U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, OR 97331, USA
[e] U.S. Geological Survey, Eastern Ecological Science Center, Kearneysville, WV 25430, USA
[f] U.S. Geological Survey, WA Water Science Center, Tacoma, WA 98402, USA
[g] USDA Forest Service, Rocky Mountain Research Station, Boise, ID 83702, USA
[h] U.S. Geological Survey, MD-DE-DC Water Science Center, Baltimore, MD 21228, USA
[i] Natural Resource Ecology Lab, Colorado State University, Fort Collins, CO 80523, USA
[j] Department of Earth and Planetary Sciences, University of California, Santa Cruz, CA 95064, USA

ARTICLE INFO

Keywords:
Headwater
Intermittent
Ephemeral
Nonperennial
Forest management
Riparian buffer

ABSTRACT

Forest management guidelines are designed to protect water quality from unintended effects of land use changes such as timber harvest, mining, or forest road construction. Although streams that periodically cease to flow (nonperennial) drain the majority of forested areas, these streams are not consistently included in forest management guidelines. This paper reviews management guidelines for nonperennial (intermittent and ephemeral) streams draining temperate forests in the continental U.S., evaluates potential impacts of land use activities on ecosystem services provided by these streams, and identifies information needed to incorporate nonperennial streams into water quality protection practices. For federally administered lands, national management guidance is deliberately nonprescriptive, deferring to regional and forest-level recommendations for both perennial and nonperennial streams. Most state guidelines recommend riparian management zone (RMZ) protection for perennial streams (48/50 states) and intermittent streams (45/50 states), but only Alaska and West Virginia require RMZs around ephemeral streams. Based on the National Hydrography Dataset, an average of 58% of forested land area in the U.S. drains to nonperennial headwater streams, making these stream types the most common connectors between forested lands and the aquatic system. Land uses that modify flow regimes in these streams can affect sediment and organic matter transport and distribution, stream temperature dynamics, and biogeochemical processing. Nonperennial streams also provide material subsidies to downstream waters and serve as temporary habitats for some aquatic species. However, limited research has examined how forest land uses affect ecosystem services and biota in these streams. Therefore we highlight a set of key questions about nonperennial streams in forests, not the least of which is simply understanding where headwater stream channels are located and associated patterns of flow duration. Although many questions remain, we also note where recent advances in data collection, modeling and process-level research provide opportunities to resolve uncertainties around nonperennial streams in forested landscapes of the continental U.S.

* Corresponding author.
E-mail addresses: stephanie.kampf@colostate.edu (S.K. Kampf), kathleen.a.dwire@usda.gov (K.A. Dwire), matthew.fairchild@usda.gov (M.P. Fairchild), jdunham@usgs.gov (J. Dunham), csnyder@usgs.gov (C.D. Snyder), kjaeger@usgs.gov (K.L. Jaeger), charles.luce@usda.gov (C.H. Luce), jhammond@usgs.gov (J.C. Hammond), codie.wilson@colostate.edu (C. Wilson), margaret.zimmer@ucsc.edu (M.A. Zimmer), marielle.sidell@colostate.edu (M. Sidell).

https://doi.org/10.1016/j.foreco.2021.119523
Received 9 April 2021; Received in revised form 4 July 2021; Accepted 7 July 2021
Available online 23 July 2021
0378-1127/© 2021 Elsevier B.V. All rights reserved.

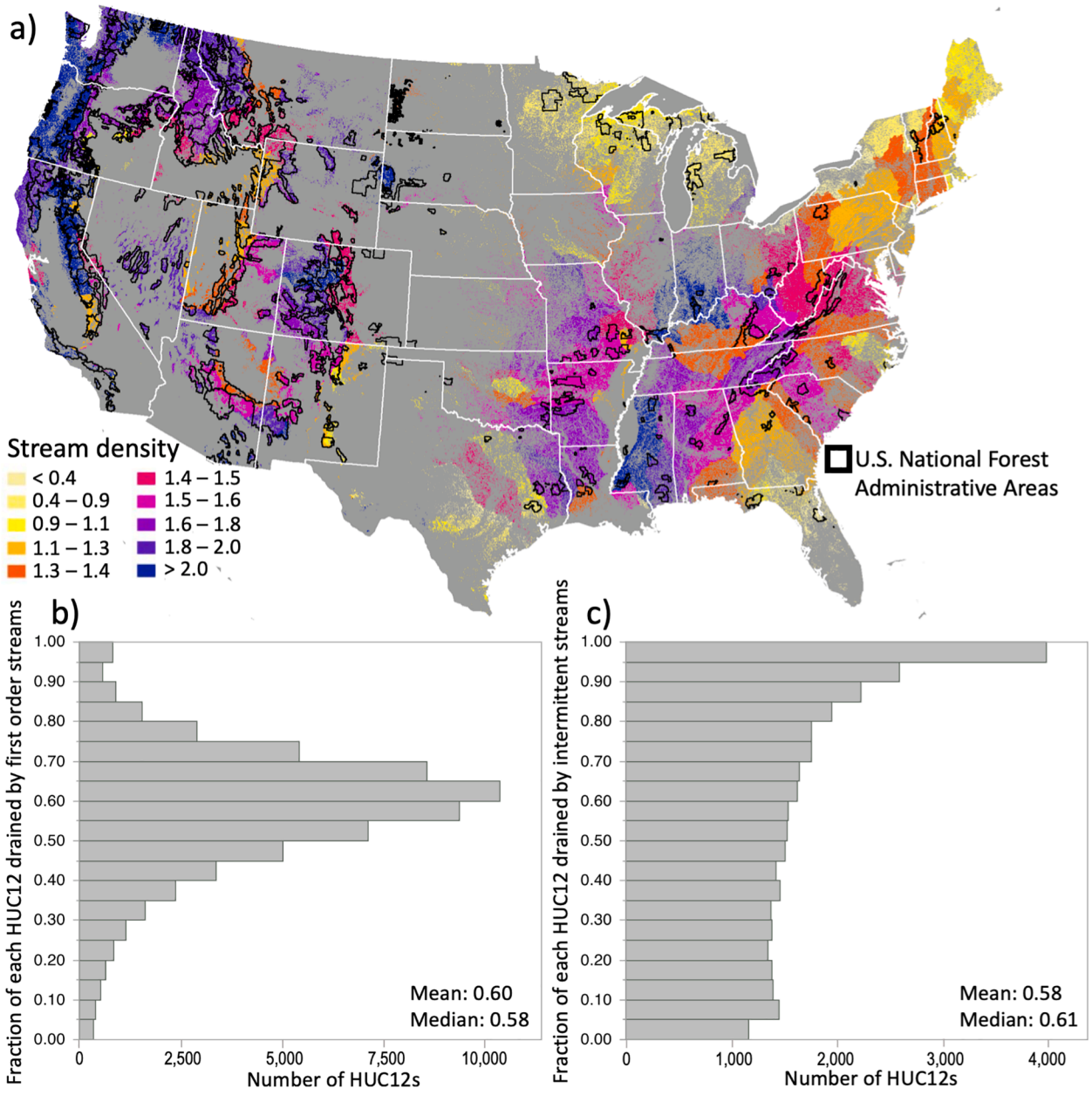


Fig. 1. Stream networks for forested watersheds of the continental U.S. showing (a) stream density (km km^{-2}), (b) fraction of forested watershed land area drained by first order headwater streams, and (c) fraction of first order streams in forested watersheds that are classified as nonperennial (intermittent or ephemeral); note that these classifications are uncertain, as described in the manuscript. Stream data from National Hydrography Dataset High Resolution (NHDHR) flowlines (USGS, 2020a) using only stream and river (Streamriver class) segments. Colored areas in (a) are forested pixels from the National Land Cover Dataset (NLCD, Yang et al., 2018), with stream densities calculated for USGS Hydrologic Unit Code (HUC) 12 watershed subdivisions aggregated to HUC4 scale for visualization. Only HUC12s with forested area > 50% are shown in (b) and (c). Black lines in (a) are boundaries of U.S. National Forest Administrative Areas. Calculations in (b) and (c) are for the same forested watersheds shown in (a), but subdivided into smaller HUC12 watershed sub-units.

1. Introduction

Forested watersheds are widely recognized as important water supply sources in temperate zones. In the United States (U.S.), streams draining land administered by the USDA Forest Service (USFS, Fig. 1a) provide more than half of the nation's water supply (Furniss et al., 2010; Brown et al., 2008). Natural resources on forested lands are managed for multiple uses such as timber harvest, grazing, mining, and recreation. Active vegetation management includes prescribed burning, pre-commercial thinning, wildfire suppression, and pesticide application. Changes in forest land uses can affect streamflow, sediment, organic matter, and thermal regimes (Wohl et al., 2015; Steel et al., 2017; Wohl et al., 2019; Segura et al., 2020), potentially disrupt aquatic and riparian ecosystems (Anderson et al., 1976; Nisbet, 2001), and ultimately degrade water quality of managed watersheds (Binkley and Brown, 1993). Accordingly, management guidelines are developed with the intent to reduce or mitigate potential impacts of land use on aquatic and riparian habitat and downstream water quality (e.g., Aust and Blinn, 2004; Ice et al., 2004; Shepard, 2006; Croke and Hairsine, 2006; Anderson and Lockaby, 2011; Cristan et al., 2016).

A major challenge for effective stream management on forested lands is lack of knowledge regarding the full extent of stream networks (Richardson and Danehy, 2007; Bishop et al., 2008). This information is critical for determining whether forest management activities will affect

Table 1
Summary of state riparian management zone (RMZ) guidelines for perennial, intermittent, and ephemeral streams, presented as number of states within each region. The states included in the four regions are shown in Fig. 3.

RMZ Details	Perennial Streams				Intermittent Streams				Ephemeral Streams			
	West Coast (n = 5)	Interior West (n = 8)	Northern (n = 24)	Southern (n = 13)	West Coast (n = 5)	Interior West (n = 8)	Northern (n = 24)	Southern (n = 13)	West Coast (n = 5)	Interior West (n = 8)	Northern (n = 24)	Southern (n = 13)
Recommended	5	7	23	13	4	7	21	13	1	1	1	1
Required by state law or statute	4	3	6	1	3	3	4	1	1	0	1	0
Adjust for adjacent slopes	3	3	12	8	3	3	13	7	1	0	0	0
Adjust for stream width	3	0	8	2	2	0	8	1	1	0	0	0
Adjust for fish	2	1	1	1	2	0	1	1	1	0	0	0
Adjust for municipal use	2	3	3	3	2	2	3	3	0	0	0	0
Allows operations within RMZ	1	5	22	13	3	5	23	13	4	8	24	13

surface water sources and downstream water quality. Locations of smaller headwater streams are often not well documented (Meyer et al., 2007; Colson et al., 2008) even though they drain the majority of land area in forests (Fig. 1b). Most current stream inventories are based on topographic maps that have limited spatial accuracy and may not correctly classify streams into perennial, intermittent, or ephemeral categories (Fritz et al., 2013; Villines et al., 2015; Hafen et al., 2020). For the purposes of this paper, we broadly define perennial streams as flowing year-round; intermittent as flowing only part of the year, with sustained groundwater contributions allowing prolonged flow, and ephemeral as flowing primarily in direct response to precipitation with variable or no inputs from shallow groundwater sources (Costigan et al., 2016; Busch et al., 2020). Collectively the intermittent and ephemeral types are nonperennial, meaning flow is not continuous in space and time (Whiting and Godsey, 2016; Jaeger et al., 2007). Current estimates indicate that these nonperennial streams make up the majority of headwater stream length in forested lands (Fig. 1c). Flow regimes in headwater streams are sensitive to changing climate (Dhungel et al., 2016), meaning that a static flow class (perennial, intermittent, ephemeral) may not capture the range of flow conditions in past, present, and future climates.

Land management decisions are based on the widely accepted premise that ecosystem services provided by streams are important, societally relevant, and worth protecting (Martin-Ortega et al., 2015; Penaluna et al., 2017). However, most of the scientific understanding of streams and their ecosystem services is based on studies of large, perennial streams (Kovach et al., 2019). Far fewer studies have focused on how land uses impact ecosystem processes in nonperennial headwater streams (e.g., Chiu et al., 2017), with fewer still attempting to relate processes in these streams to their influence on downstream perennial waters (e.g., Warrick et al., 2005). In this review we examine: (1) how current forest management guidelines apply to nonperennial streams; (2) potential impacts of forest land uses on selected processes in nonperennial streams, with a primary focus on timber harvest impacts; and (3) information needed to incorporate nonperennial streams into water quality protection practices. We focus geographically on forested headwater watersheds of the continental U.S. (CONUS) (Fig. 1a), though parts of this review may be relevant for forested watersheds across the globe.

2. Forest management guidelines for nonperennial streams

Guidelines for contemporary forest management in the U.S. are often referred to as "best" management practices (BMPs), which focus on water quality protection from nonpoint source pollution to ensure compliance with the Clean Water Act (33 U.S.C §§ 1251; Binkley and Brown, 1993; Ellefson et al., 2001). In watersheds that support rare species, guidelines also address aquatic and terrestrial habitat protection to comply with the Endangered Species Act.

A primary focus of forest management guidelines is establishing a management zone along stream segments in areas proposed for treatments to reduce chemical contamination, prevent increases in water temperature, and limit inputs of sediment, logging slash, and other large organic materials produced by forestry activities. Throughout this paper, we call these areas riparian management zones (RMZs), although many different naming conventions are used in management guidelines. On federal lands administered by the USFS, the National Core BMPs (USDA-FS, 2012) refer to streamside areas as aquatic management zones, and in regional guidance documents these areas have been termed riparian conservation areas, water influence zones, streamside management units, stream environment zones, and riparian reserves. We distinguish an RMZ from a "buffer", as some forest harvest is allowed in most RMZs, whereas "buffer" typically indicates a band of vegetation left in its pre-harvest / pre-treatment condition. The term "buffer" makes no assumptions about the composition, structure, height, or density of the vegetation left adjacent to the stream other than that it is left undisturbed by direct human activities.

On National Forests, the National Core BMPs (USDA-FS, 2012) provide general guidance for designating RMZ width and managing RMZs to protect water quality and maintain stream, aquatic, and riparian function and processes. Determining stream channel type (perennial, intermittent, ephemeral) is a key component of National Core BMP recommendations, but the guidelines are deliberately nonprescriptive, allowing managers to adapt them to local conditions. For a given region or National Forest, project-specific management plans are developed depending on local features such as presence of valued aquatic biota (e.g., species listed under the Endangered Species Act), steepness of terrain, and compliance with state, tribal, and national water quality goals. RMZ designation and BMP implementation are more prescriptively directed in forest-level management plans, with recently revised plans tending to have more specific guidance than older plans. Notable exceptions to individual forest-level or project-specific plans are the Pacific Anadromous Fish Strategy (PACFISH; U.S. Forest Service and U.S. Bureau of Land Management, 1994) and the Inland Fish Strategy (INFISH; U.S. Forest Service, 1995), which are multi-agency mandates for watershed management across vast expanses of federal lands along the Pacific Coast and in the Upper Columbia River Basin, USA. PACFISH and INFISH were developed in response to regulatory proceedings of the Endangered Species Act to protect aquatic and riparian habitat for threatened and endangered salmonid fishes. These strategies amended forest plans of 20 National Forests and 10 Bureau of Land Management Field Offices, increasing protection of intermittent streams on federal lands in the Pacific Northwest and western regions of the U.S. (Henderson et al., 2005).

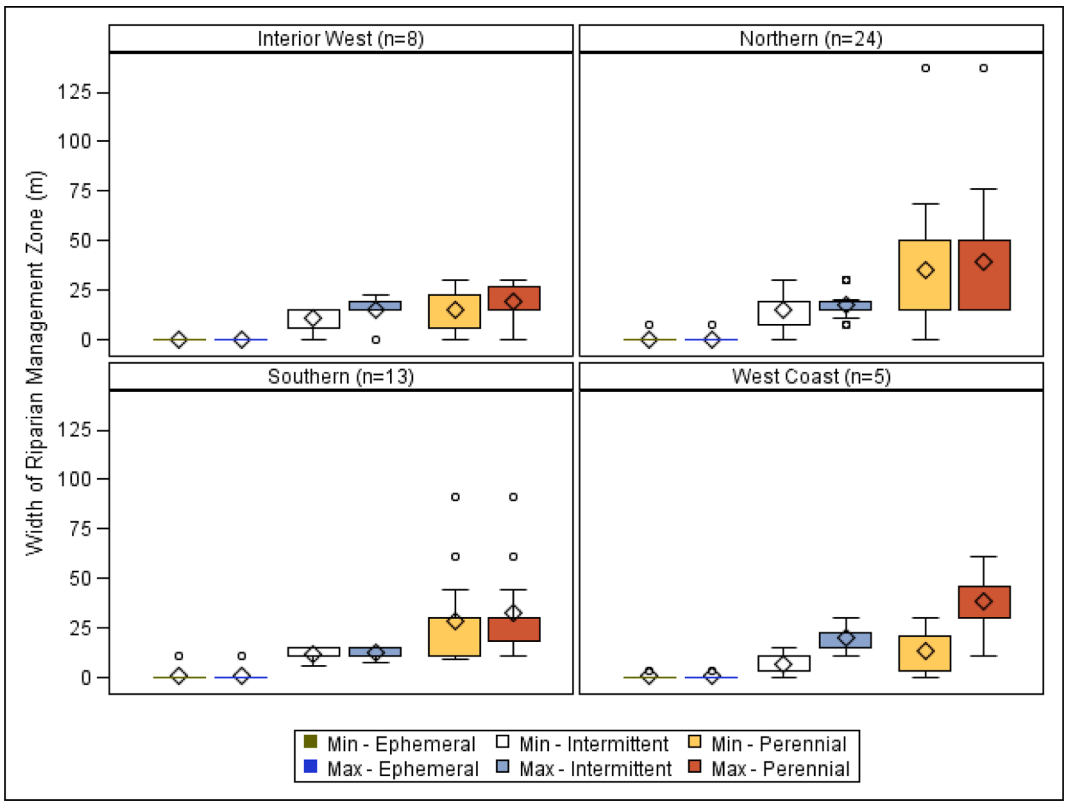


Fig. 2. Means (◊) of minimum and maximum riparian management zone (RMZ) widths surrounding ephemeral, intermittent, and perennial streams in four regions as defined by U.S. Forest Service Forest Inventory analysis (FIA, https://www.fia.fs.fed.us/regional-offices/, Fig. 3). Boxes represent the range in minimum and maximum RMZ widths among individual states in each region between the 25th and 75th percentile (the interquartile range, IQR); whiskers represent the spread of data that fall within 1.5 times the IQR, and outliers (○) are datapoints beyond 1.5 times the IQR.

Most state guidelines are more specific and prescriptive than the USFS National Core BMPs. We reviewed forest management guidelines by state and found that in most states, perennial (n = 49 states) and intermittent (n = 46 states) streams are explicitly or implicitly recognized as needing RMZ designation (Table 1). This is an increase in the number of states including intermittent streams in RMZ recommendations over the 40 that had these recommendations in 2001 (Blinn and Kilgore, 2001). Nearly all states provide forest practice guidebooks that tier to general requirements under the Clean Water Act (33 U.S.C §§ 1251), and approximately a quarter of states now have laws or statutes explicitly requiring RMZs for perennial and intermittent streams (Table 1). While 82% of states have updated guidelines over the past 20 years, only two states (Alaska, West Virginia) have revised guidelines to require RMZs for ephemeral streams; two additional states (Alabama, Montana) recommend RMZs for ephemeral streams. The minimum RMZ recommendations for intermittent streams have only changed modestly in the last two decades (Table 1).

Although we compare state guidelines using the perennial, intermittent, and ephemeral terminology (Table 1), these terms are not present in all state guidelines. For example, Washington's regulations refer to intermittent streams as "seasonal" streams. Similarly, California's guidelines include streams "capable of sediment transport", whether or not they continuously flow (California Department of Forestry and Fire Protection, 2020). Montana's streamside management zone law considers average duration of flow, with the RMZ requirements dependent on whether the streams flow fewer than six months per year (Rogers, 2006).

In most state guidelines, RMZ widths and allowable practices within RMZs are less protective for ephemeral and intermittent streams than perennial streams (Fig. 2). Recommended widths vary across regions and states depending on terrain steepness, stream size, fish occupancy, and contribution to municipal water supply (Table 1). Some state recommendations for RMZs are based on the use of the stream water (e.g., Washington, Oregon, California, Idaho, Montana), with highest level of protection for fish-bearing streams and(or) streams that are used for domestic drinking water (Washington Forest Practices Board, 2001; Oregon Department of Forestry, 2018; California Department of Forestry and Fire Protection, 2020; Barkley et al., 2015; Rogers, 2006). Where intermittent streams support fish or other species included in state guidelines, the RMZ requirements match those for perennial streams. For intermittent streams without fish, state RMZ recommendations range from including no RMZ requirement, to narrower RMZs, and in some cases RMZ widths similar to perennial streams. RMZ protections in Idaho depend on whether streamflow is present at the time of treatment operations, with reduced protection when intermittent stream channels are dry (Barkley et al., 2015). Guidelines for RMZs in Michigan vary with stream order, steepness of adjacent land, and public versus private ownership (Michigan Department of Natural Resources, 2018).

Most states allow limited harvest operations within RMZs of intermittent streams, with exceptions that prohibit some operations (Delaware, Idaho, California) or all operations (Utah, Nevada, Wisconsin, Washington, Oregon, Alaska). The requirements for retaining overstory trees can differ between intermittent and perennial streams (EMNRD, 2008; Wyoming State Forestry Division; South Carolina Forestry Commission; Stringer et al., 2018; Georgia Forestry Commission; Brogan et al., 2006; Tennessee Department of Agriculture, 2003; West Virginia Division of Forestry, 2018; Colorado State Forest Service, 2010). For ephemeral streams, some state guidelines (e.g. South Carolina, Kentucky, North Carolina, Tennessee, Michigan) recommend that disturbances be avoided within and near stream channels, but usually there are no RMZ requirements. The exception is West Virginia, which requires a reduced width RMZ for ephemeral streams as compared to

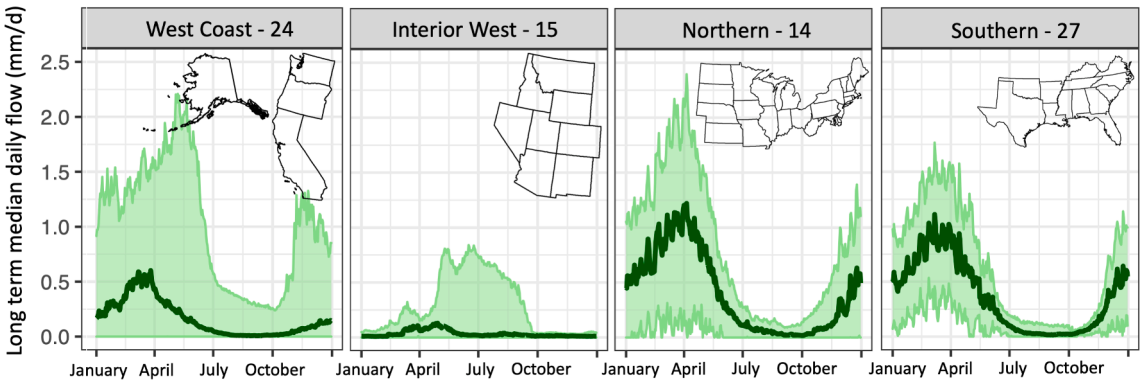


Fig. 3. Median daily flow (drainage area-normalized) for USGS reference stream gages with nonperennial flow for water years 1980–2018 (USGS, 2020b; Hammond et al., 2021). In each plot the dark line indicates the median flow for each day of year across all years of record and all nonperennial stream gages in the region, with the number above each panel indicating the number of gages used. The light green area indicates one standard deviation above and below the median. Regional subdivisions are those used by the U.S. Forest Service Forest Inventory analysis (FIA, https://www.fia.fs.fed.us/regional-offices/). Note, although Alaska and Hawaii are included in the West Coast region for Table 1 and Fig. 2, they are not part of the daily flow dataset (Hammond et al., 2021).

perennial and intermittent (West Virginia Division of Forestry, 2018). Finally, some states apply guidelines or requirements only to perennial streams (e.g., Vermont; Wilcox et al., 2019), do not specify the types of streams to consider (e.g., Nevada; Nevada State Conservation Commission, 1994; Nevada Code, 2010), or have no management guidelines at all (e.g., Arizona; Ice et al., 2004).

These varying guidelines and their level of detail regarding stream types pose contrasting management challenges. Where guidelines are explicit about the types of streams addressed in management plans, accurate information is needed on stream location, flow duration, and aquatic species present. Where guidelines are broader or more ambiguous, the decision to include a stream in a management plan is largely made at the discretion of the land manager. Management guidelines for RMZs included in state or federal forest management plans can vary in the degree to which guidelines are followed, as certain practices are considered voluntary and/or at the discretion of land managers. In other countries, examination of actual buffers used during timber harvest has shown region-wide patterns of poorly applied protections and infrequent adherence to minimum buffer guidelines for small streams when their application is voluntary or unmonitored (Kuglerová et al., 2020). Such lack of information about nonperennial stream location and use by biota could default to limited or no protection. Although BMP monitoring on federal, state, and private forest lands largely indicates the effectiveness of RMZs for perennial streams (Cristan et al., 2016), implementation and monitoring of BMPs has likely been biased toward perennial streams, given the general lack of BMP evaluation studies that focus on or even mention nonperennial streams. The variability in guidelines between states exemplifies how much management practices can vary between political jurisdictions, even though stream systems connect across political boundaries.

3. Impacts of land use and management on nonperennial forest streams

Land uses in uplands can affect streams if they change the inputs of water, sediment, and other materials to the stream network. The majority of upland area in forests drains into headwater nonperennial streams (Fig. 1b,c) rather than into higher order perennial streams, meaning that headwater nonperennial streams are often the first point of connection between uplands and stream networks. In spite of this, direct studies on the effects of land management on nonperennial streams are rare, with van Meerveld et al. (2020) recently calling nonperennial streams “Aqua temporaria incognita” to emphasize how little is known about them. In this section, we introduce how land use activities may alter streamflow regimes, sediment export, organic matter dynamics, stream temperature, and biotic ecosystems of nonperennial streams.

3.1. Streamflow regimes

3.1.1. Temporal and spatial patterns

Intermittent streamflow timing is largely driven by seasonal variability in water inputs (snowmelt, rainfall) and outputs (evapotranspiration; ET). For most streams in temperate forests of the U.S., drying is most likely during the summer and fall, when potential ET is highest (Fig. 3). In west coast forests with Mediterranean climates, the summer is commonly a time of precipitation deficit, so streams sustain flow through the summer only if they are supplied by persistent groundwater sources. Many forest streams of the drier interior West are fed by snowmelt, so highest flow is most likely during spring and summer, with driest conditions in fall and winter.

Streamflow can also be spatially intermittent, typically with reduced active (flowing) stream network extent in dry times of year. In many environments, flowing channels expand and contract seasonally, with the greatest headward extent of channels during wet times of year and (or) when ET is low (Barefoot et al., 2019; Jensen et al., 2017). Other stream networks have more stable flow locations, especially where bedrock exerts a strong control on water flow paths (Shaw, 2016; Whiting and Godsey, 2016; Lovill et al., 2018). Watersheds with varying bedrock geology may have a combination of both stable and migrating flow heads (Jaeger et al., 2007; Martin et al., 2021). Downstream of flow heads, water may move to the subsurface in stream segments with highly permeable substrates such as karst or coarse sediment deposits (Ward et al., 2018; Durighetto et al., 2020). Flow can also re-emerge downstream due to changes in channel slope, topographic convergence or valley confinement (Baxter and Hauer, 2000; Jensen et al., 2017).

3.1.2. Land use impacts

Land use activities can modify nonperennial streamflow regimes if they change the timing and/or quantity of water delivery. The timing of water delivery relates to the pathways of water from uplands to streams. In most mesic temperate forests, water reaches streams through subsurface pathways (e.g., Hewlett and Hibbert, 1967), and infiltration excess overland flow is rare. Water traveling slowly through subsurface pathways sustains flow in channels after rainfall has stopped. Land uses that reduce surface infiltration capacity can change flow paths by increasing the likelihood of infiltration excess overland flow (Wondzell and King, 2003; Larsen et al., 2009), particularly where severe ground disturbance is combined with intense rainfall (Megahan et al., 1995; Meyer and Wells, 1997; Orem and Pelletier, 2016). The ground disturbances that cause this effect may be limited to unpaved roads, skid trails

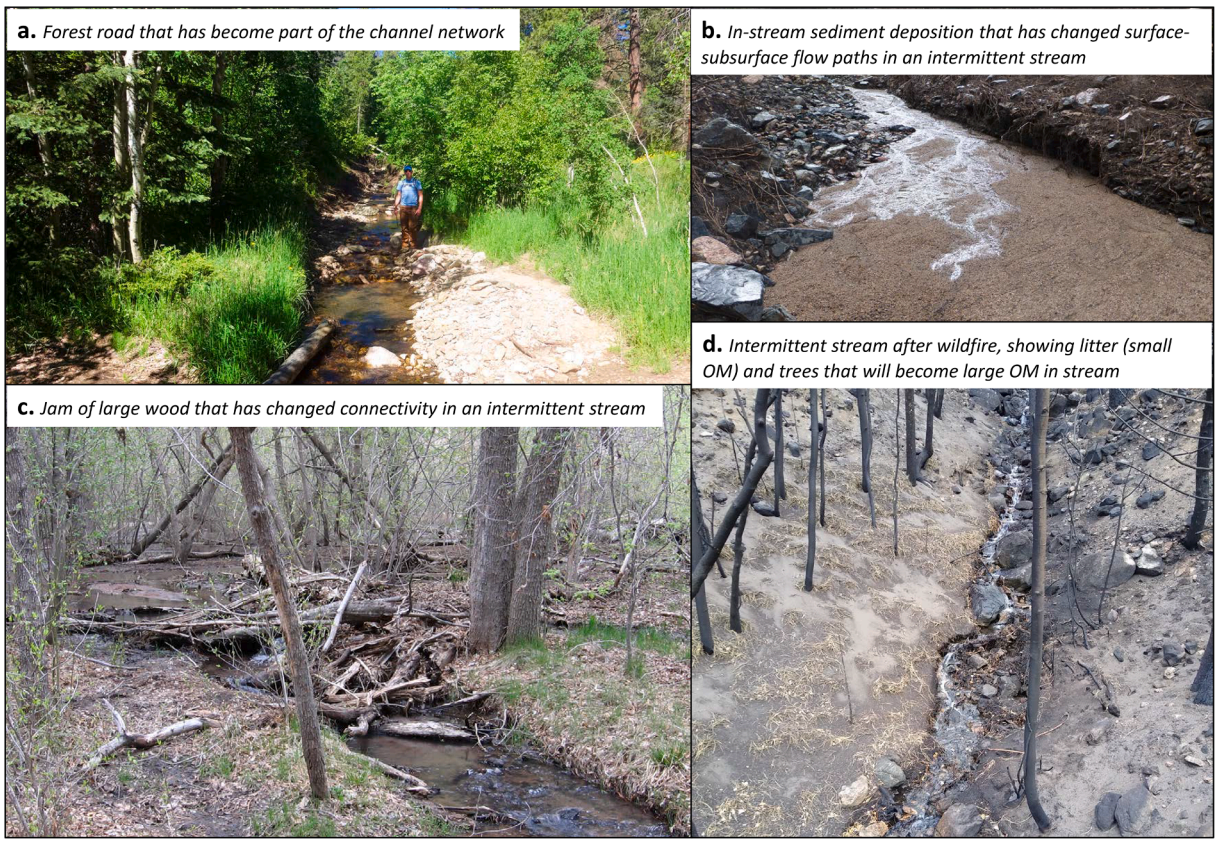


Fig. 4. Examples of nonperennial forest streams showing: (a) forest road with flowing surface water; (b) channel reach filled with recent sediment deposits, where surface flow infiltrates into the coarse sediments; (c) jam of large wood changing sediment storage and flow paths in a stream reach; (d) example of organic matter (OM) sources to stream after wildfire, including ash, litter, and eventually, burned wood when trees fall into the stream channel.

(Dickerson, 1976), or other areas where heavy equipment is operated. Cable yarding, which is commonly used for timber harvest in steep terrain, keeps heavy machinery off of slopes, and yields only small areas of compaction where logs drag. After forest harvest, a range of practices has been used historically to remove logging slash and competitive brush to prepare harvest sites for replanting, including activities like broadcast slash burning and drum chopping. Such practices can reduce infiltration and increase overland flow, at least temporarily (e.g. Hewlett and Doss, 1984; Harr et al., 1975). Post-harvest restoration activities, such as ripping or mulching skid trails and other areas disturbed by heavy equipment are now routinely used to restore infiltration capacity and reduce overland flow from disturbed patches.

Forest roads may be more permanent locations with reduced infiltration and therefore greater infiltration excess overland flow. Roads can also modify flow paths by capturing subsurface flow where roads are cut into steep slopes. Flow intercepted along cutslopes can be converted to overland flow before it would have naturally reached the stream (Wemple and Jones, 2003; Burroughs et al., 1972; Megahan, 1972; Moore and Wondzell, 2005). Depending on topography, soils, and climate, some roads capture more flow than others (Wemple and Jones, 2003; Luce, 2002). If roads capture substantial flows that are re-routed directly into streams, then the presence of roads, in effect, extends the length of the channel network, especially the nonperennial portion (Wemple et al., 1996; Croke and Mockler, 2001, Fig. 4a). By conveying overland flow rapidly to streams, roads can lead to more rapid streamflow response to rainfall.

Forest land uses can also modify the quantity of water reaching streams via changes in evapotranspiration. Trees are generally able to transpire more water than the herbaceous vegetation that grows soon after forest removal because of deeper root systems and larger leaf areas, although transpiration responses to disturbance can be highly variable (Amiro et al., 2006). The effects of changes in vegetation on streamflow have long been examined through paired catchment studies (see reviews by Bosch and Hewlett, 1982; Brown et al., 2005), which have shown that forest clear cutting over entire mesic headwater catchments leads to increases in total annual streamflow in the years immediately following forest harvest. Increases in late summer discharge have also been observed immediately after forest harvest (Perry and Jones, 2017; Robinson and Dupeyrat, 2005; Li et al., 2018) or wildfire (Kinoshita and Hogue, 2015). These types of flow changes would likely be associated with increases in flowing channel extent, with flow persisting longer in intermittent reaches.

Forest land use changes are not always detectable in streamflow, in part based on the size of the land change relative to drainage area. Prior studies have indicated that at least 20% of a catchment would need to be impacted by vegetation change before the effect would be detectable in streamflow (Bosch and Hewlett, 1982). Headwater streamflow in locations affected by vegetation change may be more sensitive than flow in larger perennial streams, for which land use changes affect a smaller portion of total drainage area. The ability to detect and quantify hydrologic effects of disturbance also depends on the magnitude of the disturbance effect relative to variability in streamflow caused by climate, and the rate and nature of vegetation recovery (Brown et al., 2005; Adams et al., 2012). Due to the heterogeneity of forest disturbances, climates, and hydrologic processes, many types and time scales of flow regime changes are possible. For example, conversion of old-growth forest to younger aged forest can cause decreased late-summer discharge in the later decades of long-running paired watershed studies because young trees may transpire more water than old-growth trees (Kuczera, 1987; Moore et al., 2004; Delzon and Loustau, 2005). Thus as forests recover from disturbance, baseflows may decline, and even be lower than the pre-disturbance condition (Perry and Jones,

2017; Segura et al., 2020; Safeeq et al., 2020; Coble et al., 2020). Natural disturbances that cause substantial forest dieoff may lead to increases, no change, or even decreases in streamflow (Adams et al., 2012; Goeking and Tarboton, 2020). Thus the effects of forest land uses on non-perennial streamflow regimes are likely to be highly variable and site-specific.

Some forested lands include areas of active or past mining, which can dramatically change the topography and alter the contributing areas to downstream rivers (Ross et al., 2016; Jaeger and Ross, 2021). Underground mining can cause land subsidence, which affects both the water reaching streams and the topographic gradients between uplands and streams (Sidle et al., 2000). In some cases, streams may be diverted below ground (Slaughter et al., 1995), while elsewhere streams may gain flow due to connections with groundwater that did not exist prior to mining (Morrison et al., 2018). The legacy effects of mining (surface and underground) and reclamation activities on streamflow patterns are highly variable and can persist for decades following mining and reclamation activities (Dickens et al., 1989; Bonta et al., 1997; Miller and Zégre, 2014). Recent modeling of reclaimed watersheds that had been surface mined indicate that changes in flow paths caused by mining would reduce streamflow during low flow periods under future climate scenarios, although this response can be mitigated by implementing different forestry reclamation approaches (Williamson and Barton, 2020).

While most forest disturbances are followed by vegetation regrowth, not all disturbances are transient. For example, although forest harvest patches are usually replanted rapidly, the road network used to access cutting units is often maintained, in which case the effects of roads on watershed hydrology persist over longer time periods. Other forest land uses such as campgrounds, day use areas, parking areas, field stations, and ski areas also have more persistent changes in forest cover. These more permanent land use conversions represent a small (<1%) portion of forested land area, but they can have localized effects on headwater streamflow regimes. For example, ski areas have been associated with sustained changes in streamflow (Wemple et al., 2007), channel network extent, and adjustments of channel morphology (David et al., 2009).

3.2. Sediment regimes

Sediment and streamflow regimes are highly inter-connected. Sediment can reach streams via erosion during overland flow, mass movements, or bank erosion (MacDonald and Coe, 2007). In undisturbed landscapes, nonperennial streams may store a large fraction of sediments produced during major storms and release these sediments gradually to downstream reaches (Dieterich and Anderson, 1998; Dewey et al., 2020), potentially limiting or moderating erosion and habitat degradation downstream. In contrast, erosion from overland flow can lead to rill and gully formation, expansion of the channel network, and more downstream sediment export (Istanbulluoglu et al., 2002; 2003; Bastola et al., 2018; Wilson et al., 2021). Although RMZs around streams are often effective at intercepting sediment from upland diffuse overland flow, concentrated flow in gullies and rills can breach RMZs (Rashin et al., 2006; Lakel et al., 2010). Where rills and gullies connect to streams, their sediment inputs can be as high as those found in streams without RMZs (Gomi et al., 2006), creating substantial changes in downstream sediment loads (Fig. 4b). If the excess overland flow that forces rill and gully incision is temporary, and vegetation recovers after disturbance, rills and gullies may disappear in a few years as side walls collapse, and channels refill with sediment (Wohl and Scott, 2017).

Roads are a ready source of chronic fine sediment to streams (Reid and Dunne, 1984; Luce and Black, 1999) and can be associated with altered stream channel morphology (Pechenick et al., 2014). Road decommissioning practices such as ripping can help restore infiltration capacity and reduce overland flow and erosion, although even after decommissioning, roads may still have reduced infiltration and elevated surface erosion compared to undisturbed forests (Luce, 1997; Sosa-Pérez and MacDonald, 2017).

Reducing surface disturbance in riparian zones is often a focus of forest management guidelines because these zones are adjacent to nearby streams. Movement of skidders or road construction equipment through riparian areas is a well-recognized source of sediment to streams, leading to restrictions on logging equipment use in RMZs (e.g. Keim and Schoenholtz, 1999). Recreational off-road vehicle use in riparian areas and stream crossings can also elevate sediment delivery to streams (e.g. Marion et al., 2014), particularly activities like “mudding” (a recreational activity involving driving off-road vehicles through mud) that disrupt soils and promote erosion of fine sediments.

Mass movements are another cause of changing sediment regimes in stream networks, in some cases leading to the greatest geomorphic changes following vegetation removal in steep uplands (Montgomery et al., 2000; Jackson and Roering, 2009). The frequency of mass movements can increase after logging (Sidle et al., 1985; Brardinoni et al., 2003; Benda et al., 2005) and along forest roads (Wemple et al., 2001; Montgomery, 1994). The sediment evacuated from steep terrain may cause substantial channel reorganization downstream by diverting or blocking channels, forming deposition fans or sediment wedges, and leading to changes in channel form (Hoffman and Gabet, 2007; Benda, 1990; Benda and Dunne, 1997). Mass movements can also lead to establishment of new channel heads by creating zones of groundwater flow convergence (Dietrich and Dunne, 1993; McNamara et al., 2006). While landslides and debris flows can be large sediment sources in many areas with steep topography, they are episodic and infrequent. Chronic, smaller magnitude sediment production is often dominated by bank erosion (Hassan et al., 2005).

Changes in the patterns of deposition and scour along streams may affect patterns of flow intermittency by shifting how water moves between the surface and subsurface. For example, deposition of fine-textured sediment within a stream can reduce hydraulic conductivity of the channel bed and hyporheic exchange with groundwater (Wharton et al., 2017). Locations of large sediment deposits can become zones of water infiltration and reduced flow duration (Ward et al., 2018; Fig. 4b).

3.3. Organic matter

Organic matter (OM) inputs to headwaters may come from wind-thrown trees, litter fall from riparian and upland vegetation, overland flow or mass wasting, leachate from organic matter in the subsurface, and dispersal of soil and canopy fauna into streams (Wipfli et al., 2007). Riparian inputs of OM per unit stream area generally decrease with increasing stream size (Conners and Naiman, 1984), making OM input particularly important in headwater streams. As with sediments, headwater nonperennial streams tend to store large amounts of OM relative to similar sized perennial streams (Dieterich and Anderson, 1998; Acuña et al., 2004), Moreover, OM decomposition rates in nonperennial streams tend to be slower due to low microbial growth rates and little physical breakdown during dry periods, as well as reduced densities of macroinvertebrate shredders (Richardson, 1990; Sabater et al., 2016). However, during flowing conditions, the resulting large standing stocks of accumulated benthic OM become available to downstream perennial reaches either gradually through seasonal flow or episodically during storm events, potentially providing increased stability to the detrital-based food webs in headwater stream networks over annual or decadal time periods (Richardson et al., 2005; Larned et al., 2010).

Coarse organic material in the form of large branches, logs, chunks of wood, and roots, can directly influence channel morphology and sediment characteristics (Fig. 4c). Studies on coarse OM specific to nonperennial streams are extremely sparse (but see Wohl et al, 2018; Galia et al., 2020 for drier climates), though prior research on forested headwater streams may not have distinguished between perennial and nonperennial streams (e.g., May and Gresswell, 2003). Because many nonperennial streams are headwaters with lower flow and smaller channel dimensions, they tend to retain much of the coarse wood that



Fig. 5. Thin RMZ retained around a nonperennial stream in an area of timber harvest.

falls in them, and more of it may initially be suspended over channels. However, episodic flash flood and debris flow events can transport substantial volumes of wood out of these channels to downstream reaches. Given the nature of these processes, we might expect the wood balance of nonperennial streams to be dominated by local inputs and decomposition, but some may occasionally release large pulses of accumulated wood to downstream segments. The changes in channel morphology caused by large wood can alter in-channel biological communities, sediment storage, and the movement and transformation of nutrients and other materials (Blaen et al., 2018; Short et al., 2015; Wipfli et al., 2007).

Smaller forms of organic material, including particulate and dissolved OM, contribute to local and downstream metabolic processes and carbon cycling (Richardson, 2019a; 2019b), with dissolved OM most likely to be transported downstream. Fine particulate and dissolved OM can be derived from direct instream growth or allochthonous inputs from riparian vegetation. Macroinvertebrates are primary consumers of fine particulate OM, and they may subsequently become food for predators. The presence of these invertebrates and therefore the breakdown of OM may be reduced when nonperennial streams are dry (Datry et al., 2011), with heterogeneous decomposition as flow paths become fragmented (Abril et al., 2016). Multiple studies have found that stream wetting and drying patterns also affect dissolved organic carbon dynamics (von Schiller et al., 2015; Hale and Godsey, 2019). Dissolved OM is available to microorganisms and constitutes a demand for oxygen that can limit habitat suitability in some intermittent streams (Larsen and Woelfle-Erskine, 2018).

Land use activities can affect all forms of OM input with subsequent implications for in-channel or downstream OM processes. The primary mechanisms of change are: 1) altering the proximal forest canopy that provides OM inputs to the stream (Fig. 4d); 2) increasing sunlight on the stream allowing greater algal growth, and 3) altering dissolved organic carbon inputs from runoff and shallow groundwater inputs from adjacent forests. Direct removal of vegetation adjacent to stream channels will substantially reduce particulate OM until vegetation regrows (Webster et al., 1992), with an even longer delay for large wood inputs (Bilby and Likens, 1980; Verry et al., 1999). Log jams may become century-scale legacies of past riparian harvest on large OM (Wohl and Goode, 2008). Roots from streamside trees also influence channel morphology; root loss after forest harvest can lead to bank failure, which can impact sediment storage and surface water expression. Changes in dissolved organic carbon inputs to streams from adjacent forest areas through runoff and leaching have complex responses to harvest, with reports of both increases and decreases depending on initial organic matter loads in the stand, moisture dynamics, changes in temperature, and time following harvest (e.g. Meyer and Tate, 1983; Laudon et al., 2011; Schelker et al., 2013; Lajtha and Jones, 2018).

3.4. Temperature

Perennial streams have been the primary focus of stream temperature research, although their temperature dynamics may be quite different from those of smaller nonperennial headwater streams (Moore et al., 2005). High stream temperatures are a water quality concern because they can limit habitat suitability for aquatic species. High stream temperatures are most likely during warmer seasons with lower flow where incoming solar radiation is a dominant energy source (Webb and Zhang, 1997, Roon et al., 2021). Consequently, loss of riparian canopy from timber harvest, removals of hazard trees, or other activities can lead to increases in warm season stream temperature (e.g. Poole and Berman, 2001).

Concerns over solar radiation and stream heating have been a primary motivation for suggesting or requiring RMZs along perennial streams. However, there have been many questions about the utility of RMZs for nonperennial channels, leading to inconsistent, optional, or ineffective application of RMZs . One example is the “compromise” of using narrower RMZs for harvest around nonperennial channels since there seems to be no “stream” to shade, and offering some nod to other values from riparian forests. Unfortunately, the riparian forest does not exist independently of the surrounding forest stand, and the thin strips prescribed for RMZs around nonperennial streams may be more vulnerable to blowdown (e.g. Jackson et al., 2001 and Fig. 5).

In some forest headwater streams, flow is supplied by shallow groundwater inputs and has relatively little opportunity for heating along the channel; in these locations, stream temperatures may be less sensitive to increased solar energy inputs from harvest or fire (e.g. Story

et al., 2003; Janisch et al., 2012; Kelleher et al., 2011; Mayer, 2012; Luce et al., 2014). Even under low flow conditions in nonperennial channels, surface water heating by solar radiation may be limited if the water is sourced by groundwater and is spatially intermittent. In some cases, subsurface flow maintains longitudinal connectivity along channels even as surface water becomes separated into disconnected pools (e.g. Ward et al., 2018). Because solar heating of subsurface water is relatively minor (e.g. Story et al., 2003), shallow groundwater inflow can cool stream temperatures during summer (Wigington et al., 2006; Larsen and Woelfle-Erskine, 2018). This can allow surface water along spatially intermittent streams and stream junctions with seemingly "dry" channels to provide locally cold habitat (Ebersole et al., 2001; Snyder et al., 2015). Temperatures of shallow subsurface water can also be sensitive to land use change such as loss of canopy to harvest or wildfire; however, the warming of groundwater is generally less than the direct warming of stream water by increased solar radiation, so even the warmed shallow groundwater inputs are still a cooling influence on peak stream temperatures (Guenther et al., 2014).

Because of the importance of groundwater for stream temperature, activities that change surface–subsurface exchanges of water along stream corridors can influence temperature regimes. Compaction of ephemeral channels during harvest (e.g. Burns, 1972), siltation of the streambed reducing down-valley transmissivity, and channel scour removing the hyporheic zone (e.g. Dunham et al., 2007) can each reduce hyporheic zone subsurface flow. This forces more flowing water to be exposed on the surface to solar radiation. Less is known about overland flow influences on stream temperatures during rain storms in forested ecosystems, although this can cause temperature spikes during summer rains in urban systems (e.g. Nelson and Palmer, 2007). Although these examples provide some insight into how disturbance may affect nonperennial stream temperatures, there is neither a formal framework nor substantial focused research on temperature in headwater nonperennial streams and their overall contribution to thermal regimes downstream perennial reaches.

3.5. Biota

Headwaters, including nonperennial streams, are vital components of upland ecosystems, potentially regulating the spatial and temporal distribution of suitable physical environmental conditions and ecosystem processes that influence terrestrial and aquatic biota (Richardson and Danehy, 2007; Studinski et al., 2012). Consequently, human-induced changes to the landscape that alter the amount, predictability, spatial distribution, and connectivity of headwater habitats can affect not only the species that intermittently use or inhabit these periodically dry stream channels, but also the species downstream in the perennial stream network (Datry et al., 2014; Leibowitz et al., 2018). Here we focus on the importance of nonperennial streams for aquatic biodiversity in general and then consider influences downstream specifically for fish, which are often the focus of management guidelines.

At the reach scale, nonperennial streams typically support lower aquatic macroinvertebrate and fish species diversity than perennial reaches due to the effects of drying on habitat availability (Poff and Ward, 1989; Stanley et al., 1997). However, recent evidence suggests that when semi-aquatic and terrestrial flora and fauna are included, biodiversity within and adjacent to nonperennial reaches is often equal to or higher than that observed for comparable perennial reaches, particularly in landscapes where seasonal drying is predictable and extensive (Larned et al., 2010). For instance, in arid landscapes, nonperennial stream valleys are oases that frequently support more productive and diverse vegetative communities than the surrounding uplands, although the processes behind these responses are not entirely clear (Katz et al., 2012). In turn, these communities create more favorable microclimates that provide primary habitat, breeding areas, temporary refuges, and movement and migration corridors for biota. Nonperennial streams can be important habitats for terrestrial invertebrates, amphibians, reptiles, birds, and mammals (Corti and Datry, 2016; Sánchez-Montoya et al., 2017).

Across river networks, nonperennial stream habitats can have a disproportionately high influence on beta- and regional diversity of both aquatic macroinvertebrate (Valente-Neto et al., 2020) and fish (Rogosch and Olden, 2019) communities. Although not fully understood, the patterns of aquatic community diversity at least partly depend on complex interactions between the length of the drying period, the spatial topology of drying within river drainages, and the predictability of drying over time (Sánchez-Montoya et al., 2018), all of which are vulnerable to changing land use. The distributions of lotic (flowing water), lentic (isolated pools), and terrestrial (dry) habitats shift seasonally thereby increasing habitat heterogeneity. Differences in communities in each phase of wetting and drying increase biodiversity at larger scales over annual cycles (Datry et al., 2014; Stubbington et al., 2017). Where seasonal drying is predictable, it can exert strong selection pressures that favor specialized behavioral, morphological, physiological, or life history adaptations that increase tolerance or resilience to drying (Lytle and Poff, 2004; Walters, 2011), sometimes resulting in higher rates of endemism and regional biodiversity (Meyer et al., 2007).

Despite the importance of nonperennial streams in maintaining biodiversity, management guidelines have focused primarily on the extent to which headwater habitats are used by fish or influence fish downstream. The role of nonperennial streams for fish has not been extensively studied in forested ecosystems (Richardson and Danehy, 2007), although in arid portions of the U.S. fish are strongly dependent on them (Minckley and Deacon, 1991; Perkin et al., 2017). Here we highlight a selected range of examples across forested ecosystems in the U.S. that demonstrate the importance of nonperennial streams for fish.

Although fish are often absent from nonperennial streams during low flow periods, several studies indicate that they do use intermmittent streams seasonally. In the northwestern U.S., fish, including salmon and trout, are known to track stream network expansions (Erman and Hawthorne, 1976; Woelfle-Erskine et al., 2017; Wigington et al., 2006). Erman and Hawthorne (1976) reported that 39–47% of nonnative rainbow trout (*O. mykiss*) spawned in a single intermittent tributary to a perennial stream in the eastern Sierra Nevada Mountains. In this study, researchers found that egg incubation, emergence, and emigration of juveniles to perennial streams occurs within the seasonal window when nonperennial streams are flowing. Emigration from these systems has not been studied extensively, but one study of eight native fish species in forested streams of the southeastern U.S. reported that the probability of emigration increased as stream networks contracted, and stream flows became intermittent (Albanese et al., 2004).

Use of nonperennial streams by many fish species in forested systems can pose important tradeoffs. These streams represent a large area of potential habitat, thus supplementing what is available to fish within the perennial network (Schlosser, 1995). In some cases, use of intermittent portions of the network allows species to avoid adverse ecological interactions with members of their own species (e.g. intraspecific competition) or other species more characteristic of the perennial network (Meyer et al., 2007). However, use of intermittent streams by fish entails risks, such as the chance that stream segments will become disconnected, dry, or otherwise unsuitable. For example, Hwan and Carlson (2016) reported that increasing intermittency was associated with declining survival in juvenile trout and salmon in a northern California stream. Thus it is not clear when use of nonperennial streams represents a net benefit to fish (e.g., Battin, 2004; Richardson, 2019a; 2019b). More research is needed to evaluate the costs and benefits of use of nonperennial streams by fish and other biota as well as the role of these streams in providing habitat and supplying cold water or trophic subsidies for different species in the context of the full range of stream types in a channel network (Richardson and Danehy, 2007; Ebersole et al., 2015).

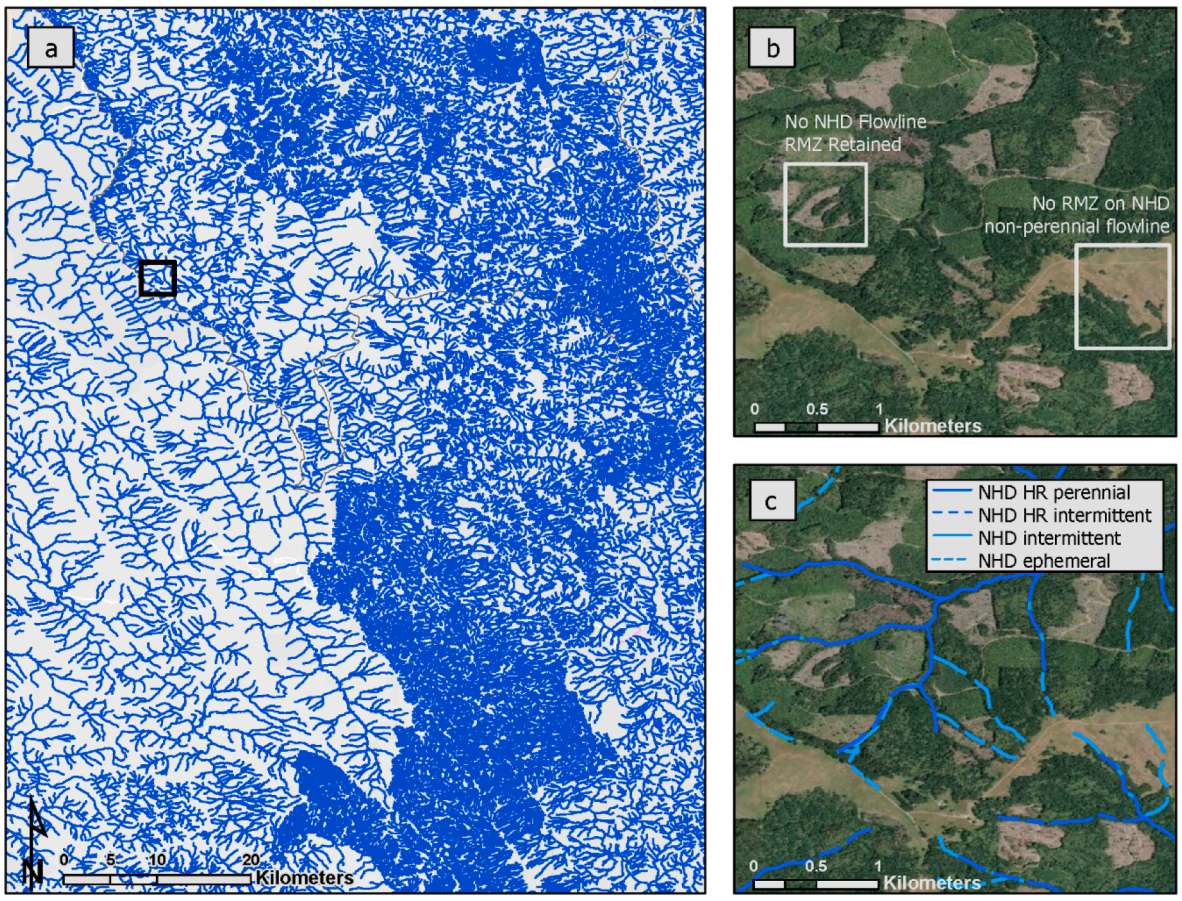


Fig. 6. Example challenges in using geospatial datalayers for management plans: (a) Inconsistencies in mapped stream density within the NHD dataset; (b and c) examples of RMZs compared to NHD HR flowlines. Some flowlines have no evident RMZ, which could be because no stream was evident in the field along these channel segments. Other locations have RMZs even though the NHD does not indicate a flowline.

4. Incorporating nonperennial streams into forest management plans

Our review and others highlight some examples of water, sediment, and organic matter connectivity between stream types and the importance of nonperennial streams for aquatic biota (Fritz et al., 2018; Leibowitz et al., 2018). Because of this connectivity, integration of nonperennial streams into forest management decisions would provide more protection for stream networks. The key aspect of management we have highlighted in this review is RMZs. Determining where to establish RMZs involves: (1) identifying nonperennial stream locations; and (2) determining stream flow duration.

A stream channel is an incised feature with a defined bed and banks (Dietrich and Dunne, 1993) generally with evidence of scour or sediment deposition from recent surface flow (Montgomery and Dietrich, 1988). If flowing water is not present, evidence of recent flow may include fluvially transported sediments, dried algae, or mesic vegetation that is distinct in species composition and(or) phenology compared to surrounding areas. In many nonperennial channels, these features are clearly visible; however, determining if a feature is a true channel is more ambiguous in other areas. For example, legacy gullies can persist for decades to centuries on the landscape without active flow; they have defined beds and banks but no recently transported sediments. Transient saturated areas may not have any clear incised channel feature (Rashin et al., 2006), even though they clearly have surface and groundwater connectivity to downstream channels. Thus the interpretation of channel presence/absence might require subjective decisions about the sensitivity of the feature to disturbance and its possible downstream impacts. For example, if a legacy gully is downstream of a heavily disturbed area that could produce infiltration excess overland flow, then an RMZ might help prevent reactivation of the gully.

Channel locations are frequently obtained from geospatial datasets. In the U.S., stream network maps are available from the National Hydrography Dataset in both Medium Resolution (NHD MR, 30 m) and High Resolution (NHD HR, 10 m) (https://www.usgs.gov/core-science-systems/ngp/national-hydrography). Because of the finer resolution of the NHD HR, this dataset generally includes more headwater streams, often considerably more. While NHD datasets are useful for illustrating regional differences in stream types (Fig. 1), they were not created in the same way across the country and can have boundary effects where stream densities vary between adjacent watersheds (Fig. 6). Field evaluations of these flow lines have found that they miss headwater streams in some regions, with prior studies reporting > 200% lower stream lengths in high resolution NHD compared to observations (Fritz et al., 2013; Villines et al., 2015; Fig. 6), while over-representing the stream network extent in others (Martin et al., 2021). There is an active stewardship program specifically aimed at updating stream information (https://www.usgs.gov/core-science-systems/ngp/national-hydrography/stewardship-and-community), and managers conducting field visits can therefore update NHD based on more detailed field reconnaissance of streams.

In addition to NHD flowlines, topographic and other geospatial data may be used to estimate stream channel locations. Techniques for mapping channels from topographic data include statistical and terrain morphology methods that search for incised features (Passalacqua et al., 2010; Sofia et al., 2011; Clubb et al., 2014; Hooshyar et al., 2016), flow routing algorithms (e.g., Moore and Grayson, 1991; Costa-Cabral and Burges, 1994; Tarboton, 1997), and topographic wetness indices (e.g.,

Beven and Kirkby, 1979; Barling et al., 1994; Hjerdt et al., 2004). These approaches have been combined with surface water features to estimate depth to groundwater, saturated areas, and potential expansion areas of surface channel networks (de Alwis et al., 2007; Ågren et al., 2015). However, topographic data alone are often insufficient for mapping stream channel networks accurately (e.g., Helmlinger et al., 1993; Orlandini et al., 2011; Hastings and Kampf, 2014) because they can miss the heterogeneity in flowpaths caused by variability in subsurface properties or by storage, infiltration, or barriers along surface flow paths (Bracken and Croke, 2007). Consequently, to design effective management plans, field site visits are usually necessary to identify surface water flow paths and their connectivity to downstream waters.

If project planning stratifies RMZs by stream channel type (perennial, intermittent, ephemeral), correctly identifying stream type poses an additional challenge. The NHD provides channel type classes, which were mainly derived from the cartographer stream type interpretation for USGS 1:24,000 topographic maps. These maps generally used solid lines for perennial streams and dashed lines for intermittent and ephemeral streams (Fishburn and Allord, 2017). Although these classes are often the best available information, classification accuracy is a notable concern because of the potential geographic inconsistencies in methods used to identify intermittent and ephemeral streams (Fig. 6). Stream type determinations are, in many cases, decades old and no longer accurate (Hafen et al., 2020).

Decisions about whether or not to apply RMZs to headwater nonperennial streams face several trade-offs. Where stream networks are dense, meaning a high length of stream per area (Fig. 1a), applying RMZs to all streams may be costly or infeasible; on the other hand, preferentially applying RMZs only to certain types of streams may require more extensive field work to determine stream type during project planning. The subjectivity in determining stream types may partly explain why implementation of RMZs is not always well aligned with management guidelines (Kuglerová et al., 2020; Fritz et al., 2020). Further, in cases of severe disturbance, erosion and mass movements can lead to creation of new channels that would not have been mapped as channels using pre-disturbance field assessments or topographic data. Thus, in addition to identifying pre-disturbance channels, managers could aim to identify locations that could develop flow and sediment connections to downstream waters. This may include topographic hollows likely to saturate during wet conditions or steep convergent slopes susceptible to rilling and gullying. Rather than prescribing fixed RMZ requirements by channel type, management plans could build on holistic watershed assessment and emphasize interventions most likely to minimize stream changes across the full channel network. Because of the heterogeneity and complexity of hydrological processes, it may not be realistic to identify fixed guidelines that apply to all landscapes. This implies the need for managers to be trained in the field, where they can observe flow locations and patterns and develop management guidelines that are most appropriate for each unique landscape.

5. Conclusions

Nonperennial headwater streams are ubiquitous on forested lands, comprising the majority of stream length. While these streams clearly influence physical and biotic processes throughout stream networks, they have proven challenging to address in a management context. Even basic information regarding the locations of nonperennial stream channels and their geomorphic and hydrologic persistence remains difficult to resolve. Accordingly, policies for managing nonperennial streams vary widely. To facilitate the path forward to addressing these issues, we conclude with a list of key questions that emerge from this review:

1. How can we identify locations within forested watersheds that are most likely to develop surface flow connectivity to stream channels after disturbance?

RMZs are most needed in locations that may produce overland flow and surface erosion after land disturbance. We need observations from streams in a variety of landscapes to determine what factors drive upland-stream connectivity and stream network expansion, both in undisturbed conditions and following different types of chronic and episodic disturbances.

2. What are the most effective methods for accurately identifying locations of stream channels and categorizing their flow durations on managed forests?

New developments in remote sensing, ground-based surveys, physically-based models and statistical models offer promising new opportunities to address this most basic question about nonperennial streams (review in Shanafield et al., 2021). Targeted efforts through community sourced field data on headwater streams (Kampf et al., 2018; Njue et al., 2019), including qualitative flow/no flow observations, can be a useful approach to meet data scarcity challenges in this portion of the stream network where streams are abundant, but data are limited. Widespread data collection is needed to improve maps of nonperennial streams across the broad range of physiographic conditions in forests.

3. To what extent do changes in flow, sediment, organic matter, and temperature regimes in nonperennial channels propagate downstream?

Nonperennial stream processes affect the larger perennial streams that are often the focus of management plans. Spatial and temporal dynamics of stream ecosystem components are inter-connected across stream networks. System-level research is needed to explore these dynamic processes in a variety of forest and stream types, both with and without management interventions.

4. To what extent do species of concern rely on nonperennial headwater streams?

Responses of aquatic and semi-aquatic species to nonperennial stream changes are difficult to anticipate, as their dependencies on these streams have not been well-studied. This equates to uncertainty regarding the vulnerability and adaptive capacity of these species to changing climate (e.g., Kovach et al. 2019) and a need for studies examining reliance of species on different stream types.

5. Where recommended, how are best management practices applied in managed forests near nonperennial streams, and how effective are these practices for protecting water quality and ecosystem services?

Relative to perennial streams, evaluations of BMP implementation for nonperennial streams are lacking. Additional monitoring studies are needed to examine RMZ effectiveness across the range of stream types and RMZ sizes. Such studies could inform decisions about which management practices to apply along nonperennial streams.

6. How will changing climate, particularly shifts in temperature and precipitation regimes, impact the spatial and temporal distribution of nonperennial streams, and how will semi-aquatic and aquatic species respond?

Nonperennial streams are sensitive to changes in temperature and precipitation, with shifts towards increased drying more likely in locations with reduced snowpack and/or reduced summer precipitation (e.g. Godsey et al. 2014; Kormos et al. 2016; Wuebbles et al. 2017). In contrast, locations with increasing precipitation / decreasing aridity may experience longer flow durations (Hammond et al., 2021). These climate-induced streamflow changes are not directly within land manager control, but understanding them is essential for developing

management strategies that maintain the resilience of streams to change. Improved understanding of all aspects of climate vulnerability in these systems could help managers craft effective climate adaptation strategies (Crausbay et al. 2020).

These broad questions have yet to be investigated systematically for nonperennial forested stream networks. Addressing them can help inform practical issues related to identifying stream types as well as shape future management guidelines. Although current management practices in the U.S. tend to include more protections for perennial than nonperennial streams, protecting nonperennial source waters may be most beneficial for the channel network as a whole because these streams are often the first point of connection between uplands and the aquatic system. Any stream in a channel network has the potential to impact ecosystem services in downstream reaches, so excluding nonperennial headwater streams from management plans can mean missing a substantial source of potential impairment to receiving waters. Streams are not static features but rather adjust to conditions within the watershed and the episodic disturbances that shape channel form. This means that streamside management in forests requires adaptive approaches that address both current and potential future changes along stream corridors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Thanks to Steve Wondzell, Ken Fritz, Sherri Johnson, Catalina Segura, Than Hitt, and Joe Wagenbrenner for contributions to conceptualization and feedback on earlier versions of this work. Thanks also to L. Kuglerová, M. Vanderhoof, and two anonymous reviewers for helpful suggestions.

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

References

U.S.C §§ 1251, Clean Water Act of 1972. Accessed at https://www.govinfo.gov/content/pkg/USCODE-2018-title33/pdf/USCODE-2018-title33-chap26.pdf.

Abril, M., Muñoz, I., Menéndez, M., 2016. Heterogeneity in leaf litter decomposition in a temporary Mediterranean stream during flow fragmentation. Sci. Total Environ. 553, 330–339. https://doi.org/10.1016/j.scitotenv.2016.02.082.

Acuña, V., Giorgi, A., Muñoz, I., Uehlinger, U., Sabater, S., 2004. Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. Freshwater Biol. 49 (7), 960–971.

Adams, H.D., Luce, C.H., Breshears, D.D., Allen, C.D., Weiler, M., Hale, V.C., Smith, A.M. S., Huxman, T.E., 2012. Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. Ecohydrology 5, 145–159. https://doi.org/10.1002/eco.233.

Ågren, A.M., Lidberg, W., Ring, E., 2015. Mapping temporal dynamics in a forest stream network—implications for riparian forest management. Forests 6 (9), 2982–3001. https://doi.org/10.3390/f6092982.

Albanese, B., Angermeier, P.L., Dorai-Raj, S., 2004. Ecological correlates of fish movement in a network of Virginia streams. Can. J. Fish. Aquat. Sci. 61 (6), 857–869. https://doi.org/10.1139/f04-096.

Amiro, B.D., Barr, A.G., Black, T.A., Iwashita, H., Kljun, N., McCaughey, J.H., Morgenstern, K., Murayama, S., Nesic, Z., Orchansky, A.L., Saigusa, N., 2006. Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada. Agric. Forest Meteorol. 136 (3–4), 237–251. https://doi.org/10.1016/j.agrformet.2004.11.012.

Anderson, C.J., Lockaby, B.G., 2011. The effectiveness of forestry best management practices for sediment control in the southeastern United States: a literature review. South. J. Appl. For. 35 (4), 170–177. https://doi.org/10.1093/sjaf/35.4.170.

Anderson, H.W., Hoover, M.D. & Reinhart, K.G., 1976. Forests and water: effects of forest management on floods, sedimentation, and water supply (Vol. 18). Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station.

Aust, W.M., Blinn, C.R., 2004. Forestry best management practices for timber harvesting and site preparation in the eastern United States: An overview of water quality and productivity research during the past 20 years (1982–2002). Water Air Soil Pollut. Focus 4 (1), 5–36.

Barefoot, E., Pavelsky, T.M., Allen, G.H., Zimmer, M.A., McGlynn, B.L., 2019. Temporally variable stream width and surface area distributions in a headwater catchment. Water Resour. Res. 55 (8), 7166–7181. https://doi.org/10.1029/2018WR023877.

Barkley, Y.C., Brooks, R., Keefe, R., Kimsey, M., McFarland, A., Schnepf, C., 2015. Idaho Forest Best Management Practices Field Guide: Using BMPs to Protect Water Quality. University of Idaho Extension.

Barling, R.D., Moore, I.D., Grayson, R.B., 1994. A quasi-dynamic wetness index for characterizing the spatial-distribution of zones of surface saturation and soil–water content. Water Resour. Res. 30, 1029–1044. https://doi.org/10.1029/93WR03346.

Bastola, S., Dialynas, Y.G., Bras, R.L., Noto, L.V., Istanbulluoglu, E., 2018. The role of vegetation on gully erosion stabilization at a severely degraded landscape: a case study from Calhoun Experimental Critical Zone Observatory. Geomorphology 308, 25–39. https://doi.org/10.1016/j.geomorph.2017.12.032.

Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conserv. Biol. 18 (6), 1482–1491. https://doi.org/10.1111/j.1523-1739.2004.00417.x.

Baxter, C.V., Hauer, F.R., 2000. Geomorphology, hyporheic exchange and selection of spawning habitat by bull trout (Salvelinus confluentus). Can. J. Fish. Aquat. Sci. 57, 1470–1481. https://doi.org/10.1139/f00-056.

Benda, L., 1990. The influence of debris flows on channels and valley floors in the Oregon Coast Range, USA. Earth Surf. Proc. Land. 15 (5), 457–466. https://doi.org/10.1002/esp.3290150508.

Benda, L., Dunne, T., 1997. Stochastic forcing of sediment routing and storage in channel networks. Water Resour. Res. 33 (12), 2865–2880. https://doi.org/10.1029/97WR02387.

Benda, L., Hassan, M.A., Church, M., May, C.L., 2005. Geomorphology of steepland headwaters: the transition from hillslopes to channels 1. JAWRA Journal of the American Water Resources Association 41 (4), 835–851. https://doi.org/10.1111/j.1752-1688.2005.tb03773.x.

Beven, K.J., Kirkby, M.J., 1979. A physically based variable contributive area model of basin hydrology. Hydrol. Sci. Bull. 24, 43–69. https://doi.org/10.1080/02626667909491834.

Bilby, R.E., Likens, G.E., 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61 (5), 1107–1113. https://doi.org/10.2307/1936830.

Binkley, D., Brown, T.C., 1993. Forest practices as nonpoint sources of pollution in North America 1. JAWRA 29 (5), 729–740. https://doi.org/10.1111/j.1752-1688.1993.tb03233.x.

Bishop, K., Buffam, I., Erlandsson, M., Folster, J., Laudon, H., Seibert, J., Temnerud, J., 2008. Aqua Incognita: the unknown headwaters. Hydrol. Processes 22 (8), 1239.

Blaen, P.J., Kurz, M.J., Drummond, J.D., Knapp, J.L., Mendoza-Lera, C., Schmadel, N.M., Klaar, M.J., Jäger, A., Folegot, S., Lee-Cullin, J., Ward, A.S., Zarnetske, J.P., Datry, T., Milner, A.M., Hannah, D.M., Krause, S., 2018. Woody debris is related to reach-scale hotspots of lowland stream ecosystem respiration under baseflow conditions. Ecohydrology 11 (5), e1952. https://doi.org/10.1002/eco.1952.

Blinn, C.R., Kilgore, M.A., 2001. Riparian management practices: a summary of state guidelines. J. Forest. 99 (8), 11–17. https://doi.org/10.1093/jof/99.8.11.

Bosch, J.M., Hewlett, J.D., 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. J. Hydrol. 55 (1–4), 3–23. https://doi.org/10.1016/0022-1694(82)90117-2.

Bonta, J.V., Amerman, C.R., Harlukowicz, T.J., Dick, W.A., 1997. Impact of coal surface mining on three Ohio watersheds. JAWRA J. Am. Water Resour. Assoc. 33 (4), 907–917.

Bracken, L.J., Croke, J., 2007. The concept of hydrological connectivity and its contribution to understanding runoff-dominated geomorphic systems. Hydrol. Process.: Int. J. 21 (13), 1749–1763. https://doi.org/10.1002/hyp.6313.

Brardinoni, F., Hassan, M.A., Slaymaker, H.O., 2003. Complex mass wasting response of drainage basins to forest management in coastal British Columbia. Geomorphology 49 (1–2), 109–124. https://doi.org/10.1016/S0169-555X(02)00166-6.

Brogan, S., Gerow, T., Gregory, J.D., Gueth, M., Hamilton, R., Hughes, K.M., Swartley, W., Swift, L., 2006. North Carolina Forestry Best Management Practices Manual to Protect Water Quality. Service publication FM-01-06, North Carolina Forest.

Brown, A.E., Zhang, L., McMahon, T.A., Western, A.W., Vertessy, R.A., 2005. A review of paired catchment studies for determining changes in water yield resulting from alterations in vegetation. J. Hydrol. 310 (1–4), 28–61. https://doi.org/10.1016/j.jhydrol.2004.12.010.

Brown, T.C., Hobbins, M.T., & Ramirez, J.A., 2008. Spatial Distribution of Water Supply in the Coterminous United States. Journal of the American Water Resources Association 44(6):1474-1487. DOI: 10.1111/j.1752-1688.2008.00252.x.

Burns, J.W., 1972. Some effects of logging and associated road construction on northern California streams. Trans. Am. Fish. Soc. 101 (1), 1–17. https://doi.org/10.1577/1548-8659(1972)101<1:SEOLAA>2.0.CO;2.

Burroughs Jr., E.R., Marsden, M.A., Haupt, H.F., 1972. Volume of snowmelt intercepted by logging roads. J. Irrigat. Drain. Divis. 98 (IR1), 1–12.

Busch, M.H., Costigan, K.H., Fritz, K.M., Datry, T., Krabbenhoft, C.A., Hammond, J.C., Zimmer, M., Olden, J.D., Burrows, R.M., Dodds, W.K., Boersma, K.S., Shanafield, M., Kampf, S.K., Mims, M.C., Bogan, M.T., Ward, A.S., Perez Rocha, M., Godsey, S., Allen, G.H., Blaszczak, J.R., Jones, C.N., Allen, D.C., 2020. What's in a name? Patterns, trends, and suggestions for defining non-perennial rivers and streams. Water 12, 1980. https://doi.org/10.3390/w12071980.

California Department of Forestry and Fire Protection, 2020. California Forest Practice Rule, Title 14, California Code of Regulations, Ch.4,4.5,10. https://bof.fire.ca.gov/media/9478/2020-forest-practice-rules-and-act_final_ada.pdf.

Chiu, M.-C., Leigh, C., Mazor, R., Cid, N., Resh, V., 2017. Anthropogenic threats to intermittent rivers and ephemeral streams. In: Datry, T., Bonada, N., Boulton, A. (Eds.), Intermittent Rivers and Ephemeral Streams: Ecology and Management. Academic Press, London, pp. 433–454. https://doi.org/10.1016/B978-0-12-803835-2.00017-6.

Clubb, F.J., Mudd, S.M., Milodowski, D.T., Hurst, M.D., Slater, L.J., 2014. Objective extraction of channel heads from high-resolution topographic data. Water Resour. Res. 50 (5), 4283–4304. https://doi.org/10.1002/2013WR015167.

Coble, A.A., Barnard, H., Du, E., Johnson, S., Jones, J., Keppeler, E., Kwon, H., Link, T.E., Penaluna, B., Reiter, M. & River, M., 2020. Long-term hydrological response to forest harvest during seasonal low flow: Potential implications for current forest practices. Science of The Total Environment, p.138926. DOI: 10.1016/j.scitotenv.2020.138926.

Colorado State Forest Service, 2010. Forestry Best Management Practices to Protect Water Quality in Colorado. https://static.colostate.edu/client-files/csfs/pdfs/ForestryBMP-CO-2010.pdf.

Colson, T., Gregory, J., Dorney, J., Russell, P., 2008. Topographic and soil maps do not accurately depict headwater stream networks. Natl. Wetlands Newsletter 30 (3), 25–28.

Conners, M.E., Naiman, R.J., 1984. Particulate allochthonous inputs: relationships with stream size in an undisturbed watershed. Can. J. Fish. Aquat. Sci. 41 (10), 1473–1484. https://doi.org/10.1139/f84-181.

Corti, R., Datry, T., 2016. Terrestrial and aquatic invertebrates in the riverbed of an intermittent river: parallels and contrasts in community organisation. Freshw. Biol. 61, 1308–1320. https://doi.org/10.1111/fwb.12692.

Costa-Cabral, M., Burges, S.J., 1994. Digital elevation model networks (DEMON): A model of flow over hillslopes for computation of contributing areas and dispersal areas. Water Resour. Res. 30 (6), 1681–1692. https://doi.org/10.1029/93WR03512.

Costigan, K.H., Jaeger, K.L., Goss, C.W., Fritz, K.M., Goebel, P.C., 2016. Understanding controls on flow permanence in intermittent rivers to aid ecological research: integrating meteorology, geology and land cover. Ecohydrology 9 (7), 1141–1153. https://doi.org/10.1002/eco.1712.

Crausbay, S.D., Betancourt, J., Bradford, J., Cartwright, J., Dennison, W.C., Dunham, J., Enquist, C.A., Frazier, A.G., Hall, K.R., Littell, J.S., Luce, C.H., 2020. Unfamiliar territory: emerging themes for ecological drought research and management. One Earth 3 (3), 337–353. https://doi.org/10.1016/j.oneear.2020.08.019.

Cristan, R., Aust, W.M., Bolding, M.C., Barrett, S.M., Munsell, J.F., Schilling, E., 2016. Effectiveness of forestry best management practices in the United States: literature review. For. Ecol. Manage. 360, 133–151. https://doi.org/10.1016/j.foreco.2015.10.025.

Croke, J., Mockler, S., 2001. Gully initiation and road-to-stream linkage in a forested catchment, southeastern Australia. Earth Surf. Proc. Land. 26 (2), 205–217. https://doi.org/10.1002/1096-9837(200102)26:2<205::AID-ESP168>3.0.CO;2-G.

Croke, J.C., Hairsine, P.B., 2006. Sediment delivery in managed forests: a review. Environ. Rev. 14 (1), 59–87. https://doi.org/10.1139/a05-016.

Datry, T., Corti, R., Claret, C., Philippe, M., 2011. Flow intermittence controls leaf litter breakdown in a French temporary alluvial river: the “drying memory”. Aquat. Sci. 73 (4), 471–483. https://doi.org/10.1007/s00027-011-0193-8.

Datry, T., Larned, S.T., Klement, T., 2014. Intermittent rivers: a challenge for freshwater ecology. Bioscience 64, 229–235. https://doi.org/10.1093/biosci/bit027.

David, G.C., Bledsoe, B.P., Merritt, D.M., Wohl, E., 2009. The impacts of ski slope development on stream channel morphology in the White River National Forest, Colorado, USA. Geomorphology 103 (3), 375–388. https://doi.org/10.1016/j.geomorph.2008.07.003.

de Alwis, D.A., Easton, Z.M., Dahlke, H.E., Philpot, W.D., Steenhuis, T.S., 2007. Unsupervised classification of saturated areas using a time series of remotely sensed images. Hydrol. Earth Syst. Sci. 11, 1609–1620. https://doi.org/10.5194/hess-11-1609-2007.

Delzon, S., Loustau, D., 2005. Age-related decline in stand water use: sap flow and transpiration in a pine forest chronosequence. Agric. For. Meteorol. 129 (3–4), 105–119. https://doi.org/10.1016/j.agrformet.2005.01.002.

Dewey, J., Hatten, J., Choi, B., Mangum, C., Ouyang, Y., 2020. Climate drives and sources of sediment and organic matter fluxes in intermittent rivers and ephemeral streams of a subtropical watershed, USA. Climate 8 (10), 117. https://doi.org/10.3390/cli8100117.

Dickens, P.S., Minear, R.A., Tschantz, B.A., 1989. Hydrologic alteration of mountain watersheds from surface mining. J. (Water Pollution Control Federation) 1249–1260.

Dickerson, B.P., 1976. Soil compaction after tree-length skidding in northern Mississippi. Soil Sci. Soc. Am. J. 40 (6), 965–966. https://doi.org/10.2136/sssaj1976.03615995004000060043x.

Dieterich, M., Anderson, N.H., 1998. Dynamics of abiotic parameters, solute removal and sediment retention in summer-dry headwater streams of western Oregon. Hydrobiologia 379, 1–15.

Dietrich, W.E., Dunne, T., 1993. The channel head. Channel Network Hydrol. 175–219.

Dhungel, S., Tarboton, D.G., Jin, J., Hawkins, C.P., 2016. Potential effects of climate change on ecologically relevant streamflow regimes. River Res. Appl. 32 (9), 1827–1840.

Dunham, J.B., Rosenberger, A.E., Luce, C.H., Rieman, B.E., 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. Ecosystems 10, 335–346.

Durighetto, N., Vingiani, F., Bertassello, L. E., Camporese, M., & Botter, G., 2020. Intraseasonal Drainage Network Dynamics in a Headwater Catchment of the Italian Alps. Water Resources Research, 56(4), e2019WR025563. DOI: 10.1029/2019WR025563.

Ebersole, J., Liss, W., Frissell, C., 2001. Relationship between stream temperature, thermal refugia and rainbow trout Oncorhynchus mykiss abundance in arid-land streams in the northwestern United States. Ecol. Freshw. Fish 10 (1), 1–10. https://doi.org/10.1034/j.1600-0633.2001.100101.x.

Ebersole, J.L., Wigington Jr, P.J., Leibowitz, S.G., Comeleo, R.L., Sickle, J.V., 2015. Predicting the occurrence of cold-water patches at intermittent and ephemeral tributary confluences with warm rivers. Freshwater Science 34 (1), 111–124.

Ellefson, P.V., Kilgore, M.A., & Phillips, M.J., 2001. Monitoring Compliance with BMPs: The Experience of State Forestry Agencies. Journal of Forestry, Volume 99, Issue 1, January 2001, Pages 11–17, https://doi.org/10.1093/jof/99.1.11.

Energy, Minerals and Natural Resources Department (EMNRD), 2008. New Mexico Forest Practices Guidelines. http://www.emnrd.state.nm.us/SFD/ForestMgt/documents/ForestPracticesGuidelines2008.pdf.

Erman, D.C., Hawthorne, V.M., 1976. The quantitative importance of an intermittent stream in the spawning of rainbow trout. Trans. Am. Fish. Soc. 105 (675–68), 1. https://doi.org/10.1577/1548-8659(1976)105<675:TQIOAI>2.0.CO;2.

Fishburn, K.A., Allord, G.J., 2017. Historical Topographic Map Collection bookmark: U. S. Geol. Survey General Informat. Product 179, 2 p. https://doi.org/10.3133/gip179.

Fritz, K.M., Hagenbuch, E., D’Amico, E., Reif, M., Wigington Jr, P.J., Leibowitz, S.G., Comeleo, R.L., Ebersole, J.L., Nadeau, T.L., 2013. Comparing the extent and permanence of headwater streams from two field surveys to values from hydrographic databases and maps. JAWRA J. Am. Water Resour. Assoc. 49 (4), 867–882. https://doi.org/10.1111/jawr.12040.

Fritz, K.M., Schofield, K.A., Alexander, L.C., McManus, M.G., Golden, H.E., Lane, C.R., Pollard, A.I., 2018. Physical and chemical connectivity of streams and riparian wetlands to downstream waters: a synthesis. JAWRA Am. Water Resour. Assoc. 54 (2), 323–345. https://doi.org/10.1111/1752-1688.12632.

Fritz, K.M., Nadeau, T.L., Kelso, J.E., Beck, W.S., Mazor, R.D., Harrington, R.A., Topping, B.J., 2020. Classifying streamflow duration: the scientific basis and an operational framework for method development. Water 12 (9), 2545. https://doi.org/10.3390/w12092545.

Furniss, M.J., Staab, B.P., Hazelhurst, S., Clifton, C.F., Roby, K.B., Ilhardt, B.L., Larry, E. B., Todd, A.H., Reid, L.M., Hines, S.J., Bennett, K.A., Luce, C.H. & Edwards, P.J., 2010. Water, climate change, and forests: Watershed stewardship for a changing climate. USFS Pacific Northwest Research Station General Technical Report PNW-GTR-812.

Galia, T., Macurová, T., Vardakas, L., Škarpich, V., Matušková, T., Kalogianni, E., 2020. Drivers of variability in large wood loads along the fluvial continuum of a Mediterranean intermittent river. Earth Surf. Proc. Land. 45 (9), 2048–2062.

Georgia Forestry Commission, Water Quality Program, Georgia’s Best Management Practices for Forestry, 2019. https://gatrees.org/wp-content/uploads/2020/02/BMP-Manual-2019-Web.pdf.

Godsey, S.E., Kirchner, J.W., Tague, C.L., 2014. Effects of changes in winter snowpacks on summer low flows: case studies in the Sierra Nevada, California, USA. Hydrol. Process. 28, 5048–5064.

Goeking, S.A., Tarboton, D.G., 2020. Forests and water yield: A synthesis of disturbance effects on streamflow and snowpack in western coniferous forests. J. Forest. 118 (2), 172–192. https://doi.org/10.1093/jofore/fvz069.

Gomi, T., Sidle, R., Noguchi, S., Negishi, J., Nik, A., Sasaki, S., 2006. Sediment and wood accumulations in humid tropical headwater streams: effects of logging and riparian buffers. For. Ecol. Manage. 224 (1–2), 166–175.

Guenther, S., Gomi, T., Moore, R., 2014. Stream and bed temperature variability in a coastal headwater catchment: influences of surface-subsurface interactions and partial-retention forest harvesting. Hydrol. Process. 28, 1238–1249.

Hafen, K.C., Blasch, K.W., Rea, A., Sando, R., Gessler, P.E., 2020. The Influence of climate variability on the accuracy of NHD perennial and nonperennial stream classifications. JAWRA J. Am. Water Resour. Assoc. 56 (5), 903–916. https://doi.org/10.1111/1752-1688.12871.

Hale, R.L., Godsey, S.E., 2019. Dynamic stream network intermittence explains emergent dissolved organic carbon chemostasis in headwaters. Hydrol. Process. 33 (13), 1926–1936. https://doi.org/10.1002/hyp.13455.

Hammond, J.C., Zimmer, M., Shanafield, M., Kaiser, K., Godsey, S.E., Mims, M.C., Zipper, S.C., Burrows, R.M., Kampf, S.K., Dodds, W., Jones, C.N., Krabbenhoft, C.A., Boersma, K.S., Datry, T., Olden, J.D., Allen, G.H., Price, A.N., Costigan, K., Hale, R., Ward, A.S., Allen, D.C., 2021. Spatial patterns and drivers of non-perennial flow regimes in the contiguous United States. Geophys. Res. Lett. 48 (2), e90794 https://doi.org/10.1029/2020GL090794.

Harr, R.D., Harper, W.C., Krygier, J.T., Hsieh, F.S., 1975. Changes in storm hydrographs after road building and clear-cutting in the Oregon Coast Range. Water Resour. Res. 11 (3), 436–444. https://doi.org/10.1029/WR011i003p00436.

Hassan, M.A., Church, M., Lisle, T.E., Brardinoni, F., Benda, L., Grant, G.E., 2005. Sediment transport and channel morphology of small, forested streams. J. Am. Water Resour. Assoc. (JAWRA) 41 (4), 853–876. https://doi.org/10.1111/j.1752-1688.2005.tb03774.x.

Hastings, B.E., Kampf, S.K., 2014. Evaluation of digital channel network derivation methods in a glaciated subalpine catchment. Earth Surf. Proc. Land. 39 (13), 1790–1802. https://doi.org/10.1002/esp.3566.

Helmlinger, K.R., Kumar, P., Foufoula-Georgiou, E., 1993. On the use of digital elevation model data for Hortonian and fractal analyses of channel networks. Water Resour. Res. 29 (8), 2599–2613. https://doi.org/10.1029/93WR00545.

Henderson, R.C.; Archer, E. K., Bouwes, B. A., Coles-Ritchie, M. S., Kershner, J. L. 2005. PACFISH/INFISH Biological Opinion (PIBO): Effectiveness Monitoring Program seven-year status report 1998 through 2004. Gen. Tech. Rep. RMRS-GTR-162. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 16 p.

Hewlett, J.D., Hibbert, A.R., 1967. Factors affecting the response of small watersheds to precipitation in humid areas. Forest Hydrol. 1, 275–290.
Hewlett, J.D., Doss, R., 1984. Forests, floods, and erosion: a watershed experiment in the southeastern Piedmont. Forest Sci. 30 (2), 424–434. https://doi.org/10.1093/forestscience/30.2.424.
Hjerdt, K.N., McDonnell, J.J., Seibert, J., Rodhe, A., 2004. A new topographic index to quantify downslope controls on local drainage. Water Resour. Res. 40, W05602. https://doi.org/10.1029/2004WR003130.
Hoffman, D.F., Gabet, E.J., 2007. Effects of sediment pulses on channel morphology in a gravel-bed river. GSA Bulletin 119 (1–2), 116–125. https://doi.org/10.1130/B25982.1.
Hooshyar, M., Wang, D., Kim, S., Medeiros, S.C., Hagen, S.C., 2016. Valley and channel networks extraction based on local topographic curvature and k-means clustering of contours. Water Resour. Res. 52 (10), 8081–8102. https://doi.org/10.1002/2015WR018479.
Hwan, J.L., Carlson, S.M., 2016. Fragmentation of an intermittent stream during seasonal drought: intra-annual and interannual patterns and biological consequences. River Res. Appl. 32 (5), 856–870. https://doi.org/10.1002/rra.2907.
Ice, G., Dent, L., Robben, J., Cafferata, P., Light, J., Sugden, B., Cundy, T., 2004. Programs assessing implementation and effectiveness of state forest practice rules and BMPs in the West. Water Air Soil Pollut. Focus 4 (1), 143–169.
Istanbulluoglu, E., Tarboton, D.G., Pack, R.T., Luce, C.H., 2002. A probabilistic approach for channel initiation. Water Resour. Res. 38 (12), 1325. https://doi.org/10.1029/2001WR000782.
Istanbulluoglu, E., Tarboton, D.G., Pack, R.T., Luce, C.H., 2003. A sediment transport model for incising gullies on steep topography. Water Resour. Res. 39 (4), 1103. https://doi.org/10.1029/2002WR001467.
Jackson, C.R., Sturm, C.A., Ward, J.M., 2001. Timber harvest impacts on small headwater stream channels in the coast ranges of washington. JAWRA Journal of the American Water Resources Association 37, 1533–1549.
Jackson, M., Roering, J.J., 2009. Post-fire geomorphic response in steep, forested landscapes: oregon Coast Range, USA. Quat. Sci. Rev. 28 (11–12), 1131–1146. https://doi.org/10.1016/j.quascirev.2008.05.003.
Jaeger, K.L., Montgomery, D.R., Bolton, S.M., 2007. Channel and perennial flow initiation in headwater streams: management implications of variability in source-area size. Environ. Manage. 40 (5), 775.
Jaeger, K.L., Ross, M.R.V., 2021. Identifying geomorphic process domains in the synthetic landscapes of West Virginia, USA. J. Geophys. Res. Earth Surf. e2020JF005851 https://doi.org/10.1029/2020JF005851.
Janisch, J.E., Wondzell, S.M., Ehinger, W.J., 2012. Headwater stream temperature: interpreting response after logging, with and without riparian buffers, Washington, USA. Forest Ecology and Management, DOI:10.1016/j.foreco.2011.12.035.
Jensen, C.K., McGuire, K.J., Prince, P.S., 2017. Headwater stream length dynamics across four physiographic provinces of the Appalachian Highlands. Hydrol. Process. 31 (19), 3350–3363. https://doi.org/10.1002/hyp.11259.
Kampf, S., Strobl, B., Hammond, J., Anenberg, A., Etter, S., Martin, C., Puntenney-Desmond, K., Seibert, J., van Meerveld, I., 2018. Testing the waters: mobile apps for crowdsourced streamflow data. EoS, 99 (2018), http://doi.org/10.1029/2018EO096355.
Katz, G.L., Denslow, M.W., Stromberg, J.C., 2012. The Goldilocks effect: Intermittent streams sustain more plant species than thoses with perennial or ephemeral flow. Freshw. Biol. 57, 467–480. https://doi.org/10.1111/j.1365-2427.2011.02714.x.
Keim, R.F., Schoenholtz, S.H., 1999. Functions and effectiveness of silvicultural streamside management zones in loessial bluff forests. For. Ecol. Manage. 118 (1–3), 197–209. https://doi.org/10.1016/S0378-1127(98)00499-X.
Kelleher, C., Wagener, T., Gooseff, M., McGlynn, B., McGuire, K., Marshall, L., 2011. Investigating controls on the thermal sensitivity of Pennsylvania streams. Hydrol. Process. 26 (5), 771–785. https://doi.org/10.1002/hyp.8186.
Kinoshita, A.M., Hogue, T.S., 2015. Increased dry season water yield in burned watersheds in Southern California. Environ. Res. Lett. 10 https://doi.org/10.1088/1748-9326/10/1/014003.
Kormos, P., Luce, C., Wenger, S.J., Berghuijs, W.R., 2016. Trends and sensitivities of low streamflow extremes to discharge timing and magnitude in pacific northwest mountain streams. Water Resour Res. 52, 4990–5007. https://doi.org/10.1002/2015WR018125.
Kovach, R.P., Dunham, J.B., Al-Chokhachy, R., Snyder, C.D., Letcher, B.H., Young, J.A., Beever, E.A., Pederson, G.T., Lynch, A.J., Hitt, N.P., Konrad, C.P., 2019. An integrated framework for ecological drought across riverscapes of North America. Bioscience 69 (6), 418–431. https://doi.org/10.1093/biosci/biz040.
Kuczera, G., 1987. Prediction of water yield reductions following a bushfire in ash-mixed species eucalypt forest. J. Hydrol. 94 (3–4), 215–236. https://doi.org/10.1016/0022-1694(87)90054-0.
Kuglerová, L., Jyväsjärvi, J., Ruffing, C., Muotka, T., Jonsson, A., Andersson, E., Richardson, J.S., 2020. Cutting Edge: A Comparison of Contemporary Practices of Riparian Buffer Retention Around Small Streams in Canada, Finland, and Sweden. Water Resources Research, 56(9), e2019WR026381. DOI: 10.1029/2019WR026381.
Lajtha, K., Jones, J., 2018. Forest harvest legacies control dissolved organic carbon export in small watersheds, western Oregon. Biogeochemistry 140, 299–315.
Lakel III, W.A., Aust, W.M., Bolding, M.C., Dolloff, C.A., Keyser, P., Feldt, R., 2010. Sediment trapping by streamside management zones of various widths after forest harvest and site preparation. Forest Sci. 56 (6), 541–551. https://doi.org/10.1093/forestscience/56.6.541.
Larned, S.T., Datry, T., Arscott, D.B., Tockner, K., 2010. Emerging concepts in temporary-river ecology. Freshw. Biol. 5, 717–738. https://doi.org/10.1111/j.1365-2427.2009.02322.x.
Larsen, I.J., MacDonald, L.H., Brown, E., Rough, D., Welsh, M.J., Pietraszek, J.H., Libohova, Z., de Dios Benavides-Solorio, J., Schaffrath, K., 2009. Causes of post-fire runoff and erosion: water repellency, cover, or soil sealing? Soil Sci. Soc. Am. J. 73 (4), 1393–1407. https://doi.org/10.2136/sssaj2007.0432.
Larsen, L.G., Woelfle-Erskine, C., 2018. Groundwater is key to salmonid persistence and recruitment in intermittent Mediterranean-climate streams. Water Resour. Res. 54 (11), 8909–8930. https://doi.org/10.1029/2018WR023324.
Laudon, H., Sponseller, R.A., Lucas, R.W., Futter, M.N., Egnell, G., Bishop, K., Ågren, A., Ring, E., Högberg, P., 2011. Consequences of more intensive forestry for the sustainable management of forest soils and waters. Forests 2, 243–260.
Leibowitz, S.G., Wigington Jr., P.J., Schofield, K.A., Alexander, L.C., Vanderhoof, M.K., Golden, H.E., 2018. Connectivity of streams and wetlands to downstream waters: An integrated systems framework. J. Am. Water Resour. Assoc. 1–25 https://doi.org/10.1111/1752-1688.12631.
Li, Q., Wei, X., Zhang, M., Liu, W., Giles-Hansen, K., Wang, Y., 2018. The cumulative effects of forest disturbance and climate variability on streamflow components in a large forest-dominated watershed. J. Hydrol. 557, 448–459. https://doi.org/10.1016/j.jhydrol.2017.12.056.
Lovill, S.M., Hahm, W.J., Dietrich, W.E., 2018. Drainage from the critical zone: Lithologic controls on the persistence and spatial extent of wetted channels during the summer dry season. Water Resour. Res. 54 (8), 5702–5726. https://doi.org/10.1029/2017WR021903.
Luce, C.H., Black, T.A., 1999. Sediment production from forest roads in western oregon. Water Resour. Res. 35 (8), 2561–2570. https://doi.org/10.1029/1999WR900135.
Luce, C.H., 1997. Effectiveness of road ripping in restoring infiltration capacity of forest roads. Restor. Ecol. 5 (3), 265–270. https://doi.org/10.1046/j.1526-100X.1997.09731.x.
Luce, C.H., 2002. Hydrological processes and pathways affected by forest roads: what do we still need to learn? Hydrol. Process. 16 (1), 2901–2904. https://doi.org/10.1002/hyp.5061.
Luce, C.H., Staab, B., Kramer, M., Wenger, S., Isaak, D., McConnell, C., 2014. Sensitivity of summer stream temperatures to climate variability in the pacific northwest. Water Resour. Res 50 (4), 3428–3443. https://doi.org/10.1002/2013WR014329.
Lytle, D.A., Poff, N.L., 2004. Adaptation to natural flow regimes. Trends Ecol. Evol. 19, 94–100. https://doi.org/10.1016/j.tree.2003.10.002.
MacDonald, L.H., Coe, D., 2007. Influence of headwater streams on downstream reaches in forested areas. Forest Science 53 (2), 148–168. https://doi.org/10.1093/forestscience/53.2.148.
Marion, D.A., Phillips, J.D., Yocum, C., Mehlhope, S.H., 2014. Stream channel responses and soil loss at off-highway vehicle stream crossings in the Ouachita National Forest. Geomorphology 216, 40–52. https://doi.org/10.1016/j.geomorph.2014.03.034.
Martin, C., Kampf, S.K., Hammond, J.C., Wilson, C., Anderson, S.P., 2021. Controls on streamflow densities in semiarid rocky mountain catchments. Water 13 (4), 521. https://doi.org/10.3390/w13040521.
Martin-Ortega, J., Ferrier, R.C., Gordon, I.J., Khan, S., 2015. Water Ecosystem Services: A Global Perspective. UNESCO Publishing.
May, C.L., Gresswell, R.F., 2003. Processes and rates of sediment and wood accumulation in headwater streams of the Oregon Coast Range, USA. Earth Surface Process. Landforms: J. Brit. Geomorphol. Res. Group 28 (4), 409–424. https://doi.org/10.1002/esp.450.
Mayer, T., 2012. Controls of summer stream temperature in the Pacific Northwest. J. Hydrol. 475, 323–335. https://doi.org/10.1016/j.jhydrol.2012.10.012.
McNamara, J.P., Ziegler, A.D., Wood, S.H., Vogler, J.B., 2006. Channel head locations with respect to geomorphologic thresholds derived from a digital elevation model: a case study in northern Thailand. For. Ecol. Manage. 224 (1–2), 147–156. https://doi.org/10.1016/j.foreco.2005.12.014.
Megahan, W.F., 1972. Subsurface flow interception by a logging road in mountains of central Idaho. Paper presented at the Proceedings, National Symposium on Watersheds in Transition, Fort Collins, Colorado.
Megahan, W.F., King, J.G., Seyedbagheri, K.A., 1995. Hydrologic and erosional responses of a granitic watershed to helicopter logging and broadcast burning. For. Sci. 41, 777–795. https://doi.org/10.1093/forestscience/41.4.777.
Meyer, G.A., Wells, S.G., 1997. Fire-related sedimentation events on alluvial fans, Yellowstone National Park, USA. J. Sediment. Res. 67, 776–791. https://doi.org/10.1306/D426863A-2B26-11D7-8648000102C1865D.
Meyer, J.L., Strayer, D.L., Wallace, J.B., Eggert, S.L., Helfman, G.S., Leonard, N.E., 2007. The contribution of headwater streams to biodiversity in river networks 1. JAWRA J. Am. Water Resources Assoc. 43 (1), 86–103. https://doi.org/10.1111/j.1752-1688.2007.00008.x.
Meyer, J.L., Tate, C.M., 1983. The effects of watershed disturbance on dissolved organic carbon dynamics of a stream. Ecology 64, 33–44.
Michigan Department of Natural Resources and Michigan Department of Environmental Quality, 2018. Michigan Forestry Best Management Practices for Soil and Water Quality.
Miller, A.J., Zégre, N.P., 2014. Mountaintop removal mining and catchment hydrology. Water 6 (3), 472–499. https://doi.org/10.3390/w6030472.
Minckley, W.L., Deacon, J.E., eds., 1991. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson, AZ.
Montgomery, D.R., Dietrich, W.E., 1988. Where do channels begin. Nature 336, 232–234.
Montgomery, D.R., 1994. Road surface drainage, channel initiation, and slope instability. Water Resour. Res. 30 (6), 1925–1932. https://doi.org/10.1029/94WR00538.
Montgomery, D.R., Schmidt, K.M., Greenberg, H.M., Dietrich, W.E., 2000. Forest clearing and regional landsliding. Geology 28 (4), 311–314. https://doi.org/10.1130/0091-7613(2000)28<311:FCARL>2.0.CO;2.

Moore, D.R., Wondzell, S.M., 2005. Physical hydrology and the effects of forest harvesting in the Pacific Northwest: a review 1. JAWRA J. Am. Water Resources Assoc. 41 (4), 763–784. https://doi.org/10.1111/j.1752-1688.2005.tb03770.x.
Moore, I.D., Grayson, R.B., 1991. Terrain-based catchment partitioning and runoff prediction using vector elevation data. Water Resour. Res. 27 (6), 1177–1191. https://doi.org/10.1029/91WR00090.
Moore, G.W., Bond, B.J., Jones, J.A., Phillips, N., Meinzer, F.C., 2004. Structural and compositional controls on transpiration in 40-and 450-year-old riparian forests in western Oregon, USA. Tree Physiol. 24 (5), 481–491. https://doi.org/10.1093/treephys/24.5.481.
Moore,.D., R., Spittlehouse, D.L., Story, A., 2005. Riparian microclimate and stream temperature response to harvesting: a review. JAWRA J. Am. Water Resources Assoc. 41(4), pp.813-834. DOI: 10.1111/j.1752-1688.2005.tb03772.x.
Morrison, K.G., Reynolds, J.K., Wright, I.A., 2018. Underground coal mining and subsidence, channel fracturing and water pollution: A five-year investigation. In: In Proceedings of the 9th Australian Stream Management Conference, pp. 12–15.
Nelson, K.C., Palmer, M.A., 2007. Stream temperature surges under urbanization and climate change: data, models, and responses 1. JAWRA J. Am. Water Resources Assoc. 43 (2), 440–452. https://doi.org/10.1111/j.1752-1688.2007.00034.x.
Nevada Code, 2010. Title 47 Forestry; Forest Products and Flora, Ch. 528 Forest practice and reforestation NRS 528.053 Certain activities prohibited near bodies of water, exceptions.
Nevada State Conservation Commission, 1994. Best Management Practices Handbook. https://ndep.nv.gov/uploads/water-nonpoint-docs/NVBMPHandbook1994.pdf.
Nisbet, T.R., 2001. The role of forest management in controlling diffuse pollution in UK forestry. For. Ecol. Manage. 143 (1–3), 215–226. https://doi.org/10.1016/S0378-1127(00)00519-3.
Njue, N., Kroese, J.S., Gräf, J., Jacobs, S.R., Weeser, B., Breuer, L., Rufino, M.C., 2019. Citizen science in hydrological monitoring and ecosystem services management: State of the art and future prospects. Sci. Total Environ. 693, 133531.
Oregon Department of Forestry Forest Practice Administrative Rules and Forest Practices Act. 2018.
Orem, C.A., Pelletier, J.D., 2016. The predominance of post-wildfire erosion in the long-term denudation of the Valles Caldera, New Mexico. J. Geophys. Res. Earth Surf. 121, 843–864. https://doi.org/10.1002/2015JF003663.
Orlandini, S., Tarolli, P., Moretti, G., Dalla Fontana, G., 2011. On the prediction of channel heads in a complex alpine terrain using gridded elevation data. Water Resour. Res. 47 (2) https://doi.org/10.1029/2010WR009648.
Passalacqua, P., Tarolli, P., Foufoula-Georgiou, E., 2010. Testing space-scale methodologies for automatic geomorphic feature extraction from lidar in a complex mountainous landscape. Water Resour. Res. 46 (11) https://doi.org/10.1029/2009WR008812.
Pechenick, A.M., Rizzo, D.M., Morrissey, L.A., Garvey, K.M., Underwood, K.L., Wemple, B.C., 2014. A multi-scale statistical approach to assess the effects of connectivity of road and stream networks on geomorphic channel condition. Earth Surf. Proc. Land. 39 (11), 1538–1549. https://doi.org/10.1002/esp.3611.
Penaluna, B.E., Olson, D.H., Flitcroft, R.L., Weber, M.A., Bellmore, J.R., Wondzell, S.M., Dunham, J.B., Johnson, S.L., Reeves, G.H., 2017. Aquatic biodiversity in forests: a weak link in ecosystem services resilience. Biodivers. Conserv. 26 (13), 3125–3155.
Perkin, J.S., Gido, K.B., Falke, J.A., Fausch, K.D., Crockett, H., Johnson, E.R., Sanderson, J., 2017. Groundwater declines are linked to changes in Great Plains stream fish assemblages. Proc. Natl. Acad. Sci. 114 (28), 7373–7378.
Perry, T.D., Jones, J.A., 2017. Summer streamflow deficits from regenerating Douglas-fir forest in the Pacific Northwest, USA. Ecohydrology. 10 (2), 1–13. https://doi.org/10.1002/eco.1790.
Poff, N.L., Ward, J.V., 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Can. J. Fish. Aquat. Sci. 46, 1805–1818. https://doi.org/10.1139/f89-228.
Poole, G.C., Berman, C.H., 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. Environ. Manage. 27 (6), 787–802. https://doi.org/10.1007/s002670010188.
Rashin, E.B., Clishe, C.J., Loch, A.T., Bell, J.M., 2006. Effectiveness of timber harvest practices for controlling sediment related water quality impacts 1. JAWRA J. Am. Water Resources Assoc. 42 (5), 1307–1327. https://doi.org/10.1111/j.1752-1688.2006.tb05303.x.
Reid, L.M., Dunne, T., 1984. Sediment production from forest road surfaces. Water Resour. Res. 20 (11), 1753–1761. https://doi.org/10.1029/WR020i011p01753.
Richardson, W., 1990. A comparison of detritus processing between permanent and intermittent headwater streams. J. Freshwater Ecol. 5 (3), 341–347. https://doi.org/10.1080/02705060.
Richardson, J.S., 2019a. Biological diversity in headwater streams. Water 11 (2), 366. https://doi.org/10.3390/w11020366.
Richardson, J., Bilby, R., Bondar, C., 2005. Organic mattern dynamics in small streams of the pacific northwest. JAWRA J. Am. Water Resour. Assoc. 41 (4), 921–934.
Richardson, J.S., Danehy, R.J., 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. Forest Science 53 (2), 131–147. https://doi.org/10.1093/forestscience/53.2.131.
Richardson, J.S., 2019b. Biological diversity in headwater streams. Water 11, 1–19. https://doi.org/10.3390/w11020366.
Robinson, M., Dupeyrat, A., 2005. Effects of commercial timber harvesting on streamflow regimes in the Plynlimon catchments, mid-Wales. Hydrol. Process. 19 (6), 1213–1226. https://doi.org/10.1002/hyp.5561.
Rogers D., 2006. Montana Guide to the Streamside Management Zone Law and Rules. Montana Department of Natural Resources. http://dnrc.mt.gov/divisions/forestry/docs/assistance/practices/smz.pdf.
Rogosch, J.S., Olden, J.D., 2019. Dynamic contributions of intermittent and perennial streams to fish beta diversity in dryland rivers. J. Biogeogr. 46, 6421. https://doi.org/10.1111/jbi.13673.
Roon, D.A., Dunham, J.B., Groom, J.D., 2021. Shade, light, and stream temperature responses to riparian thinning in second-growth redwood forests of northern California. PLoS ONE 16 (2), e0246822. https://doi.org/10.1371/journal.pone.0246822.
Ross, M.R., McGlynn, B.L., Bernhardt, E.S., 2016. Deep impact: effects of mountaintop mining on surface topography, bedrock structure, and downstream waters. Environ. Sci. Technol. 50 (4), 2064–2074. https://doi.org/10.1021/acs.est.5b04532.
Sabater, S., Timoner, X., Borrego, C., Acuña, V., 2016. Stream biofilm responses to flow intermittency: from cells to ecosystems. Front. Environ. Sci. 4 (4) https://doi.org/10.3389/fenvs.2016.00014.
Safeeq, M., Grant, G.E., Lewis, S.L., Hayes, S.K., 2020. Disentangling effects of forest harvest on long-term hydrologic and sediment dynamics, western Cascades, Oregon. J. Hydrol. 580, 124259 https://doi.org/10.1016/j.jhydrol.2019.124259.
Sánchez-Montoya, M.M., Moleón, M., Sánchez-Zapata, J.A., Escoriza, D., 2017. The biota of intermittent and ephemeral rivers: Amphibians; reptiles; birds; and mammals. In Intermittent Rivers and Ephemeral Streams: Ecology and Management; Datry, T., Bonada, N., Boulton, A.J., Eds.; Elsevier B.V.: Amsterdam, The Netherlands, pp. 299–322.
Sánchez-Montoya, M.M., von Schiller, D., Barbera, G.G., Diaz, A.M., Arce, M.I., del Campo, Ruben, Tockner, K., 2018. Understanding the effects of predictability, duration, and spatial pattern of drying on benthic invertebrate assemblages in two contrasting intermittent streams. PLoS ONE 13, e0193933. https://doi.org/10.1371/journal.pone.0193933.
Schelker, J., Grabs, T., Bishop, K., Laudon, H., 2013. Drivers of increased organic carbon concentrations in stream water following forest disturbance: Separating effects of changes in flow pathways and soil warming. J. Geophys. Res. Biogeosci. 118, 1814–1827.
Schlosser, I.J., 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303 (1–3), 71–81.
Segura, C., Bladon, K.D., Hatten, J.A., Jones, J.A., Hale, V.C., Ice, G.G., 2020. Long-term effects of forest harvesting on summer low flow deficits in the Coast Range of Oregon. J. Hydrol. 124749 https://doi.org/10.1016/j.jhydrol.2020.124749.
Shanafield, M., Bourke, S.A., Zimmer, M.A., Costigan, K.H., 2021. An overview of the hydrology of non-perennial rivers and streams. Wiley Interdisciplinary Reviews: Water 8 (2), e1504.
Shaw, S.B., 2016. Investigating the linkage between streamflow recession rates and channel network contraction in a mesoscale catchment in New York state. Hydrol. Process. 30 (3), 479–492. https://doi.org/10.1002/hyp.10626.
Shepard, J.P., 2006. Water quality protection in bioenergy production: the US system of forestry best management practices. Biomass Bioenergy 30 (4), 378–384. https://doi.org/10.1016/j.biombioe.2005.07.018.
Short, L.E., Gabet, E.J., Hoffman, D.F., 2015. The role of large woody debris in modulating the dispersal of a post-fire sediment pulse. Geomorphology 246, 351–358. https://doi.org/10.1016/j.geomorph.2015.06.031.
Sidle, R.C., Kamil, I., Sharma, A., Yamashita, S., 2000. Stream response to subsidence from underground coal mining in central Utah. Environ. Geol. 39 (3–4), 279–291.
Sidle, R.C., Pearce, A.J., O'Loughlin, C.L.. 1985. Hillslope stability and land use. Water Resources Monograph Series 11, American Geophysical Union, Washington, DC.
Slaughter, C.B., Freethey, G.W., Spangler, L.E., 1995. Hydrology of the North Fork of the Right Fork of Millar Creek, Carbon County, Utah, before, during, and after underground coal mining. US Geol Surv Water Resour Invest Rep 95–4025, US Geol Surv, Denver, Colo.
Snyder, C.D., Hitt, N.P., Young, J.A., 2015. Accounting for groundwater in stream fish thermal habitat responses to climate change. Ecol. Appl. 25, 1397–1419. https://doi.org/10.1890/14-1354.1.
Sofia, G., Tarolli, P., Cazorzi, F., Fontana, G.D., 2011. An objective approach for feature extraction: distribution analysis and statistical descriptors for scale choice and channel network identification. Hydrol. Earth Syst. Sci. 15 (5) https://doi.org/10.5194/hess-15-1387-2011.
Sosa-Pérez, G., MacDonald, L.H., 2017. Effects of closed roads, traffic, and road decommissioning on infiltration and sediment production: a comparative study using rainfall simulations. Catena 159, 93–105. https://doi.org/10.1016/j.catena.2017.08.004.
South Carolina Forestry Commission Best Management Practices, Streamside Management Zones. https://www.state.sc.us/forest/rbsmz.htm.
Stanley, E.H., Fisher, S.G., Grimm, N.B., 1997. Ecosystem expansion and contraction in streams. Bioscience 47, 427–435. https://doi.org/10.2307/1313058.
Steel, E.A., Beechie, T.J., Torgersen, C.E., Fullerton, A.H., 2017. Envisioning, quantifying, and managing thermal regimes on river networks. Bioscience 67 (6), 506–522. https://doi.org/10.1093/biosci/bix047.
Story, A., Moore, R., Macdonald, J., 2003. Stream temperatures in two shaded reaches below cutblocks and logging roads: downstream cooling linked to subsurface hydrology. Can. J. For. Res. 33 (8), 1383–1396. https://doi.org/10.1139/x03-087.
Stringer, J.W., Lowe, L., Metzger, T., 2018. Kentucky Logging BMP Field Guide, FOR-130. University of Kentucky.
Stubbington, R., Bogan, M.T., Bonada, N., Boulton, A.J., Datry, T., Leigh, C., Vander Vorste, R., 2017. The biota of intermittent rivers and ephemeral streams: aquatic invertebrates. In: Intermittent rivers and ephemeral streams. Academic Press, pp. 217–243.
Studinski, J.M., Hartman, K.J., Niles, J.M., Keyser, P., 2012. The effects of riparian forest disturbance on stream temperature, sedimentation, and morphology. Hydrobiologia 686 (1), 107–117.

Tarboton, D.G., 1997. A new method for the determination of flow directions and contributing areas in grid digital elevation models. Water Resour. Res. 33, 309–319. https://doi.org/10.1029/96WR03137.
Tennessee Department of Agriculture Division of Forestry, 2003. Guide to Forestry Best Management Practices in Tennessee. https://www.tn.gov/content/dam/tn/agriculture/documents/forestry/AgForBMPs.pdf.
U.S. Forest Service and U.S. Bureau of Land Management, 1994. Environmental assessment for the implementation of interim strategies for managing anadromous fish-producing watersheds in eastern Oregon, Washington, Idaho, and portions of California. U.S. Department of Agriculture, Forest Service, Washington, D.C.
U.S. Forest Service, 1995. Environmental Assessment for the Inland Native Fish Strategy: Interirm strategies for managing fish-producing watersheds in eastern Oregon and Washington, Idaho, western Montana, and portions of Nevada. U.S. Department of Agriculture, Forest Service, Washington, D.C.
USDA-FS 2012 National Best Management Practices for Water Quality Management on National Forest System Lands Volume 1: National Core BMP Technical Guide, United States Department of Agriculture Forest Service FS-990a April 2012.
U.S. Geological Survey, 2020a, National Hydrography Dataset (ver. USGS National Hydrography Dataset Plus version 2 for the contiguous U.S.), accessed July, 1, 2020 at URL https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products.
U.S. Geological Survey, 2020b, USGS water data for the Nation: U.S. Geological Survey National Water Information System database, accessed October, 2020 at https://doi.org/10.5066/F7P55KJN.
Valente-Neto, F., da Silva, F.H., Covich, A.P., de Oliveira Roque, F., 2020. Streams dry and ecological uniqueness rise: environmental selection drives aquatic insect patterns in a stream network prone to intermittence. Hydrobiologia 847, 617–628.
van Meerveld, H.J., Sauquet, E., Gallart, F., Sefton, C., Seibert, J., Bishop, K., 2020. Aqua temporaria incognita. Hydrol. Process. 34 (26), 5704–5711. https://doi.org/10.1002/hyp.13979.
Verry, E.S., Hornbeck, J.W., Dolloff, C.A. (Eds.), 1999. Riparian management in forests of the continental eastern United States. CRC Press.
Villines, J.A., Agouridis, C.T., Warner, R.C., Barton, C.D., 2015. Using GIS to delineate headwater stream origins in the Appalachian Coalfields of Kentucky. JAWRA J. Am. Water Resources Assoc. 51 (6), 1667–1687. https://doi.org/10.1111/1752-1688.12350.
von Schiller, D., Graeber, D., Ribot, M., Timoner, X., Acuña, V., Martí, E., Sabater, S., Tockner, K., 2015. Hydrological transitions drive dissolved organic matter quantity and composition in a temporary Mediterranean stream. Biogeochemistry 123 (3), 429–446.
Walters, A.W., 2011. Resistance of aquatic insects to a low-flow disturbance: exploring a trait-based approach. J. North Am. Benthol. Soc. 30, 346–356.
Ward, A.S., Schmadel, N.M., Wondzell, S.M., 2018. Simulation of dynamic expansion, contraction, and connectivity in a mountain stream network. Adv. Water Resour. 114, 64–82. https://doi.org/10.1016/j.advwatres.2018.01.018.
Warrick, J.A., Washburn, L., Brzezinski, M.A., Siegel, D.A., 2005. Nutrient contributions to the Santa Barbara Channel from the ephemeral Santa Clara River. Estuar. Coast. Shelf Sci. 62, 559–574. https://doi.org/10.1016/j.ecss.2004.09.033.
Washington Forest Practices Board: 2001, Watershed Analysis under Chapter 222–22 WAC, https://www.dnr.wa.gov/publications/fp_rules_ch222-22wac.pdf?8vi59l.
Webb, B.W., Zhang, Y., 1997. Spatial and seasonal variability in the components of the river heat budget. Hydrol. Process. 11, 79–101. https://doi.org/10.1002/(SICI)1099-1085(199701)11:1<79::AID-HYP404>3.0.CO;2-N.
Webster, J.R., Golladay, S.W., Benfield, E.F., Meyer, J.L., Swank, W.T., Wallace, J.B., 1992. Catchment disturbance and stream response: an overview of stream research at Coweeta Hydrologic Laboratory. River Conserv. Manage. 15, 232–253.
Wemple, B.C., Jones, J.A., Grant, G.E., 1996. Channel network extension by logging roads in two basins, Western Cascades, Oregon 1. JAWRA J Am. Water Resour. Assoc. 32 (6), 1195–1207. https://doi.org/10.1111/j.1752-1688.1996.tb03490.x.
Wemple, B., Shanley, J., Denner, J., Ross, D., Mills, K., 2007. Hydrology and water quality in two mountain basins of the northeastern US: assessing baseline conditions and effects of ski area development. Hydrol. Processes 21 (12), 1639–1650.
Wemple, B.C., Swanson, F.J., Jones, J.A., 2001. Forest roads and geomorphic process interactions, Cascade Range, Oregon. Earth Surface Processes and Landforms: J. Brit. Geomorphol. Res. Group 26 (2), 191–204. https://doi.org/10.1002/1096-9837(200102)26:2<191::AID-ESP175>3.0.CO;2-U.
Wemple, B.C., Jones, J.A., 2003. Runoff production on forest roads in a steep, mountain catchment. Water Resour. Res. 39 (8), 1220. https://doi.org/10.1029/2002WR001744.
West Virginia Division of Forestry, 2018. West Virginia Silvicultural Best Management Practices for Controlling Soil Erosion and Sedimentation from Logging Operations. https://www.wvforestry.com/pdf/DOFbmpManual2018.pdf.
Wharton, G., Mohajeri, S.H., Righetti, M., 2017. The pernicious problem of streambed colmation: a multi-disciplinary reflection on the mechanisms, causes, impacts, and management challenges. Wiley Interdisciplinary Reviews: Water 4 (5), e1231. https://doi.org/10.1002/wat2.1231.
Whiting, J.A., Godsey, S.E., 2016. Discontinuous headwater stream networks with stable flowheads, Salmon River basin, Idaho. Hydrol. Process. 30 (13), 2305–2316. https://doi.org/10.1002/hyp.10790.
Wigington Jr, P., Ebersole, J., Colvin, M., Leibowitz, S., Miller, B., Hansen, B., Lavigne, H., White, D., Baker, J., Church, M., 2006. Coho salmon dependence on intermittent streams. Front. Ecol. Environ. 4 (10), 513–518.
Wilcox, D., Sabourin, G., Greenough, B., Lones, J., & White, R., 2019. Vermont Water Quality: Acceptable Management Practices Manual for Logging Professionals. Vermont Agency of Natural Resources, Department of Forests, Parks and Recreation. https://fpr.vermont.gov/sites/fpr/files/Forest_and_Forestry/Forest_Management/Library/FullDocument-7.29.pdf.
Williamson, T.N., Barton, C.D., 2020. Hydrologic modeling to examine the influence of the forestry reclamation approach and climate change on mineland hydrology. Sci. Total Environ. 743, 140605.
Wilson, C., Kampf, S., Ryan, S., Covino, T., MacDonald, L., Gleason, H., 2021. Connectivity of post-fire runoff and sediment from nested hillslopes and watersheds. Hydrol. Processes 35 (1).
Wipfli, M.S., Richardson, J.S., Naiman, R.J., 2007. Ecological linkages between headwaters and downstream ecosystems: transport of organic matter, invertebrates, and wood down headwater channels 1. JAWRA J. Am. Water Resour. Assoc. 43 (1), 72–85. https://doi.org/10.1111/j.1752-1688.2007.00007.x.
Woelfle-Erskine, C., Larsen, L.G., Carlson, S.M., 2017. Abiotic habitat thresholds for salmonid over-summer survival in intermittent streams. Ecosphere 8 (2), e01645. https://doi.org/10.1002/ecs2.1645.
Wohl, E., Goode, J.R., 2008. Wood dynamics in headwater streams of the Colorado Rocky Mountains. Water Resour. Res. 44, W09429. https://doi.org/10.1029/2007WR006522.
Wohl, E., Bledsoe, B.P., Jacobson, R.B., Poff, N.L., Rathburn, S.L., Walters, D.M., Wilcox, A.C., 2015. The natural sediment regime in rivers: broadening the foundation for ecosystem management. Bioscience 65 (4), 358–371. https://doi.org/10.1093/biosci/biv002.
Wohl, E., Cadol, D., Pfeiffer, A., Jackson, K., Laurel, D., 2018. Distribution of large wood within river corridors in relation to flow regime in the semiarid western US. Water Resour. Res. 54 (3), 1890–1904.
Wohl, E., Kramer, N., Ruiz-Villanueva, V., Scott, D.N., Comiti, F., Gurnell, A.M., Piegay, H., Lininger, K.B., Jaeger, K.L., Walters, D.M., Fausch, K.D., 2019. The natural wood regime in rivers. Bioscience 69 (4), 259–273. https://doi.org/10.1093/biosci/biz013.
Wohl, E., Scott, D.N., 2017. Wood and sediment storage and dynamics in river corridors. Earth Surf. Proc. Land. 42 (1), 5–23. https://doi.org/10.1002/esp.3909.
Wondzell, S.M., King, J.G., 2003. Postfire erosional processes in the Pacific Northwest and Rocky Mountain regions. For. Ecol. Manage. 178 (1–2), 75–87. https://doi.org/10.1016/S0378-1127(03)00054-9.
Wuebbles, D. J., Fahey, D. W., Hibbard, K. A., Dokken, D. J., Stewart, B. C., Maycock, T. K. (Eds.), 2017. Climate science special report: Fourth national climate assessment, Volume I. U.S. Global Change Research Program, Washington, DC.
Wyoming State Forestry Division. Wyoming Forestry Best Management Practices, Forestry BMPs Water Quality Protection Guidelines, https://wsfd.wyo.gov/forest-management/bmp-s.
Yang, L., Jin, S., Danielson, P., Homer, C., Gass, L., Bender, S.M., Case, A., Costello, C., Dewitz, J., Fry, J., Funk, M., Granneman, B., Liknes, G.C., Rigge, M., Xian, G., 2018. A new generation of the United States National Land Cover Database: requirements, research priorities, design, and implementation strategies. ISPRS J. Photogramm. Remote Sens. 146, 108–123. https://doi.org/10.1016/j.isprsjprs.2018.09.006.

An Ecological Perspective of Riparian and Stream Restoration in the Western United States

By J. Boone Kauffman, Robert L. Beschta, Nick Otting, and Danna Lytjen

ABSTRACT

There is an unprecedented need to preserve and restore aquatic and riparian biological diversity before extinction eliminates the opportunity. *Ecological restoration* is the reestablishment of processes, functions, and related biological, chemical, and physical linkages between the aquatic and associated riparian ecosystems; it is the repairing of damage caused by human activities. The first and most critical step in ecological restoration is *passive restoration*, the cessation of those anthropogenic activities that are causing degradation or preventing recovery. Given the capacity of riparian ecosystems to naturally recover, often this is all that is needed to achieve successful restoration. Prior to implementation of active restoration approaches (e.g., instream structures, channel and streambank reconfiguration, and planting programs), a period of time sufficient for natural recovery is recommended. Unfortunately, structural additions and active manipulations are frequently undertaken without halting degrading land use activities or allowing sufficient time for natural recovery to occur. These scenarios represent a misinterpretation of ecosystem needs, can exacerbate the degree of degradation, and can cause further difficulties in restoration. Restoration should be undertaken at the watershed or landscape scale. Riparian and stream ecosystems have largely been degraded by ecosystemwide, off-channel activities and, therefore, cannot be restored by focusing solely on manipulations within the channel. While ecological restoration comes at a high cost, it also is an investment in the natural capital of riparian and aquatic systems and the environmental wealth of the nation.

J. B. Kauffman



A fence-line contrast of a five-year-old exclosure (without livestock grazing) and an area grazed season-long on a tributary of the Deschutes River, Oregon. The cessation of those activities that are causing degradation or preventing recovery is the most important step in ecological restoration. Given the natural resilience capacity of riparian ecosystems, passive restoration such as halting excessive livestock grazing is all that is needed to restore degraded riparian ecosystems.

Traditionally, the use and management of rivers, riparian zones, and wetlands have focused on activities that led to increases in the social well-being or material wealth of a society. These included such endeavors as transportation, hydroelectric power generation, flood control, and the use of water for agricultural, industrial, and municipal uses (National Research Council 1992).

J. Boone Kauffman is an associate professor at Oregon State University's Department of Fisheries and Wildlife, 541/737-1625; Kauffmab@ccmail.orst.edu. Robert L. Beschta is a professor at the Department of Forest Engineering. Nick Otting and Danna Lytjen are graduate research assistants for the Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97330.

As a result of these practices, as well as activities such as channelization, road construction, timber harvesting, livestock grazing, mining, and water diversion, numerous riparian zones in the western United States have been extensively altered since Euro-American settlement (National Research Council 1995, 1996). The resulting decreases in diversity, functions, and productivity of riparian and aquatic ecosystems limit their future integrity, value, and use. This is an important societal concern since riparian zones are among the nation's most highly valued, yet threatened natural ecosystems (Johnson and McCormick 1979; National Research Council 1995).

Riparian and aquatic ecosystems are currently being altered, impacted, or destroyed at a greater rate than any time in history (National Research Council 1992).

An estimated 70%–90% of all natural riparian areas in the United States have been extensively altered (Hirsch and Segelquist 1978); approximately 47.3 million ha (117 million acres) or 53% of all U.S. wetlands have been lost since the 1780s (Dahl 1990). Some widespread land uses that occur in both uplands and riparian systems exert their greatest impacts on streamside areas. For example, in the 11 western states, livestock grazing is permitted on 91% of all public lands. On the 64 million ha (158 million acres) of Bureau of Land Management-administered lands, 58% is classified in fair to poor condition (i.e., the lands have been moderately to severely desertified) as a result of long-term grazing (U.S. General Accounting Office 1988). Historical grazing impacts to riparian systems have been even more severe. On these public lands, 25,700 km (16,000 miles) of sportfishing streams have declined in quality as a result of land use practices (Armour et al. 1991).

Degradation of riparian zones and streams diminishes their capacity to provide critical ecosystem functions, including the cycling and chemical transformation of nutrients, purification of water, attenuation of floods, maintenance of stream flows and stream temperatures, recharging of groundwater, and establishment and maintenance of habitats for fish and wildlife. The most important factor contributing to the decline of aquatic biodiversity is the loss or degradation of habitats (i.e., habitat alteration, introduced species, and water pollution; Miller et al. 1989). Almost 40% of the perennial streams in the United States are affected by reduced flows, and 41% are influenced by siltation, bank erosion, and channelization (National Research Council 1992). More than half of the nation's rivers have fish communities harmed by turbidity, high temperatures, toxins, and low levels of dissolved oxygen (Council on Environmental Quality 1989). Almost 85% of historical Pacific Northwest anadromous salmon stocks are either extinct, endangered, threatened, or of special concern (National Research Council 1996). The current threat to aquatic biodiversity in North America is greater than the threat to terrestrial diversity (Naiman et al. 1995). While 11%–15% of the terrestrial vertebrates are considered rare or nearly extinct, 34% of the fishes, 65% of the crayfishes, and 75% of the bivalve mussels fall into these categories (Naiman et al 1995). To date, not a single aquatic species has been delisted through Endangered Species Act procedures because of implementation of a successful recovery plan; in fact, the majority of the listed species do not have a formal recovery plan (Williams et al. 1989). An unprecedented need exists for ecological restoration of riparian ecosystems and their closely associated aquatic ecosystems.

What Is Ecological Restoration?

Ecological restoration in riparian ecosystems is defined as the reestablishment of predisturbance riparian functions and related chemical, biological, and physical processes (National Research Council 1992). *Restoration* is the process of repairing damage caused by humans to the diversity and dynamics of indigenous ecosystems (Jackson et al. 1995). While ecological restoration attempts to return riparian zones as closely as possible to predisturbance functions and processes, scientists must recognize that ecosystems are in a constant state of flux due to ever-changing environmental conditions. These changes, sometimes coupled with irreversible human impacts (e.g., soil loss, biotic invasions, air pollution), may preclude our capability to precisely re-create ecosystem structure and functions that previously existed. Thus, the goal of restoration projects is to ensure that the dynamics of natural ecosystem processes are again operating efficiently so that both ecosystem structure and function can be recovered (National Research Council 1992).

Riparian areas are three-dimensional zones of biological, physical, and chemical interactions between terrestrial and aquatic ecosystems (Gregory et al. 1991). Because of landscape-level interactions between terrestrial and aquatic systems, ecological restoration of riparian zones requires a holistic approach whereby activities and conditions across an entire watershed should be considered. Problems affecting riparian and aquatic resources are unlikely to be solved by ignoring deleterious land management practices, either historical or current, that occur at landscape or watershed scales.

While scientists strongly recognize the need to restore or conserve native fish throughout the Pacific Northwest and other nearby regions, less appreciation exists for how local geomorphic settings and natural

hydrologic disturbance regimes interact with native riparian plant communities to create sustainable habitats (Figure 1). Restoration of degraded riparian zones and their subsequent conservation after recovery requires knowledge of how these ecosystems function as well as the attributes responsible for their composition, structure, and productivity. The character and value of riparian zones arise as a result of an infinite number of complex interactions among three fundamental ecosystem features: (1) soils/geomorphology; (2) hydrology; and (3) biota (Figure 1). The soils/geomorphology features include streambank and floodplain form and development, channel gradient, geologic substrates influencing soil and channel composition, and subsoil features of the floodplain (e.g., gravel lenses important for hyporheic or subsurface flows). Hydrological features include the frequency, magnitude, and temporal distribution of stream flow (including peak and low flows), sediment availability and transport, subsurface hydrology, and water quality. Biotic features include vegetation, vertebrates, invertebrates, and microorganisms. In addition to live plants, the vegetation component also includes dead materials (necromass) such as snags, fallen logs, and fine organic debris (litter). Anthropogenic activities that either alter these components or sever the linkages between them will disrupt ecosystem dynamics, including species composition, productivity, structure, and function.

Among the most important ecosystem linkages are those interactions among vegetation, hydrology, and substrates as they influence geomorphic features such as channel morphology and channel dynamics (Figure 1). For example, naturally occurring pool habitats typically form as a result of interactions of hydrologic disturbance regimes, substrates, and streamside vegetation. If hydrologic patterns, sediment availability, or streamside vegetation are altered by land use activities, then channel morphology will subsequently adjust to these new conditions. This is often expressed by a simplification in stream structure (e.g., loss of pools, decreased channel sinuosity, and loss of channel diversity).

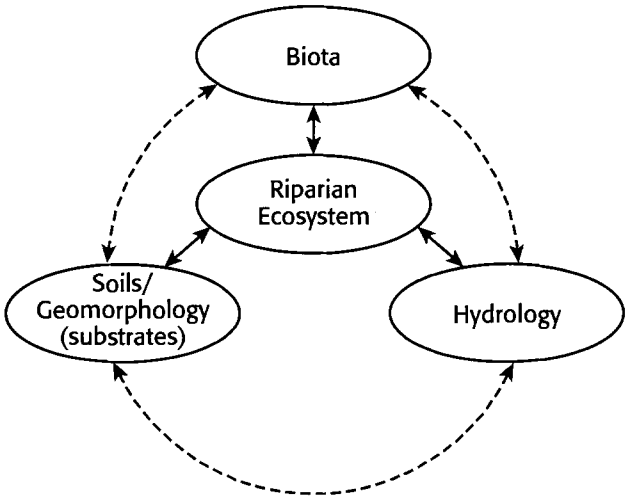


Figure 1 illustrates the linkages of the biotic, hydrologic, and geomorphic components combined to shape the unique structure and function of riparian and stream ecosystems. Each arrow represents an infinite number of biological and physical processes and interrelationships among these ecosystem features. Because of these inextricable linkages, human or natural actions that alter any one component or process will have feed-forward influences that can affect all other components of the ecosystem.

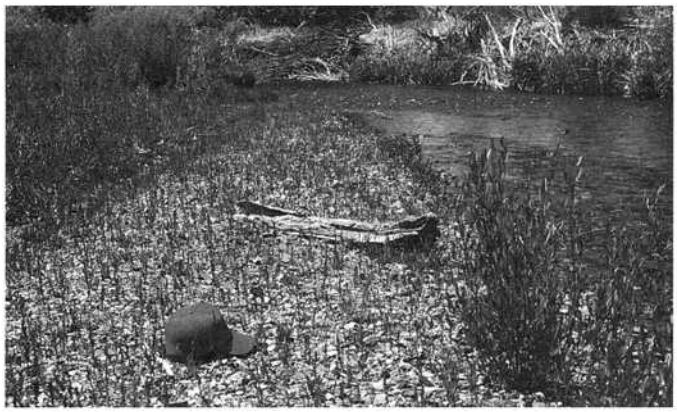
Another important interaction represented in Figure 1 is the influence of substrate characteristics and hydrology on plant community composition. For example, many riparian-obligate trees and shrubs have specific micro-site requirements for establishment. Successful natural establishment of cottonwood trees (*Populus* spp.) and willows (*Salix* spp.) commonly occurs on point bars of newly deposited, coarsely textured, well-aerated substrates within the 2- to 10-year floodplain (McBride and Strahan 1984; Bradley and Smith 1986); high flows are needed to create these conditions. Seed dispersal and germination are timed to coincide with late-spring flows when water tables are high, and fresh alluvium has been deposited (Noble 1979). Successful establishment also may be limited to areas where the rate and extent of water table decline does not exceed the biological capacity of root growth (Mahoney and Rood 1992). At the lower limits of the floodplain, establishment is often not possible because high water in subsequent years destroys the young plants (Bradley and Smith 1986).

Saturated, finely textured soils associated with low-gradient riparian zones are often sites of anaerobic conditions; such sites are typically unsuitable for the establishment of cottonwoods or willows. Under these hydrologic and geomorphic conditions, the natural plant communities are dominated by sedges (*Carex* spp.), rushes (*Juncus* spp.), or hydrophytic grasses. At the opposite extreme, where coarse materials (cobbles and boulders) occur in elevated and excessively drained situations, riparian-obligate vegetation will not establish. These conditions rarely occur naturally in western riparian ecosystems. However, they may be found after extreme human perturbations (e.g., dredge mining, channelization, or other in-channel modifications) deposit spoils on streambanks and floodplains.

Ecological restoration begins with identification of those land use practices that are damaging ecosystems or preventing recovery, followed by implementation of land management strategies that allow for natural recovery to occur (National Research Council 1992, 1996; Jackson et al. 1995). Thus, ecological restoration aims to ensure the occurrence of (1) those physical and biotic processes facilitating persistence of species through natural recruitment and survival; (2) functioning food webs and systemwide nutrient conservation via relationships among plants, animals, and detritivores; and (3) the integrity of watersheds through linkages with the hydrologic, geomorphic, and climatic disturbance regimes that shape plant and animal communities (Jackson et al. 1995).

What Isn't Ecological Restoration?

Ecological restoration results in the reestablishment of linkages between organisms and their environment. Because an entire suite of organisms, physical features, and processes comprise an ecosystem, a species-only or single-process approach to restoration will likely fail (Beschta et al.





Photos by J. B. Kauffman

The influence of restoring streamflow and halting grazing on Rush Creek, California, (1992–1996) is illustrated above. The small willow in the foreground in 1992 (left) is the same willow to the left of the third author in 1996. In 1992, a high density (50 m^{-2}) of willow seedlings, was established on the gravel bar the first year without livestock. By 1996, a dense willow community had formed, with many willows becoming more than 2 m in height.

1994; Jackson et al. 1995). For example, the reintroduction of an extirpated fish species or the installation of log weirs and large boulders into a degraded stream reach does not constitute restoration. While attempts to revive a single species are likely to target only a few of its more obvious habitat requirements, less-apparent needs and important processes and functions are often ignored. In the case of declining anadromous salmonids, a technological perspective has prevailed (Bottom 1997); first fish hatcheries, then fish ladders, and finally in-stream manipulations were looked on as solutions. However, increasingly apparent is that there is a remarkable complexity of environmental phenomena that affect salmon viability, and the cumulative losses of various biotic and physical components are what must be addressed (National Research Council 1996). By shifting the focus to the integrity of ecological processes and functions, we are more likely to successfully attain the restoration both of habitats and species of interest.

Ecological restoration also should be distinguished from architectural and mechanical approaches to ecosystem management. Such "restoration" methodologies often call for the systematic reconstruction of a stream according to specific human perspectives of what the stream "should look like." More often than not, this will not achieve the goal of ecological restoration or species recovery. Merely re-creating a form without the function or the function in an artificial configuration does not constitute restoration (National Research Council 1992). A long-term perspective regarding ecosystem sustainability is not inherent with these approaches. For example, the placement of artificial structures (boulders, rock gabions) does not replace many of the multiple functions of large, woody debris, nor does it ensure or promote the future recruitment of woody debris into the stream system. Such structures are commonly engineered and constructed with the false assumption that they and the stream channel are static. High flows can be destructive when rigid structures are placed in degraded alluvial channels (Beschta et al. 1991; Gregory and Bisson 1997). The underlying failure of this approach rests in a lack of recognition regarding the natural dynamics of high-flow disturbances, bedload transport, local scour and fill, lateral channel movements, and particularly the interactions of streamside vegetation with fluvial disturbance regimes.

Fish hatcheries, fish ladders, and barging salmon downstream in dammed rivers are artificial means of maintaining anadromous fish in systems (functions with no natural form). These approaches seldom address fundamental problems associated with restoring the habitats of natural fish runs. Such activities could be construed to be mitigation or aquaculture but not restoration since they do nothing to restore habitat or reverse barriers to migration.

Preservation

Preservation is the maintenance of intact ecosystems; it is distinct from ecological restoration, which only addresses degraded ecosystems. Ecosystems that exist in a desired natural state warrant preservation (National Research Council 1992, 1996). The protection and preservation of intact ecosystems are of great importance, both environmentally and economically. Restoring the natural structure and function of riparian and stream ecosystems requires an understanding of the complex processes and linkages between the biotic and physical components of intact systems. Intact ecosystems are necessary as reference reaches from which to compare the efficacy of restoration programs (Case 1995; Beschta 1997). Furthermore, they are sources of natural genetic material for the reestablishment or reintroduction of the native biota to nearby areas in need of restoration.

Preservation is a management strategy that entails more than simply preventing human-induced alterations. For example, management actions may be necessary to maintain natural functions and characteristics (e.g., prescribed fire, management of exotic species invasions, and large herbivore management). Measures to protect intact ecosystems (preservation) are important because they are often easier to implement, have greater rates of success, and are less expensive than restoration. Preserving intact ecosystems also may be less expensive than restoring them, just as preventative medicine is nearly always less expensive than corrective medicine (National Research Council 1992; Cairns 1993).

Various other land management approaches seek to alter and improve riparian conditions or specific habitat features, yet they may not represent ecological restoration. Activities often confused with ecological restoration include creation, rehabilitation, reclamation, mitigation, replacement, and enhancement. These activities typically emphasize altering ecosystem components for a particular human purpose (National Research Council 1992, 1996).

Creation

Creation is defined as establishing a new ecosystem that previously did not exist on a particular site. For example, developing a sustainable wetland in an area formerly occupied by upland plant communities would represent creation. Creation also includes attempts to create specific riparian features that previously did not exist on the treated site. Examples include the planting of willows or alders (*Alnus* spp.) on riparian wetland sites naturally occupied by sedges or rushes, placement of boulders in streams with floodplains comprised of fine sediment, and construction of secondary channels where none existed previously (Quammen 1986) .

Reclamation

Reclamation is traditionally defined as the process of adapting wild or natural resources to serve a utilitarian human purpose (National Research Council 1992). Historically, this often included the conversion of riparian or wetland ecosystems to agricultural, industrial, or urban uses. More recently, however, *reclamation* has been defined as the process resulting in a stable, self-sustaining ecosystem that may or may not include some exotic species. Reclaimed sites may have similar, although not identical, structure and function of the original land (Jackson et al. 1995).

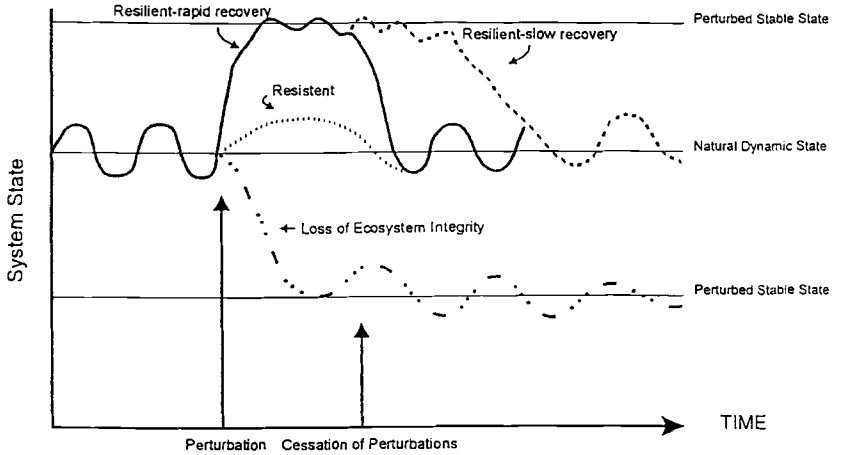


Figure 2 represents the conceptual responses of individual riparian plant communities to human perturbations and response pathways after cessation of perturbations. Resistant plant communities exhibit few deviations from natural equilibria when exposed to a perturbation. In contrast, nonresistant communities shift to a perturbed state unlike that of the natural dynamic state (i.e, changes in composition, structure, or productivity). After activities that caused ecosystem degradation (perturbations) stop, resilient communities will recover to natural system states. *Nonresilient communities* are those lacking potential for natural recovery and are characterized as having lost ecosystem integrity. In the absence of active restoration activities, they may remain indefinitely in an altered ecosystem state.

Rehabilitation

Rehabilitation implies making the land useful again after natural or anthropogenic disturbances. Restoration to predisturbance conditions and functions is not implied in the definition of *rehabilitation*. The creation of a crested wheatgrass (*Agropyron cristatum*) stand where sagebrush steppe (*Artemisia tridentata*) once existed or the planting of exotic grass species after a forest fire could be construed as rehabilitation but is not ecological restoration.

Replacement

Replacement is the substitution of a native species or ecosystem feature with an exotic species or foreign object; often, it is considered another form of rehabilitation. Examples of replacement would include the planting of nonnative trees or the placement of boulders, gabions, or weirs to substitute for natural features. The introduction of brook trout (*Salvelinus fontinalis*) or smallmouth bass (*Micropteris dolomieui*) in streams historically occupied by native salmonids is an example of ecological replacement.

Mitigation

Mitigation is an attempt to alleviate any or all of the detrimental effects or environmental damage that arise from anthropogenic actions. The construction of fish hatcheries or the modification of headwater fish habitats to compensate for losses caused by dams is a mitigation approach. Wetland creation is often suggested as mitigation for the destruction of natural wetlands from construction, fill, or other human activities. However, these constructed wetlands seldom display the structural or functional attributes of the native wetlands they replaced (Quammen 1986; M. Kentula, U.S. Environmental Protection Agency, personal communication).

Enhancement

Enhancement is any improvement of a structural or functional attribute for a species or habitat. However, when enhancement activities are focused only on a single species or specific component of an ecosystem, they may create conditions outside the context of a natural riparian and stream system. For example, in-stream structures (e.g., rock jetties, gabions, pool excavations) are often used with the objective of fish habitat enhancement. However, these structures can severely alter streambank structure, sediment transport dynamics, and hydrologic connectivity with riparian vegetation, resulting in disruptions or losses of riparian-stream linkages. When in-stream spoils, rocks, or boulders are piled on a streambank, conditions may no longer be suitable for natural establishment of riparian vegetation nor for adjustments in channel morphology to natural variations in sediment transport and stream flow. Such physical

alterations may further limit the future recruitment potential of large, woody debris as well as degrade riparian wildlife habitat. The ecological costs and benefits to physical processes, biological diversity, and ecosystem functions should be considered before such actions are initiated.

Resistance and Resilience

In undertaking restoration, it is important to understand the response of riparian ecosystems to anthropogenic perturbations (resistance) as well as the capacity to recover after cessation or removal of the problem-causing activities (resilience). *Resistance* is the capacity of an ecosystem to maintain natural function and structure after a natural disturbance or an introduction of an anthropogenic perturbation. For example, some riparian meadow plants will maintain productivity with moderate levels of livestock grazing because of their adaptive capacities or tolerance to herbivory. These would be considered *resistant communities*. In contrast, even low levels of herbivory can retard community development on gravel bars dominated by young willow or cottonwoods (Case and Kauffman, in press; Green and Kauffman 1995); these are *nonresistant communities*.

Resilience is the capacity of species or ecosystems to recover after a natural disturbance or following the cessation of an anthropogenic perturbation. Because riparian species evolved in areas with frequent fluvial disturbances, they represent classic examples of a resilient biota. Not only do many riparian plants depend on natural disturbances for establishment, but rates of recovery or establishment following disturbances can be remarkably high (Busse 1989; Gecy and Wilson 1990; Case 1995). Paradoxically, while riparian ecosystems are often resilient to natural disturbance regimes, many rapidly degrade with the curtailment of these disturbances. For example, water impoundment and diversion projects have resulted in dramatic losses in riparian floodplain forests throughout North America (Bradley and Smith 1986; Rood and Mahoney 1990; Howe and Knopf 1991).

The conceptual pathways of riparian community response to the initiation and cessation of anthropogenic perturbations are illustrated in Figure 2. A severe anthropogenic perturbation (e.g., overgrazing, clear-cutting, channelization, dams, diversions) may sufficiently alter a riparian ecosystem such that it will attain a dynamic equilibrium different than what would occur under natural conditions. A *resistant ecosystem* is one that displays few changes in composition or structure following the initiation of a perturbation. In contrast, nonresistant riparian zones or communities will change to a new system state or equilibrium typified by a different composition (e.g., dominance by exotics), different structure (e.g., losses of the woody component), altered productivity (e.g., shifts in above- and below-ground biomass), or a change in ecosystem functions (e.g., influences on water quality).

After cessation of perturbations, resilient riparian ecosystems usually show signs of recovery through measurable changes in composition, structure, or function (Figure 2). In these situations, cessation of those human perturbations that harm the riparian ecosystem may be all that is necessary to achieve restoration. Because some ecosystems recover more quickly than others, it is important to monitor changes before implementing other, often more costly, measures. Failure to wait minimally may result in wasting limited funds; at worst, it may exacerbate the extent of degradation.

When losses in ecosystem structure, composition, or function reach a sufficient magnitude, the simple cessation of perturbations may not be sufficient for ecosystem recovery (Figure 2). Factors that may diminish resilience and, hence, prevent recovery include species extinctions, introductions of exotics, excessive soil erosion, pollution, and severe changes in geomorphology or hydrology. In these situations, the ecosystem may remain degraded indefinitely even after the cessation of activities that caused degradation. In this scenario a concerted and active effort will be needed to accomplish restoration.

Rather than referring to a handbook, land managers should obtain the "blueprints" for the ultimate outcomes of planned restoration activities from intact streams.

Conceptual Approaches to Restoration

The basic goal of riparian restoration is to facilitate a self-sustaining occurrence of natural processes and linkages among the terrestrial, riparian, and aquatic ecosystems. An important initial component of any restoration plan should be an evaluation of the ecological status of existing riparian and aquatic systems. Ideally, this assessment should be conducted at the watershed scale, while still being sufficiently detailed to depict specific reaches or channel units where particular restoration activities might ultimately occur. The objectives of the initial resource analysis should be to identify (1) those reaches that are relatively intact (few anthropogenic impacts evident) and worthy of protection or preservation management strategies; (2) those reaches where restoration is feasible with changes in current land use activities or without large expenditures of money; (3) those areas that could be restored but only at high costs and with a high probability of failure, and (4) those reaches that are in a condition where restoration is not technically feasible due to extreme conditions of alteration, degradation, or sociopolitical limitations.

When planning for ecosystem restoration, it may be useful from a strategic perspective to partition riparian zones into those capable of rapid recovery, those with a slow rate of natural recovery, and those with little or no resilience capacity (i.e., loss of ecosystem integrity, Figure 2). The greatest efforts should be initially focused on the former because of a greater potential for successful restoration with lowered risk or expenditures. Only after areas

with a high-resilience capacity are improving or have been restored should restoration efforts focus on areas that have generally lost the capability of natural recovery, even after the cessation of human perturbations. However, special situations may exist in which degraded habitats of species near extinction can only be restored at high risk and cost; such areas assume a high priority for improvement.

Where possible, managers should emphasize preservation because preservation of intact ecosystems is typically less expensive than restoring degraded systems (Cairns 1993). Intact ecosystems are not only valuable sources of biological diversity, but they also provide important reference sites that land managers may seek to emulate in their restoration activities. Rather than referring to a handbook, land managers should obtain the "blueprints" for the ultimate outcomes of planned restoration activities in adjacent sites from intact streams. Because the failure rate of restoring degraded ecosystems is far greater than that of simply protecting fully functional sites, protecting and preserving intact ecosystems should represent the first priority of any watershed-scale restoration plan.

At the other extreme, many areas exist where ecological restoration in the strictest sense is neither economically, socially, nor technologically feasible (e.g., metropolitan reaches, dredged mine sites, etc.). If restoration practices are pursued in these situations, they may be costly. However, stream enhancement activities should not be ruled out in these scenarios, particularly if such activities would diminish harm to downstream or upstream riparian and aquatic ecosystems.

Reviews of instream habitat management projects throughout the western United States clearly indicate that passive restoration has been the critical first step in successful riparian restoration programs.

The domain of riparian and stream restoration lies between these two extremes (Figure 2). A successful riparian restoration program will result in the perpetuation of processes that determine ecosystem structure, function, and evolutionary trajectory. However, this operating principle is stated with the recognition that the intact wildlands of today and the future will exist in a fragmented landscape and will require specific preservation management activities such as prescribed fires, suppression of arson fires, control of biotic invasions, and maintenance of natural hydrologic disturbance regimes.

After identifying those degraded sites where restoration is deemed feasible, scientists must determine the causes of degradation and the activities preventing recovery (Beschta 1997). Also important is the identification of biotic components of the ecosystem that have been extirpated and the presence of biotic invaders that may prevent recovery. In addition to biotic considerations, scientists must determine the degree to which the hydrologic and geomorphic features of the ecosystem have been (or are being) altered. This includes determining the influences of past management activities on channel morphology, channel incision, hyporheic flows, water table dynamics, and water quality (i.e., the linkages between the terrestrial and aquatic system). From this initial analysis, not only can the extent and causes of ecosystem degradation be addressed, but potential restoration options may become evident. Obviously, even at this stage, restoration is a multidisciplinary effort.

The desired endpoints of restoration efforts are naturally dynamic and self-sustaining ecosystems (Figure 2). Given the fluctuating nature of environmental factors inherent to all natural systems, restoration managers should emphasize ecosystem processes and function rather than some preconceived landscape form. Fisheries professionals should recognize that because of the likely permanence of many exotic species, extinctions of native species, long-term changes in soil productivity due to erosion, and other severe environmental perturbations, complete recovery may not always be possible. In such cases, goals of restoration are to return a riparian system to a "potential natural community," whereby the ecosystem is naturally functioning in a manner as closely as possible to that in which it evolved.

Passive Restoration

Once professionals have decided where to implement restoration activities, the first and most critical step is to halt activities causing degradation or preventing recovery, an approach referred to as *passive* or *natural restoration* (Kauffman et al. 1993; Kauffman et al. 1995). Many riparian zones are capable of rapid recovery after human perturbations stop because the biota has evolved adaptations to survive and even reproduce despite frequent natural disturbance events characteristic of riverine systems (Barnes 1983; Wilson 1970; Gecy and Wilson 1990).

In western riparian zones the two most common examples of successful passive ecological restoration are the rewatering of streams after years of withdrawal for agricultural or municipal purposes and the cessation of livestock grazing in riparian areas. Stream flow diversion, combined with heavy livestock grazing, can result in severe degradation of riparian and stream ecosystems. With the return of perennial instream flows and the halt of livestock grazing, the recovery of riparian vegetation can be dramatic. For example, in the Mono basin of California, 24% of the area of riparian vegetation lost during a 50-yr period of water diversion (1940–1989) had reestablished after only 4 years following rewatering (Jones and Stokes Associates, Inc., and Trihey Associates, personal communication). Along these recovering streams, willow and cottonwood seedling densities were often >50 m^{-2} with annual growth rates of 0.6 to 1.5 m high (B. Kauffman and R. Beschta, Oregon State University, personal communication). Now, vegetation establishment is beginning to influence channel diversity through the creation of narrower channels, bank undercuts, and pools. In contrast, while several million dollars has been spent on engineering manipulations

in and around stream channels, the influence of those manipulations on trout densities was insignificant and actually hurt the natural restoration process of the riparian and stream ecosystem (Beschta et al. 1994; Inter-Fluve 1995; W. S. Platts, Don Chapman and Consultants, personal communications).

Livestock grazing has been perhaps the most prevalent cause of ecological degradation for many western riparian and stream ecosystems (Kauffman and Krueger 1984; Kauffman 1988; Fleischner 1994). After extensive field reviews of fish habitat improvement projects in eastern Oregon, Beschta et al. (1991) and Kauffman et al. (1993) concluded that the cessation of livestock grazing in riparian zones of eastern Oregon was the single most ecologically effective approach to restoring salmonid habitats.

While many reviews of grazing effects on riparian vegetation have been general in nature (e.g., Platts 1991; Elmore and Kauffman 1994), recent research is providing improved insights into the effects of grazing on woody riparian species. This research is important because willows, cottonwoods, and alders are significant features of terrestrial wildlife habitat, stream channel morphology, and aquatic habitat. In central Oregon, Busse (1989) found a lack of willow and cottonwood reproduction in grazed

misinterpreting ecosystem needs is common with many instream rehabilitation and enhancement programs

riparian zones of the Crooked River National Grassland. After constructing corridor fencing, she recorded a widespread and rapid rate of willow and cottonwood establishment. In northeast Oregon, similar rates of woody species recovery after cattle grazing stopped have been quantified (Green and Kauffman 1995; Case and Kauffman, in press). Three years after cattle grazing stopped on Meadow Creek (a tributary of the Grande Ronde River), Case and Kauffman (in press) reported that the average crown volume of willows increased nearly 300%. Average crown volume of black cottonwood and alder increased 800% and 200%, respectively. Comparing 10 years of no grazing with light to moderate late-season grazing use in northeast Oregon, Green and Kauffman (1995) reported significant increases in both the density and structural complexity of willows and cottonwoods in ungrazed exclosures. Although positive trends in willow density and height also occurred in the lightly to moderately grazed areas (three weeks annually late in the season), recovery rates were significantly less than those of the ungrazed areas.

Reviews of instream habitat management projects throughout the western United States clearly indicate that passive restoration has been the critical first step in successful riparian restoration programs (Beschta et al. 1991; Kauffman et al. 1993; Beschta et al. 1994). In many cases, this was all that was needed to initiate restoration of riparian ecosystems. Because of the high costs and potential for failure with active restoration and manipulation, we recommended that project managers monitor and observe the natural recovery process for an appropriate period of time (e.g., 10 years) after implementing passive restoration. Then, if managers ascertain that natural recovery is limited or not occurring, implementation of active restoration projects might begin.

Active Restoration

After implementing passive restoration, a site still may remain in an ecological state that is unlike what would occur naturally (Figures 2 and 3). These situations can occur when an ecosystem is sufficiently degraded such that the inherent capacity to recover has been lost. To achieve ecological restoration in such situations, active manipulations will be necessary.

Many factors may prevent a return to a natural dynamic system when using only passive restoration—species extinctions [particularly keystone species such as cottonwood or beaver (*Castor canadensis*)], exotic predators [smallmouth bass or bullfrogs (*Rana catesbeiana*)], exotic competitors [carp (*Cyprinus carpio*), reed canary grass (*Phalaris arundinacea*), or knapweeds (*Centaurea* spp.)], loss of hydrologic function and alteration of hydrologic disturbance regimes (e.g., diversions, regulated flows by dams, disruptions of groundwater flow patterns), and alteration of geomorphic features (e.g., channel incision, soil erosion, compaction). While some of these barriers to recovery might be easily ameliorated, others can be sufficiently severe in their magnitude and persistence that restoration may not be technologically feasible.

Biotic manipulations representing active ecological restoration include the reintroduction of beaver or plant species that have been extirpated from the area. Reintroductions are most successful when a feasibility analysis has confirmed that suitable habitat is present for the organism to be reintroduced. In the case of beaver, adequate habitat conditions include sufficient availability of forage and suitable structure of riparian plant communities. If introduced into degraded or recovering ecosystems before woody species have sufficiently reestablished, beaver can actually limit ecological recovery (Kauffman et al. 1982; Case 1995). Alternatively, when reintroduced in suitable riparian habitat conditions, the beaver can dramatically accelerate the restoration process through its influence on the hydrology, wetland extent, species composition, and quality of salmonid habitats (Naiman et al. 1988; Lowry 1993).

Vegetation plantings are a commonly proposed restoration technique. However, after passive restoration is implemented, the natural capacity for rapid reinvasion of woody species on suitable sites often makes artificial plantings unnecessary (Busse 1989; Schulz and Leineger 1990; Case and Kauffman, in press). Where shrubs and other woody species have been eliminated and the potential for natural reinvasion no longer exists, active revegetation will be required. For example, where high-flow regimes have been significantly altered (e.g., below a

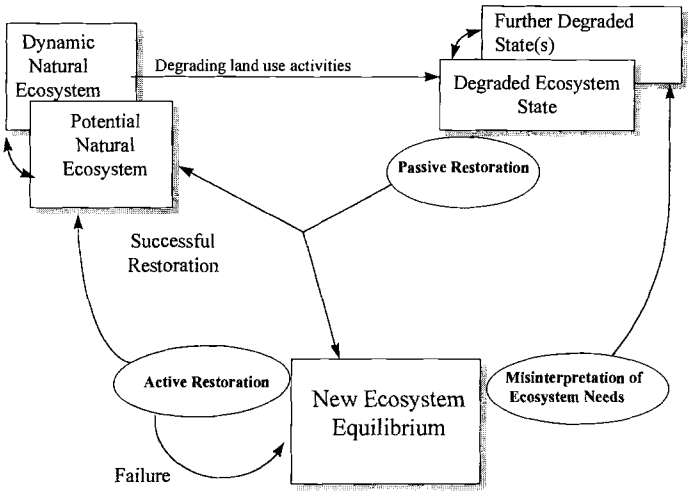


Figure 3 explores the conceptual pathways or ecosystem response to ecological restoration of western North American riparian and stream ecosystems.

major dam), the natural regeneration of riparian-obligate trees and other woody species may be severely limited (Bradley and Smith 1986; Rood and Mahoney 1990). Without a recovery of high-flow regimes, artificial revegetation will likely be necessary to perpetuate forests within the historic floodplains. Gallery forests can be naturally perpetuated only if flow management allows high-water events to create conditions for regeneration.

By definition, ecological restoration of riparian vegetation entails the planting of only native species. The use of exotic plant species to "improve" riparian habitats associated with native fisheries is tantamount to introducing brook trout (*Salvelinus fontinalis*) or some other exotic fish as a substitute for extirpated native bull trout (*Salvelinus confluentus*) populations. In addition, revegetation with native species should focus on those areas of the riparian zone that contain appropriate substrates and microclimates. The planting of willows or conifers in native sedge meadows will likely result in failure or the creation of an unnatural, unsustainable plant community.

In addition to revegetation, a suite of silvicultural options to accelerate riparian forest development can be implemented. Creation of small canopy gaps, small clearings, and placement of coarse wood debris on the floodplain to serve as nurse logs can enhance growth rates of existing trees or provide conditions for establishment of desirable trees. Overstory manipulations should be done in a patchy, irregular manner to mimic natural disturbances and forest structure. In some instances, the products of thinning can be used as a source of instream wood or nurse logs. Prescribed burning also can be an important activity when used to mimic the disturbance regime of natural fires.

Appropriate livestock grazing management is of major importance for the proper functioning of many western riparian zones, particularly where grazing is deemed a primary use (e.g., private ranch lands). While some have suggested that livestock can be used as a "tool" in riparian enhancement, there is no ecological basis to indicate that livestock grazing, under any management strategy, can accelerate riparian recovery more rapidly than total exclusion (Platts 1991; Elmore and Kauffman 1994). The passive restoration approach of livestock exclusion demonstrably has resulted in a rapid recovery of riparian vegetation (U.S. General Accounting Office 1988; Beschta et al. 1991; Kauffman et al. 1993); however, less is known regarding rates of channel morphology recovery (P. McDowell, University of Oregon, personal communications). Although moderate levels of winter grazing, late-season (autumn) grazing, or early-season (spring) grazing have been demonstrated to reduce harm by livestock in some riparian zones (Platts 1991; Elmore and Kauffman 1994), any grazing practice must include close monitoring of wood use and bank conditions so that livestock can be promptly removed before significant damage occurs. The variety of approaches to active restoration is potentially large and beyond the scope of this document, but what is important regarding active restoration procedures is that any approach reestablish the disturbance regimes and conditions so natural hydrologic, geomorphic, and biotic processes can occur. In some cases, active restoration may require removing or altering artificial structures contributing to degradation or preventing natural ecosystem processes from occurring. These practices might include obliterating roads that are contributing excessive amounts of sediment, removing instream or streambank structures (e.g., rip-rap, gabions, and anchored structures) that limit channel dynamics, reconfiguring channelized reaches to increase their sinuosity and floodplain connectivity, and removing mainstem dams to eliminate barriers to fish migration.

Instream Structures

A general deficiency of large, woody debris within streams draining forested watersheds is common throughout much of the Pacific Northwest, primarily because of historical practices of timber harvesting of riparian forests, splash damming, agricultural conversion, livestock grazing, and stream "cleaning" (i.e., the purposeful removal of wood debris). The natural recruitment of coarse, woody debris in such streams often requires much time (Gregory and Ashkenas 1990). As a result, managers often add large, woody debris. Where such practices are needed, the primary goal should be to provide natural amounts, types,

sizes, and spatial distributions of wood both in and along stream channels. During the inevitable high-water events that follow, added wood should function effectively in channel development and sediment and hydrologic routing (Gregory and Bisson 1997). Managers should place logs in or along channels so they resemble natural accumulations of debris, and should use complex wood debris (e.g., whole trees with branches and root wads if at all possible) to maximize habitat values and minimize potential for movement. The placement should enhance conditions that facilitate natural establishment of woody species (e.g., point-bar formation or nurse logs) so wood recruitment will become a self-perpetuating process. Anchoring or cabling complex pieces should be done sparingly, if at all, because it does not allow for the natural behavior of log accumulations during high-flow events. In this respect log length is critical; logs longer than the active channel width are not likely to move very far downstream (Lienkaemper and Swanson 1986).

Unfortunately, structural additions to channels (e.g., logs, boulders) are too often undertaken before anthropogenic impacts causing degradation have been eliminated or before significant natural recovery of riparian plant communities has occurred. In both situations, artificial structural additions are premature and can cause additional degradation to riparian and aquatic ecosystems. Of particular importance is the concern that placement activities should not diminish the natural regrowth capacity of riparian forests and should not severely curtail or accelerate natural channel dynamics such as channel migration, pool development, and streambank building. Riparian and stream ecosystems degraded from off-channel activities cannot be restored by focusing only on manipulations within a channel.

Throughout the western United States, inchannel placement of habitat structures has become one of the most common and widespread stream "enhancement" activities. Although instream structures have been commonly used in attempts to control channel erosion and rehabilitate fish habitat since the early twentieth century (Elmore and Kauffman 1994), systematic evaluation of their success has been limited. Furthermore, instream habitat handbooks (e.g., U.S. Forest Service 1952; Seehorn 1985, 1992) generally provide no ecological or geomorphic perspective as to where various habitat manipulations are appropriate (or inappropriate). A summary of instream enhancement projects throughout the region (Beschta et al. 1994) indicated little or no positive fisheries response to structural approaches. Clearly, the widespread practice of engineered structural modifications to streams with little or no scientific evidence of biological benefits represents a management paradox of immense proportions.

Misinterpretation of Ecosystem Needs

Active restoration should be undertaken to facilitate recovery of natural ecosystem processes (Kauffman et al. 1995). Riparian and instream activities that do not address ecosystem function and linkages are likely to fail or even exacerbate degradation of the ecosystem—a result of misinterpretation of ecosystem needs. Examples of such misinterpretation might include outplanting hatchery fish of nonindigenous genetic strains and introducing nonnative plant species. Implementation of riparian or inchannel activities that further degrade or prevent reestablishment of hydrologic, geomorphic, or biotic functions also represents a misinterpretation of ecosystem needs (Figure 3). Such activities may involve habitat manipulations such as blasting bedrock channels; adding logs and boulders in channels formed in floodplains of finely textured meadow systems; implementing in-channel engineering approaches that are heavily anchored by cable, metal rods, or boulders (structures that rely on geotextile fabrics to maintain their integrity); armoring streambanks with large boulders; and placing excavated sediments on streambanks and floodplains. Many of these approaches not only severely limit the capacity for streams to undergo natural adjustments in channel morphology and stream sinuosity through time, but they also may create conditions that suppress or stop the recovery of riparian vegetation.

Ecological restoration is a holistic approach not achieved through isolated manipulations of individual elements but through approaches ensuring that natural ecological processes occur...

Unfortunately, misinterpretating ecosystem needs is common with many instream rehabilitation and enhancement programs (Beschta et al. 1991; Kauffman et al. 1993). Stream manipulations targeted to fish habitat enhancement often exacerbate riparian and stream degradation for many reasons (Beschta et al. 1994):

- An inadequate understanding of riparian and stream ecology, particularly how stream-side vegetation and disturbance patterns shape both channels and habitat features;
- Sociopolitical pressures (e.g., it is socially or politically unacceptable to change ongoing land use practices that are causing degradation);
- Institutional limitations regarding the use of available funds (e.g., appropriations are designated only for mechanical or engineering approaches to stream manipulation with little or no appreciation of the effectiveness of improved stewardship);
- Management philosophies that emphasize immediately quantifiable project results (e.g., the number of instream structures built during a fiscal year) rather than ecological improvement or improved stewardship;
- Emphasis on a "landscaping" approach (e.g., designing channels or building structures based on preconceived plans rather than addressing factors limiting the processes that create these habitat features);
- A presumption that engineering approaches (e.g., placement of boulders, woody debris, gabions,

spawning gravels) are equivalent or superior to natural processes and structure;
- A presumption that inchannel structures can mitigate for riparian and aquatic degradation caused by land use practices (e.g., installing structures while allowing continued overgrazing, logging, or agricultural or industrial practices); and
- Current paradigms of land stewardship (e.g., a lack of a social or political land ethic that implicitly recognizes the value of natural or noncommodity products associated with naturally functioning and intact riparian ecosystems).

The rationale behind these reasons forms a common managerial paradigm: Stream, riparian, and fish habitat degradation brought about by anthropogenic activities, both locally and throughout a watershed, can be remedied solely through inchannel habitat manipulations. We suggest that the philosophy that natural habitat structure can be "improved" by engineering approaches misinterprets ecosystem needs and is an inadequate solution for fish habitat restoration. These approaches include activities that attempt to enhance fisheries habitat by eliminating natural barriers to fish passage, placing structures in intact ecosystems (old-growth forests), and putting spawning gravels or structural features such as logs or boulders in reaches where they would not naturally exist. Such activities not only carry a high risk of biological failure, but also risk a loss of capital resources, labor resources, and public credibility.

Sustainable and successful ecological restoration of degraded riparian systems is most likely to be achieved by considering the potential influences of proposed activities. Prior to the implementation of instream or riparian manipulations, the following questions should be addressed:
- Has passive restoration (e.g., changes in grazing, logging, etc.) been implemented, monitored, and evaluated prior to choosing structural manipulations?
- Will manipulations ultimately provide shade and thermally moderate stream temperature?
- Will they ultimately provide allocthonous inputs similar to that of stream-side vegetation?
- Will they ultimately provide the range of microhabitats typical of a particular stream?
- Will activities facilitate restoration of riparian vegetation that will restore natural channel morphology (e.g., overhanging banks, width-to-depth ratios, pool/riffle morphology)?
- Will they decrease time-rate dissipation of a stream's potential energy (i.e., stream power) by providing increased flow resistance from stream-side vegetation along a reach as compared with energy dissipation at localized points associated with inchannel structures?
- Will they allow for increased channel sinuosity from increased hydraulic roughness (as would occur with recovery of riparian vegetation)?
- Will biogeochemical and nutrient cycling influences on water chemistry—the results of the unique functional linkages between hydrologic and biotic features of intact riparian zones—be preserved or restored?
- Will the activities improve woody-debris recruitment and, hence, channel diversity because of enhanced vegetation establishment and growth?
- Are the restoration activities composed of naturally occurring materials? Are their characteristics and functions within the natural context of the riparian and stream reach to be treated?

Conclusions

Riparian zones are rich ecosystems in terms of biological diversity, unique biogeochemical processes, and productivity. For humans, riparian and stream ecosystems are a foci of commodity, recreational, and aesthetic values. The preservation and maintenance of intact riparian ecosystems and the restoration of degraded ones are important to local, regional, and global societies as well as to future generations.

While we recognize that ecological restoration sometimes comes at a high cost, we also note that ecological restoration is an investment in the natural capital of stream and aquatic systems and, hence, the environmental wealth of the nation. Healthy riparian ecosystems are a subsidy of nature. Conversely, degradation is the squandering of this natural wealth through the depletion of the productive capacity of ecosystems. Clearly, restoring once-productive riparian and aquatic ecosystems in the western United States is in the best long-term environmental and economic interests of the nation. Restored riparian and aquatic systems essentially will be self-maintaining and, therefore, useful in perpetuity (Cairns 1993). Because these ecosystems are a fundamental component of our life-support system, restoration should represent an important priority for both public and private landowners.

Complex ecosystems and associated habitat features cannot be created via simple and artificial construction of selected components. Ecological restoration is a holistic approach not achieved through isolated manipulations of individual elements but through approaches ensuring that natural ecological processes occur (National Research Council 1992). If society is to use, enjoy, and benefit from the wide range of values and products associated with western riparian and stream ecosystems, concerted efforts of ecological restoration should begin before their productive potential, diversity, and beauty are forever lost.

Acknowledgments

We wish to thank all of the biologists, hydrologists, landowners, and others dedicated to the restoration of the riparian and stream ecosystems of the world. Much of the research that generated the hypotheses and ideas presented in this paper was funded by the U.S.D.A. Pacific Northwest Research Station-Land and Water Interactions Team. We especially thank Peter Bisson, Nick Gerhardt, and Gordon Reeves for their helpful reviews of this paper.

References

Armour, C. L., D. A. Duff, and **W. Elmore.** 1991. The effects of livestock grazing on riparian and stream ecosystems. Fisheries 16:7–11.

Barnes, W. J. 1983. Population dynamics of woody plants on a river island. Can. J. Bot. 63:647–655.

Beschta, R. L. 1994. Opportunities and challenges in the restoration of riverine/riparian wetlands. Pages 18–27 *in* Partnerships and opportunities in wetland restoration. EPA 910/R-94-003. U.S. Environmental Protection Agency, Region 10, Seattle, WA.

———. 1997. Restoration of riparian and aquatic systems for improved aquatic habitats in the upper Columbia River basin. Pages 475–491 *in* D. J. Stouter, P. A. Bisson, and R. J. Naiman, eds. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Beschta, R. L., W. S. Platts, and **J. B. Kauffman.** 1991. Field review of fish habitat improvement projects in the Grande Ronde and John Day River basins of eastern Oregon. DOE/BP-21493-1. U.S. Department of Energy, Bonneville Power Administration, Portland, OR.

Beschta, R. L., W. S. Platts, J. B. Kauffman, and **M. T. Hill.** 1994. Artificial stream restoration—money well-spent or an expensive failure? Universities Council on Water Resources Annual (UCWR) Conference, Big Sky, Montana, 2–5 August 1994. UCWR, University of Illinois, Carbondale.

Bottom D. L. 1997. To till the water—a history of ideas in fisheries conservation. Pages 569–597 *in* D. J. Stouter, P. A. Bisson, and R. J. Naiman, eds. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Bradley, C. E., and **D. G. Smith.** 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. Can. J. Bot. 64:1,433–1,442.

Busse, C. G. 1989. Ecology of the *Salix* and *Populus* species of the Crooked River National Grassland. M.S. thesis. Oregon State University, Corvallis.

Cairns, J. Jr. 1993. Is restoration ecology practical? Restor. Ecol. 1:3–6.

Case, R. L. 1995. Structure, biomass, and successional dynamics of forested riparian ecosystems of the Upper Grande Ronde basin. M.S. thesis. Oregon State University, Corvallis.

Case, R. L., and **J. B. Kauffman.** In press. Wild ungulate influences on the recovery of willows, black cottonwood, and thin-leaf alder following cessation of cattle grazing in northeastern Oregon. Northwest Sci.

Council on Environmental Quality. 1989. Environmental trends—chapter 2. Water. Interagency Advisory Committee on Environmental Trends. Executive Office of the President, Council on Environmental Quality, Washington, DC.

Dahl, T. E. 1990. Wetland losses in the United States: 1780s to 1980s. FR 36-2. U.S. Fish and Wildlife Service, Washington, DC.

Elmore, W., and **J. B. Kauffman.** 1994. Riparian and watershed systems: degradation and restoration. Pages 211–232 *in* M. Vavra, W. A. Laycock, and R. D. Piper, eds. Ecological implications of herbivory in the West. Society of Range Management, Denver, CO.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. Conserv. Biol. 8:629–644.

Gecy, J. L., and **M. V. Wilson.** 1990. Initial establishment of riparian vegetation after disturbance by debris flows in Oregon. Am. Midl. Nat. 123:282–291.

Green, D. M., and **J. B. Kauffman.** 1995. Succession and livestock grazing in a Northeast Oregon riparian ecosystem. J. Range Manage. 48:307–313.

Gregory, S. V., and **P. A. Bisson.** 1997. Degradation and loss of anadromous salmonid habitat in the Pacific Northwest. Pages 277–314 in D. J. Stouder, P. A. Bisson, and R. J. Naiman, eds. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Gregory, S. V., F. J. Swanson, W. A. McKee, and **K. W. Cummins.** 1991. An ecosystem perspective of riparian zones. Bioscience 41(8):540–550.

Gregory, S. V., and **L. R. Ashkenas.** 1990. Riparian management guide. Willamette National Forest, U.S. Forest Service, Region 6, Portland, OR.

Hirsch, A., and **C. A. Segelquist.** 1978. Protection and management of riparian ecosystems: activities and views of the U.S. Fish and Wildlife Service. Pages 344–352 *in* R. R. Johnson and J. F. McCormack, tech. coords. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. U.S. For. Serv. Gen. Tech. Rep. WO-12.

Howe, W. H., and **F. L. Knopf.** 1991. On the imminent decline of Rio Grande cottonwoods in central New Mexico. Southwest. Nat. 36:218–224.

Inter-Fluve, Inc. 1995. Mono basin stream projects. Report on the strategy, quality, and success of existing stream recovery projects. Inter-Fluve, Inc., Bozeman, MT.

Jackson, L. L., N. Lopoukhine, and **D. Hillyard.** 1995. Ecological restoration: a definition and comments. Restor. Ecol. 3:71–75.

Johnson, R. R., and **J. F. McCormack.** 1979. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. General Technical Report WO-12. U.S. Forest Service, Washington, DC.

Kauffman, J. B. 1988. The status of riparian habitats in Pacific Northwest forests. Pages 45–55 *in* K. J. Raedeke, ed. Streamside management: riparian wildlife and forestry interactions. College of Forest Resources, Contribution No. 59, University of Washington, Seattle.

Kauffman, J. B., and **W. C. Krueger.** 1984. Livestock impacts on riparian ecosystems and stream management implications: a review. J. Range Manage. 37:430–437.

Kauffman, J. B., R. L. Beschta, and **W. S. Platts.** 1993. Fish habitat improvement projects in the Fifteenmile Creek and Trout Creek basins of central Oregon: field review and management recommendations. DOE/BP-18955-1. U.S. Department of Energy, Bonneville Power Administration, Portland, OR.

Kauffman, J. B., R. L. Case, D. Lytjen, N. Otting, and **D. L. Cummings.** 1995. Ecological approaches to riparian restoration in northeastern Oregon. Restoration and Management Notes 13:12–15.

Kauffman, J. B., W. C. Krueger, and **M. Vavra.** 1982. Impacts of a late-season grazing scheme on nongame wildlife habitat in a Wallowa mountain riparian ecosystem. Pages 208–209 *in* Wildlife-livestock relationships symposium. Couer d'Alene, ID.

Lienkaemper, G. W., and **F. J. Swanson.** 1986. Dynamics of large woody debris in streams in old-growth Douglas-fir forests. Can J. For. Res. 17:150–156.

Lowry, M. M. 1993. Groundwater elevations and temperature adjacent to a beaver pond in central Oregon. M.S. thesis. Oregon State University, Corvallis.

Mahoney, J. M., and **S. B. Rood.** 1992. Response of a hybrid poplar to water table decline in different substrates. For. Ecol. Manage. 54:141–156.

McBride, J. R., and **J. Strahan.** 1984. Establishment and survival of woody riparian species on gravel bars of an intermittent stream. Am. Midl. Nat. 112:235–245.

Miller, R. R., J. D. Williams, and **J. E. Williams.** 1989. Extinctions of North American fishes during the past century. Fisheries 14:22–38.

Naiman, R. J., C. A. Johnston, and **J. C. Kelley.** 1988. Alteration of North American streams by beaver. Bioscience 38:753–762.

Naiman, R. J., J. J. Magnuson, D. M. McKnight, and **J. A. Stanford.** 1995. The freshwater imperative: a research agenda. Island Press, Washington, DC.

National Research Council. (U.S.) Committee on restoration of aquatic ecosystems—science, technology and public policy. 1992. Restoration of aquatic ecosystems. National Academy Press, Washington, DC.

———. (U.S.) Committee on characterization of wetlands. 1995. Wetlands—characteristics and boundaries. National Academy Press, Washington, DC.

———. (U.S.) Committee on protection and management of Pacific Northwest salmonids. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, DC.

Noble, M. G. 1979. The origin of *Populus deltoides* and *Salix interior* zones on point bars along the Minnesota River. Am. Midl. Nat. 102(1):59–67.

Platts, W. S. 1991. Livestock grazing. Pages 389–483 *in* Influences of forest and rangeland management on salmonid fishes and their habitats. Am. Fish. Soc. Spec. Publ. 19, Bethesda, MD.

Quammen, M. L. 1986. Measuring the success of wetlands mitigation. National Wetlands Newsletter 8(5):6–8.

Rood, S. B., and **J. M. Mahoney.** 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. Environ. Manage. 14:451–464.

Schulz, T. T., and **W. C. Leininger.** 1990. Differences in riparian vegetation structure between grazed areas and exclosures. J. Range Manage. 43(4):295–299.

Seehorn, M. E. 1985. Stream habitat improvement handbook. R8-T-7. U.S. Forest Service, Southern Region, Atlanta, GA.

———. 1992. Stream habitat improvement handbook. U.S. Forest Service, Southern Region, Atlanta, GA.

U.S. Forest Service. 1952. Fish stream improvement handbook. U.S. Forest Service, Washington, DC.

U.S. General Accounting Office. 1988. Public rangelands: Some riparian areas restored, but widespread improvement will be slow. RCED-88-105. U.S. General Accounting Office, Washington, DC.

Williams J. E., J. E. Johnson, D. A. Hendrickson, S. Contreras-Balderas, J. D. Williams, M. Navarro-Mendoza, D. E. McAllister, and **J. E. Deacon.** 1989. Fishes of North America: endangered, threatened, or of special concern. Fisheries 14:2–20.

Wilson, R. E. 1970. Succession in stands of *Populus deltoides* along the Missouri River in southeastern South Dakota. Am. Midl. Nat. 83:330–342.

Annals of Forest Science (2015) 72:145–167
DOI 10.1007/s13595-014-0446-5

REVIEW PAPER

Climate change impacts and adaptation in forest management: a review

Rodney J. Keenan

Received: 1 September 2014 / Accepted: 10 December 2014 / Published online: 14 January 2015
© INRA and Springer-Verlag France 2015. This article is published with open access at Springerlink.com

Abstract

• ***Key message*** **Adaptation of forest management to climate change requires an understanding of the effects of climate on forests, industries and communities; prediction of how these effects might change over time; and incorporation of this knowledge into management decisions. This requires multiple forms of knowledge and new approaches to forest management decisions. Partnerships that integrate researchers from multiple disciplines with forest managers and local actors can build a shared understanding of future challenges and facilitate improved decision making in the face of climate change.**

• ***Context*** Climate change presents significant potential risks to forests and challenges for forest managers. Adaptation to climate change involves monitoring and anticipating change and undertaking actions to avoid the negative consequences and to take advantage of potential benefits of those changes.

• ***Aims*** This paper aimed to review recent research on climate change impacts and management options for adaptation to climate change and to identify key themes for researchers and for forest managers.

• ***Methods*** The study is based on a review of literature on climate change impacts on forests and adaptation options for forest management identified in the Web of Science database, focusing on papers and reports published between 1945 and 2013.

• ***Results*** One thousand one hundred seventy-two papers were identified in the search, with the vast majority of papers published from 1986 to 2013. Seventy-six percent of papers involved assessment of climate change impacts or the sensitivity or vulnerability of forests to climate change and 11 % (130) considered adaptation. Important themes from the analysis included (i) predicting species and ecosystem responses to future climate, (ii) adaptation actions in forest management, (iii) new approaches and tools for decision making under uncertainty and stronger partnerships between researchers and practitioners and (iv) policy arrangements for adaptation in forest management.

• ***Conclusions*** Research to support adaptation to climate change is still heavily focused on assessing impacts and vulnerability. However, more refined impact assessments are not necessarily leading to better management decisions. Multi-disciplinary research approaches are emerging that integrate traditional forest ecosystem sciences with social, economic and behavioural sciences to improve decision making. Implementing adaptation options is best achieved by building a shared understanding of future challenges among different institutions, agencies, forest owners and stakeholders. Research-policy-practice partnerships that recognise local management needs and indigenous knowledge and integrate these with climate and ecosystem science can facilitate improved decision making.

Keywords Climate change · Adaptation · Vulnerability · Policy · Forest management · Impacts · Effects · Responses

Handling Editor: Erwin Dreyer

This research was partly undertaken during the period the author was Director of the Victorian Centre for Climate Change Adaptation Research and part-funded by the Victorian Government. It was completed with support from the University of Melbourne under a Special Studies Program grant.

R. J. Keenan (✉)
Department of Forest and Ecosystem Science, The University of Melbourne, 221 Bouverie St., Carlton, VIC 3010, Australia
e-mail: rkeenan@unimelb.edu.au

1 Introduction

Anthropogenic climate change presents potential risks to forests and future challenges for forest managers. Responding to

climate change, through both mitigation and adaptation, may represent a paradigm shift for forest managers and researchers (Schoene and Bernier 2012). Climate change is resulting in increasing air temperature and changing precipitation regimes, including changes to snowfall and to the timing, amount and inter-annual variability of rainfall (IPCC 2013). Forests are widespread, long-lived ecosystems that are both intensively and extensively managed. They are potentially sensitive to these longer term climatic changes, as are the societies and economies that depend on them (Bernier and Schöne 2009). Climate change increases the potential consequences of many existing challenges associated with environmental, social or economic change.

Whilst forest ecosystems are resilient and many species and ecosystems have adapted historically to changing conditions, future changes are potentially of such magnitudes or will occur at rates that are beyond the natural adaptive capacity of forest species or ecosystems, leading to local extinctions and the loss of important functions and services, including reduced forest carbon stocks and sequestration capacity (Seppälä et al. 2009).

Recent global warming has already caused many changes in forests (Lucier et al. 2009). Aspects of climate change may be positive for some tree species in some locations. Tree growth is observed to be increasing in some locations under longer growing seasons, warmer temperatures and increased levels of CO_2. However, many projected future changes in climate and their indirect effects are likely to have negative consequences for forests. Observed shifts in vegetation distribution (Kelly and Goulden 2008; Lenoir et al. 2010) or increased tree mortality due to drought and heat in forests worldwide (Allen et al. 2010) may not be due to human-induced climate change but demonstrate the potential impacts of rapid climate change. These impacts may be aggravated by other human-induced environmental changes such as increases in low elevation ozone concentrations, nitrogenous pollutant deposition, the introduction of exotic insect pests and pathogens, habitat fragmentation and increased disturbances such as fire (Bernier and Schöne 2009). Other effects of climate change may also be important for forests. Sea level rise is already impacting on tidal freshwater forests (Doyle et al. 2010) and tidal saltwater forests (mangroves) are expanding landward in sub-tropical coastal reaches taking over freshwater marsh and forest zones (Di Nitto et al. 2014).

With projected future change, species ranges will expand or contract, the geographic location of ecological zones will shift, forest ecosystem productivity will change and ecosystems could reorganise following disturbances into ecological systems with no current analogue (Campbell et al. 2009; Fischlin et al. 2009). Forests types differ in their sensitivity to climatic change. Bernier and Schöne (2009) considered boreal, mountain, Mediterranean, mangrove and tropical moist forests most vulnerable to climate change. However, there has been recent debate about the vulnerability of tropical moist forests (Corlett 2011; Huntingford et al. 2013; Feeley et al. 2012), and temperate forests in areas subject to drier climates may be more at risk (Choat et al. 2012).

Adapting to these changing and uncertain future conditions can be considered from a number of perspectives (McEvoy et al. 2013). Policy and management might be directed at avoiding or reducing the impact of climate-related events, reducing vulnerability to future climatic conditions, managing a broader suite of climate 'risks' or increasing resilience and capacity in forest ecological and production systems to recover from climate 'shocks'.

Adapting forest management to climate change involves monitoring and anticipating change and undertaking actions to avoid the negative consequences or take advantage of potential benefits of those changes (Levina and Tirpak 2006). Adopting the principles and practices of sustainable forest management (SFM) can provide a sound basis for addressing the challenges of climate change. However, Innes et al. (2009) pointed out that our failure to implement the multi-faceted components of sustainable forest management in many forests around the world is likely to limit capacity to adapt to climate change. Forest managers will need to plan at multiple spatial and temporal scales and adopt more adaptive and collaborative management approaches to meet future challenges.

Whilst forest managers are accustomed to thinking in long time scales—considering the long-term implications of their decisions and factoring in uncertainty and unknowns into management—many are now responding to much shorter term social or economic imperatives. Local forestry practices are often based on an implicit assumption that local climate conditions will remain constant (Guariguata et al. 2008). Other social and economic changes will also continue to drive changes in forest management (Ince et al. 2011). For example, a growing global population, rapid economic development and increased wealth are driving demand for food and fibre crops and forest conversion to agriculture in many developing countries (Gibbs et al. 2010). Climate change mitigation objectives are increasing demands for wood-based bioenergy and the use of wood in construction and industrial systems. Increasing urbanisation is changing the nature of social demands on forests, and decreasing rural populations is limiting the availability of labour and capacity for intensive forest management interventions.

Ecosystem-based adaptation is being promoted as having the potential to incorporate sustainable management, conservation and restoration of ecosystems into adaptation to climate change (IUCN 2008). This can be achieved more effectively by integrating ecosystem management and adaptation into national development policies through education and outreach to raise societal awareness about the value of ecosystem services (Vignola et al. 2009).

Kimmins (2002) invoked the term 'future shock', first coined by Toffler (1970) to describe the situation where

societal expectations from forests were changing faster than the institutional capacity for change in forest management organisations. The pace of climate change is likely to intensify this phenomenon. Empirically based management based on traditional 'evidence-based' approaches therefore will potentially not develop quickly enough for development of effective future management options. How can managers consider rapid change and incorporate the prospect of very different, but uncertain, future climatic conditions into their management decisions? What types of tools are needed to improve decision making capacity?

This study aimed to review the literature on studies to support forest management in a changing climate. It builds on the major review of Seppala (2009), in particular Chapter 6 of that report by Innes et al. (2009).

2 Methods

The study involved a systematic assessment of the literature based on the database Web of Science (Thomson-Reuters 2014), an online scientific citation indexing service that provides the capacity to search multiple databases, allowing in-depth exploration of the literature within an academic or scientific discipline.

The following search terms were used in the titles of publications:

(forest or tree* or (terrestrial and ecosystem)) and climat* and (adapt* or impact* or effect* or respons*) and*

(forest or tree*) and climat* and vulnerabilit* or sensitivit*)*

The search was restricted to publications between 1945 and 2013. References related solely to climate change mitigation were excluded, as were references where the word 'climate' simply referred to a study in a particular climatic zone. This left a database of 1172 publications for analyses (a spreadsheet of the papers revealed in the search can be obtained from the author). References were classified into various types of studies and different regions, again based on the titles. Not all papers identified in the search are referenced. The selection of themes for discussion and papers for citation was a subjective one, based on scanning abstracts and results from relevant individual papers. The focus was important themes from key papers and literature from the last 5 years. The review includes additional papers not revealed in the search relating to these themes including selected papers from the literature in the year 2014.

3 Results

Of the published papers relating to climate impacts or adaptation selected for analysis, the vast majority of papers were published from 1986 onwards. The earliest paper dated from 1949 (Gentilli 1949) analysing the effects of trees on climate, water and soil. Most studies prior to 1986 (and even some published later) focused on the effects of trees on local or wider regional climate (Lal and Cummings 1979; Otterman et al. 1984; Bonan et al. 1992), the implications of climate variability (Hansenbristow et al. 1988; Ettl and Peterson 1995; Chen et al. 1999), studies of tree and forest responses across climatic gradients (Grubb and Whitmore 1966; Bongers et al. 1999; Davidar et al. 2007) or responses to historical climate (Macdonald et al. 1993; Huntley 1990; Graumlich 1993).

One thousand twenty-six papers specifically addressed future climate change (rather than historical climate or gradient analysis). Of these, 88 % studied impacts, effects, vulnerability or responses to climate change in tree species, forests, forest ecosystems or the forest sector (Fig. 1). The first study analysing the potential impacts of future climate change on terrestrial ecosystems was published in 1985 (Emanuel et al. 1985) with other highly cited papers soon after (Pastor and Post 1988; Cannell et al. 1989).

Twelve percent of papers (129) considered adaptation options, including 10 papers on adaptation in the forest sector. The first papers to focus on adaptation in the context of climate change were in 1996 with a number of papers published in that year (Kienast et al. 1996; Kobak et al. 1996; Dixon et al. 1996). Publications were then relatively few each year until the late 2000s with numbers increasing to 11 in 2009, 22 in 2010 and 27 in 2011. Publications on adaptation dropped to 14 papers in 2013. The ratio of adaptation-related papers has increased more recently, with 19 % of total publications on adaptation in the last 5 years. Most papers considering adaptation since the early 2000s have related to the integration of adaptation and forest management (e.g. Lindner 2000; Spittlehouse 2005; Kellomaki et al. 2008; Guariguata 2009; Bolte et al. 2009; Keskitalo 2011; Keenan 2012; Temperli et al. 2012).

Analyses of the implications of climate change for the forest sector have focused heavily on North America: Canada (Ohlson et al. 2005; Van Damme 2008; Rayner et al. 2013; Johnston et al. 2012) and the USA (Joyce et al. 1995; Blate et al. 2009; Kerhoulas et al. 2013); and Europe (Karjalainen et al. 2003; von Detten and Faber 2013). There has been a stronger consideration in recent years of social, institutional and policy issues (Ogden and Innes 2007b; Kalame et al. 2011; Nkem et al. 2010; Spies et al. 2010; Somorin et al. 2012) and the assessment of adaptive capacity in forest management organisations and in society more generally (Keskitalo 2008; Lindner et al. 2010; Bele et al. 2013a).

Regionally, there have been relatively few published journal articles on impacts or adaptation in forests in the Southern Hemisphere (Hughes et al. 1996; Williams 2000; Pinkard et al. 2010; Gonzalez et al. 2011; Mok et al. 2012; Breed et al. 2013), although there have been more studies in the grey literature for Australian forests (Battaglia et al. 2009; Cockfield et al. 2011; Medlyn et al. 2011; Stephens et al.

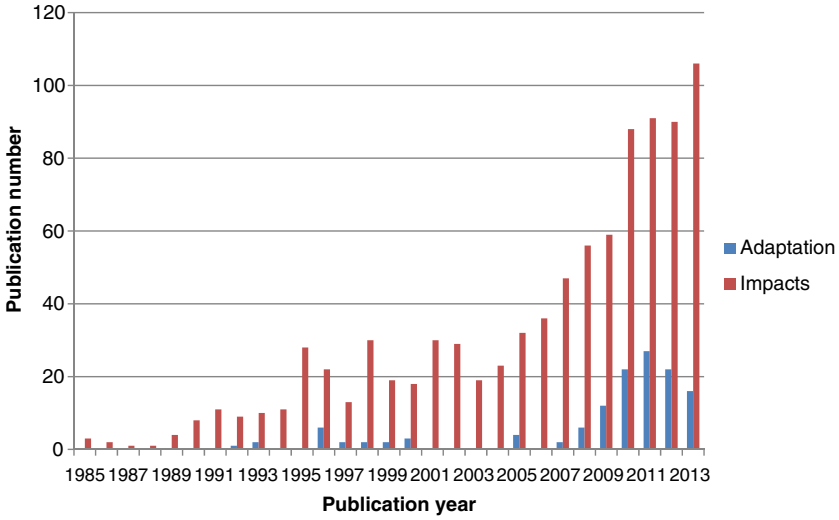


Fig. 1 Publication numbers by publication year for publications relating to climate change and forests from a search of the Web of Science database to the end of 2013 (1025 in total, 896 publications studied climate change impacts, responses or vulnerability, 129 studied adaptation)

2012). There have been some valuable analyses for the tropics (Guariguata et al. 2008, 2012; Somorin et al. 2012; Feeley et al. 2012).

Analysis of the publications identified the following key themes: (i) predicting species and ecosystem responses to future climate, (ii) adaptation actions in forest management, (iii) new approaches and tools for decision making under uncertainty and stronger partnerships between researchers and practitioners and (iv) policy arrangements for adaptation in forest management. These are discussed in more detail below.

3.1 Predicting species and ecosystem responses to future climate

Forest managers have long used climatic information in a range of ways in planning and decision making. Climate information has been used extensively to define and map vegetation types and ecological zones and for modelling habitat distributions of vertebrates and invertebrates (Daubenmire 1978; Pojar et al. 1987; Thackway and Cresswell 1992), for species and provenance selection (Booth et al. 1988; Booth 1990) and seed zone identification (Johnson et al. 2004), for forest fire weather risk assessment and fire behaviour modelling (Carvalho et al. 2008), for modelling forest productivity (Battaglia et al. 2004) and analysing the dynamics of a range of ecological processes (Anderson 1991; Breymeyer and Melillo 1991). Predicting species responses to future climate change presents a different set of challenges, involving consideration of predictions of future climate that are often outside the historical range of variability of many species. These challenges are discussed in the next section.

3.1.1 Species responses to climate

Aitken et al. (2008) argued that there were three possible fates for forest tree populations in rapidly changing climatic conditions: persistence through spatial migration to track their ecological niches, persistence through adaptation to new conditions in current locations or the extirpation of the species. Predicting the potential fate of populations in these conditions requires the integration of knowledge across biological scales from individual genes to ecosystems, across spatial scales (for example, seed and pollen dispersal distances or breadth of species ranges) and across temporal scales from the phenology of annual developmental cycle traits to glacial and interglacial cycles.

Whilst there has been widespread use of climatic information to predict future distributions in species distribution models (SDMs, Pearson and Dawson 2003; Attorre et al. 2008; Wang et al. 2012; Ruiz-Labourdette et al. 2013), understanding of the range of climatic and non-climatic factors that will determine the future range of a particular species remains limited. Many now feel that SDMs are of limited value in adaptation decision making or species conservation strategies. Some of these limitations are summarised in Table 1.

For example, models indicate significant shifts in patterns of tree species distribution over the next century but usually without any intrinsic consideration of the biological capacity of populations to move, internal population dynamics, the extent and role of local adaptation or the effects of climate and land use (Aitken et al. 2008; Thuiller et al. 2008). In a recent study, Dobrowski et al. (2013) found that the predicted speed of movement of species to match the predicted rate of climate change appears to be well beyond the historical rates of migration. Whilst modelled outputs suggest that migration rates of 1000 m per year or higher will be necessary to track changing habitat conditions (Malcolm et al. 2002), actual migration rates in response to past change are generally considered to have been less than 100 m per year. This was reinforced by model predictions that incorporate species dispersal characteristics for five tree species in the eastern USA indicated very low probabilities of dispersal beyond 10–20 km from current species boundaries by 2100 (Iverson et al. 2004).

Table 1 Limitations to species distribution models (SDMs) for predicting the impacts of climate change on forest tree species

Challenge	Examples	References
Predicting capacity of species to move	Species have historically moved much more slowly than future climate is projected to change. Humans may have a role in shifting species distributions. Fragmentation or lack of suitable habitat can limit movement	Iverson et al. (2004), Dobrowski et al. (2013), Clark (2007), Corlett and Westcott (2013)
Local adaptation	Many species have the capacity to adapt to changes in local conditions through refugia	Aitken et al. (2008)
Uncertainty in predicting future climate, particularly precipitation or aridity	Water balance and aridity can be major factor in determining future tree growth	Dobrowski et al. (2013), Wang et al. (2012)
Predicting and incorporating effects of extreme events on tree species populations	Extreme events (frost, fire, flood, high temperatures) can be a major determinant of species survival	Zimmermann et al. (2009)
Lag effects and gene flow within species	Species are generally still responding to past changes in climate and not optimally suited to current conditions	Thuiller et al. (2008), Kuparinen et al. (2010), Kremer et al. (2012)
Epigenetic effects	The growing conditions of the parents can affect the capacity of progeny to cope with drier or warmer conditions	Brautigam et al. (2013)
Biotic effects	Insect pests and diseases can be strong determinants of species distribution	Anderson et al. (2012), (Brooker et al. 2007)
Phenology and life history traits	Age to sexual maturity, fecundity, seed dispersal, or chilling or dormancy requirements	Nitschke and Innes (2008b)
Mutual benefits with plants or animals	Some species have strong interactions with other plants, animals or micro-organisms that may respond differentially to climate	Six (2009), Gilman et al. (2012)
Competition effects	SDMs generally assume open-grown conditions. Competition with other tree species can determine species distribution	Castagneri and Motta (2010)

Corlett and Westcott (2013) also argued that plant movements are not realistically represented in models used to predict future vegetation or carbon-cycle feedbacks and that fragmentation of natural systems is likely to slow migration rates.

However, these estimates do not account for the role of humans in influencing tree species distributions, which they have done for thousands of years (Clark 2007), and managed translocation may be an option for conserving many tree species, but there are significant unresolved technical and social questions about implementing translocation at a larger scale (Corlett and Westcott 2013).

Most early SDMs relied primarily on temperature envelopes to model future distribution, but factors such as precipitation and soil moisture are potentially more limiting and more important in determining distribution patterns (Dobrowski et al. 2013). Aitken et al. (2008) found that the degree to which variation in precipitation explains phenotypic variation among populations is greater in general for populations from continental than from maritime climates and greater for lower latitude than higher latitude populations. However, precipitation alone is often not a good predictor of variation and there is often a strong interaction with temperature (Andalo et al. 2005). Heat to moisture index or aridity is probably more important in determining future distribution or productivity than precipitation alone (Aitken et al. 2008; Harper et al. 2009; Wang et al. 2012). Soil properties (depth, texture and organic matter content) have a major influence on plant-available water, but few SDMs incorporate these.

Future precipitation is proving more difficult to model than temperature, due to the complex effects of topography, and there are more widely varying estimates between global circulation models (GCMs) of future change in precipitation (IPCC 2013). As such, there is more uncertainty around the extent to which moisture stress will change with warming and the extent to which natural selection pressures will change as a result. Even without changes in precipitation, increased temperatures will increase the length of growing season and potential evapotranspiration (PET) resulting in more water use over the year and greater risk plant water shortage and drought death.

Changes in the intervals of extreme events (extreme heat, cold, precipitation, humidity, wind) may also matter more than changes in the mean. Current forecasting approaches that produce future climate averages may make it difficult to detect non-linear ecosystem dynamics, or threshold effects, that could trigger abrupt ecosystem change (Campbell et al. 2009). Zimmermann et al. (2009) found that predictions of spatial patterns of tree species in Switzerland were improved by incorporating measures of extremes in addition to means in SDMs.

The risks of future climate will also depend on the management goal. If the aim is simply to conserve genetic diversity, risks of extinction or reduction in genetic diversity may be overstated by SDMs because much of the genetic variation within tree species is found within rather than among their populations, and the extinction of a relatively large proportion

of a population is generally likely to result in relatively little overall loss of genetic diversity (Hamrick 2004). Local habitat heterogeneity (elevation, slope aspect, moisture, etc.) can preserve adaptive genetic variation that, when recombined and exposed to selection in newly colonised habitats, can provide for local adaptation. The longevity of individual trees can also retard population extinction and allow individuals and populations to survive until habitat recovery or because animal and wind pollination can provide levels of pollen flow that are sufficient to counteract the effects of genetic drift in fragmented populations. Consequently, widespread species with large populations, high fecundity and higher levels of phenotypic plasticity are likely to persist and adapt and have an overall greater tolerance to changing climates than predicted by SDMs (Alberto et al. 2013).

Tree species distributions have always been dynamic, responding to changing environmental conditions, and populations are likely to be sub-optimal for their current environments (Namkoong 2001; Wu and Ying 2004). These lag effects are important in predicting species responses to climate change. In a modelling study of Scots pine and silver birch, Kuparinen et al. (2010) predicted that after 100 years of climate change, the genotypic growth period length of both species will lag more than 50 % behind the climatically determined optimum. This lag is reduced by increased mortality of established trees, whereas earlier maturation and higher dispersal ability had comparatively minor effects. Thuiller et al. (2008) suggest that mechanisms for incorporating these 'trailing edge' effects into SDMs are a major area of research potential.

Trees are also capable of long-distance gene flow, which can have both adaptive evolution benefits and disadvantages. Kremer et al. (2012) found that there may be greater positive effects of gene flow for adaptation but that the balance of positive to negative consequences of gene flow differs for leading edge, core and rear sections of forest distributions.

Epigenetics—heritable changes that are not caused by changes in genetic sequences but by differences in the way DNA methylation controls the degree of gene expression—is another complicating factor in determining evolutionary response to climate change (Brautigam et al. 2013). For example, a recent study in Norway spruce (*Picea abies*) showed that the temperature during embryo development can dramatically affect cold hardiness and bud phenology in the offspring. In some cases, the offspring's phenotype varied by the equivalent of 6° of latitude from what was expected given the geographic origin of the parents. It remains uncertain whether these traits are persistent, both within an individual's lifetime and in its offspring and subsequent generations (Aitken et al. 2008). It is suggested that analysis of the epigenetic processes in an ecological context, or 'ecological epigenetics', is set to transform our understanding of the way in which organisms function in the landscape. Increased understanding of these processes can inform efforts to manage and breed tree species to help them cope with environmental stresses (Brautigam et al. 2013). Others argue that whilst investigating this evolutionary capacity to adapt is important, understanding responses of species to their changing biotic community is imperative (Anderson et al. 2012) and 'landscape genomics' may offer a better approach for informing management of tree populations under climate change (Sork et al. 2013).

These recent results indicate the importance of accounting for evolutionary processes in forecasts of the future dynamics and productivity of forests. Species experiencing high mortality rates or populations that are subject to regular disturbances such as storms or fires might actually be the quickest to adapt to a warming climate.

Species life history characteristics are also not usually well represented in most climate-based distribution models. Important factors include age to sexual maturity, fecundity, seed dispersal, competition or chilling or dormancy requirements (Nitschke and Innes 2008b).

Competitive relationships within and between species are likely to be altered by climate change. Most models also assume open site growth conditions, rather than those within a forest, where the growth environment will be quite different. However, increased disturbance associated with climate change may create stand reinitiation conditions more often than has occurred in the past, altering competitive interactions.

Process-based models of species range shifts and ecosystem change may capture more of the life history variables and competition effects that will be important in determining responses to climate change (Kimmins 2008; Nitschke and Innes 2008a, b). These can provide the basis for a more robust assessment framework that integrates biological characteristics (e.g. shade tolerance and seedling establishment) and disturbance characteristics (e.g. insect pests, drought and fire topkill). Matthews et al. (2011) integrated these factors into a decision support system that communicates uncertainty inherent in GCM outputs, emissions scenarios and species responses. This demonstrated a greater diversity among species to adapt to climate change and provides a more practical assessment of future species projections.

In summary, whilst SDMs and other climate-based modelling approaches can provide a guide to potential species responses, the extent to which future climate conditions will result in major range shifts or extinction of species is unclear and the value of this approach in adaptation and decision making is limited. The evidence from genetic studies seems to suggest that many species are reasonably robust to potential future climate change. Those with a wide geographic range, large populations and high fecundity may suffer local population extinction but are likely to persist and adapt whilst suffering adaptational lag for a few generations. For example, Booth (2013) considered that many eucalyptus

species, some of which are widely planted around the world, had a high adaptive capacity even though their natural ranges are quite small.

However, large contractions or shifts in distribution could have significant consequences for different forest values and species with small populations, fragmented ranges, low fecundity or suffering declines due to introduced insects or diseases may have a higher sensitivity and are at greater risk in a changing climate (Aitken et al. 2008).

3.1.2 Ecosystem responses to climate

Projecting the fate of forest ecosystems under a changing climate is more challenging than for species. It has been well understood for some time that species will respond individualistically to climate change, rather than moving in concert, and that this is likely to result in 'novel' ecosystems, or groups of species, that are not represented in current classifications (Davis 1986). Forecasts need to consider the importance of these new species interactions and the confounding effects of future human activities.

Climate change affects a wide range of ecosystem functions and processes (Table 2). These include direct effects of temperature and precipitation on physiological and reproductive processes such as photosynthesis, water use, flowering, fruiting and regeneration, growth and mortality and litter decomposition. Changes in these processes will have effects on species attributes such as wood density or foliar nutrient status. Indirect effects will be exhibited through changing fire and other climate-driven disturbances. These will ultimately have impacts on stand composition, habitat structure, timber supply capacity, soil erosion and water yield.

Most early studies of forest ecosystem responses to climate change were built around ecosystem process models at various scales (Graham et al. 1990; Running and Nemani 1991; Rastetter et al. 1991). A number of recent studies have investigated the effects of past and current climate change on forest processes, often with surprising effects (Groffman et al. 2012).

Observed forest growth has increased recently in a number of regions, for example over the last 100 years in Europe (Pretzsch et al. 2014; Kint et al. 2012), and for more recent observations in Amazon forests (Phillips et al. 2008). In a major review, Boisvenue and Running (2006) found that at finer spatial scales, a trend is difficult to decipher, but globally, based on both satellite and ground-based data, climatic changes seemed to have a generally positive impact on forest productivity when water was not limiting. However, there can be a strong difference between species, complicating ecosystem level assessments (Michelot et al. 2012), and there are areas with little observed change (Schwartz et al. 2013). Generally, there are significant challenges in detecting the response of forests to climate change. For example, in the tropics, the lack of historical context, long-term growth records and access to data are real barriers (Clark 2007) and temperate regions also have challenges, even with well-designed, long-term experiments (Leites et al. 2012).

Table 2 Forest ecosystem responses to elevated CO_2 and climate change

	Faster response	Slower response
Direct	• Photosynthesis	• Litter decomposition
	• Water use/transport	• Foliar nutrient status
	• Flowering/phenology	• Genetic change
	• Regeneration	• Tree species distribution and stand composition
	• Growth and mortality	
	• Wood density/quality	
	• Frost/storm damage	
Indirect	• Increased fire frequency/intensity	• Habitat composition and structure
	• Disease impacts	• Wood supply
	• More insect pests	• Erosion and soil loss
	• Increased invasive species	• Water yield
	• Water quality	

Projections of net primary productivity (NPP) under climate change indicate that there is likely to be a high level of regional variation (Zhao et al. 2013). Using a process model and climate scenario projections, Peters et al. (2013) predicted that average regional productivity in forests in the Great Lakes region of North America could increase from 67 to 142 %, runoff could potentially increase from 2 to 22 % and net N mineralization from 10 to 12 %. Increased productivity was almost entirely driven by potential CO_2 fertilization effects, rather than by increased temperature or changing precipitation. Productivity in these forests could shift from temperature limited to water limited by the end of the century. Reyer et al. (2014) also found strong regional differences in future NPP in European forests, with potential growth increases in the north but reduced growth in southern Europe, where forests are likely to be more water limited in the future. Again, assumptions about the impact of increasing CO_2 were a significant factor in this study.

In a different type of study using analysis of over 2400 long-term measurement plots, Bowman et al. (2014) found that there was a peaked response to temperature in temperate and sub-tropical eucalypt forests, with maximum growth occurring at a mean annual temperature of 11 °C and maximum temperature of the warmest month of 25–27 °C. Lower temperatures directly constrain growth, whilst high temperatures primarily reduced growth by reducing water availability but they also appeared to exert a direct negative effect. Overall, the productivity of Australia's temperate eucalypt forests could decline substantially as the climate warms, given that 87 % of these forests currently experience a mean annual temperature above the 'optimal' temperature.

Incorporating the effects of rising CO_2 in models of future tree growth continues to be a major challenge. The sensitivity of projected productivity to assumptions regarding increased CO_2 was high in modelling studies of climate change impacts in commercial timber plantations in the Southern Hemisphere (Kirschbaum et al. 2012; Battaglia et al. 2009), and a recent analysis indicated a general convergence of different model predictions for future tree species distribution in Europe, with most of the difference between models due to the way in which this effect is incorporated (Cheaib et al. 2012). Increased CO_2 has been shown to increase the water-use efficiency of trees, but this is unlikely to entirely offset the effects of increased water stress on tree growth in drying climates (Leuzinger et al. 2011; Booth 2013). In general, despite studies extending over decades and improved understanding of biochemical processes (Franks et al. 2013), the impacts of increased CO_2 on tree and stand growth are still unresolved (Kallarackal and Roby 2012).

Integrating process model outputs with spatially explicit landscape models can improve understanding and projection of responses and landscape planning and this could provide for simulations of changes in ecological processes (e.g. tree growth, succession, disturbance cycles, dispersal) with other human-induced changes to landscapes (Campbell et al. 2009).

Investigation of current species responses to changing climate conditions may also guide improved prediction of patterns of future change in ecosystem distribution. For example, Allen et al. (2010) suggest that spatially explicit documentation of environmental conditions in areas of forest die-off is necessary to link mortality to causal climate drivers, including precipitation, temperature and vapour pressure deficit. Better prediction of climate responses will also require improved knowledge of belowground processes and soil moisture conditions. Assessments of future productivity will depend on accurate measurements of rates (net ecosystem exchange and NPP), changes in ecosystem level storage (net ecosystem production) and quantification of disturbances effects to determine net biome production (Boisvenue and Running 2006).

Hydrological conditions, runoff and stream flow are of critical importance for humans and aquatic organisms, and many studies have focused on the implications of climate change for these ecosystem processes. However, most of these have been undertaken at small catchment scale (Mahat and Anderson 2013; Neukum and Azzam 2012; Zhou et al. 2011) with few basin-scale assessments (van Dijk and Keenan 2007). However, the effects of climate and forest cover change on hydrology are complicated. Loss of tree cover may increase stream flow but can also increase evaporation and water loss (Guardiola-Claramonte et al. 2011). The extent of increasing wildfire will also be a major factor determining hydrological responses to climate change (Versini et al. 2013; Feikema et al. 2013).

Changing forest composition will also affect the habitat of vertebrate and invertebrate species. The implications of climate change for biodiversity conservation have been subject to extensive analysis (Garcia et al. 2014; Vihervaara et al. 2013; Schaich and Milad 2013; Clark et al. 2011; Heller and Zavaleta 2009; Miles et al. 2004). An integrated analytical approach, considering both impacts on species and habitat is important. For example, in a study of climate change impacts on bird habitat in the north-eastern USA, the combination of changes in tree distribution and habitat for birds resulted in significant impacts for 60 % of the species. However, the strong association of birds with certain vegetation tempers their response to climate change because localised areas of suitable habitat may persist even after the redistribution of tree species (Matthews et al. 2011).

Understanding thresholds in changing climate conditions that are likely to result in a switch to a different ecosystem state, and the mechanisms that underlie ecosystem responses, will be critical for forest managers (Campbell et al. 2009). Identifying these thresholds of change is challenging. Detailed process-based ecosystem research that identifies and studies critical species interactions and feedback loops, coupled with scenario modelling of future conditions, could provide valuable insights (Kimmins et al. 1999, 2008; Walker and Meyers 2004). Also, rather than pushing systems across thresholds into alternative states, climate change may create a stepwise progression to unknown transitional states that track changing climate conditions, requiring a more graduated approach in management decisions (Lin and Petersen 2013).

Ultimately, management decisions may not be driven by whether we can determine future thresholds of change, but by observing the stressors that determine physiological limits of species distributions. These thresholds will depend on species physiology and local site conditions, with recent research demonstrating already observed ecosystem responses to climate change, including die-back of some species (Allen et al. 2010; Rigling et al. 2013).

3.1.3 Fire, pests, invasive species and disturbance risks

Many of the impacts of a changing future climate are likely to be felt through changing disturbance regimes, in particular fire. Forest fire weather risk and fire behaviour prediction have been two areas where there has been strong historical interaction between climate science and forest management and where we may see major tipping points driving change in ecosystem composition (Adams 2013). Fire weather is fundamentally under the control of large-scale climate conditions with antecedent moisture anomalies and large-scale atmospheric circulation patterns, further exacerbated by configuration of local winds, driving fire weather (Brotak and Reifsnyder 1977; Westerling et al. 2002, 2006). It is therefore important to improve understanding of both short- and long-

term atmospheric conditions in determining meteorological fire risk (Amraoui et al. 2013).

Increased fuel loads and changes to forest structure due to long periods of fire exclusion and suppression are increasing fire intensity and limiting capacity to control fires under severe conditions (Williams 2004, 2013). Increasing urbanisation is increasing the interface between urban populations and forests in high fire risk regions, resulting in greater impacts of wildfire on human populations, infrastructure and assets (Williams 2004). Deforestation and burning of debris and other types of human activities are also introducing fire in areas where it was historically relatively rare (Tacconi et al. 2007).

In a recent study, Chuvieco et al. (2014) assessed ecosystem vulnerability to fire using an index based on ecological richness and fragility, provision of ecosystem services and value of houses in the wildland–urban interface. The most vulnerable areas were found to be the rainforests of the Amazon Basin, Central Africa and Southeast Asia; the temperate forest of Europe, South America and north-east America; and the ecological corridors of Central America and Southeast Asia.

In general, fire management policies in many parts of the world will need to cope with longer and more severe fire seasons, increasing fire frequency, and larger areas exposed to fire risk. This will especially be the case in the Mediterranean region of Europe (Kolström et al. 2011) and other fire-prone parts of the world such as South Eastern Australia (Hennessy et al. 2005). This will require improved approaches to fire weather modelling and behaviour prediction that integrate a more sophisticated understanding of the climate system with local knowledge of topography, vegetation and wind patterns. It will also require the development of fire management capacity where it had previously not been necessary. Increased fire weather severity could push current suppression capacity beyond a tipping point, resulting in a substantial increase in large fires (de Groot et al. 2013; Liu et al. 2010) and increased investment in resources and management efforts for disaster prevention and recovery.

Biotic factors may be more important than direct climate effects on tree populations in a changing climate. For example, insects and diseases have much shorter generation length and are able to adapt to new climatic conditions more rapidly than trees. However, if insects move more rapidly to a new environment whilst tree species lag, some parts of the tree population may be impacted less in the future (Regniere 2009).

The interaction of pests, diseases and fire will also be important. For example, this interaction will potentially determine the vulnerability of western white pine (*Pinus monticola*) ecosystems in Montana in the USA. Loehman et al. (2011) found that warmer temperatures will favour western white pine over existing climax and shade tolerant species, mainly because warmer conditions will lead to increased frequency and extent of wildfires that facilitates regeneration of this species.

3.2 Adaptation actions in forest management

The large majority of published studies relating to forests and climate change have been on vulnerability and impacts. These have increased understanding of the various relationships between forest ecosystems and climate and improved capacity to predict and assess ecosystem responses. However, managers need greater guidance in anticipating and responding to potential impacts of climate change and methods to determine the efficiency and efficacy of different management responses because they are generally not responding sufficiently to potential climate risks.

3.2.1 Adaptation actions at different management levels

A number of recent reviews have described adaptation actions and their potential application in different forest ecosystems being managed for different types of goods or services (Bernier and Schöne 2009; Innes et al. 2009; Lindner et al. 2010; Kolström et al. 2011), and adaptation guides and manuals have been developed (Peterson et al. 2011; Stephens et al. 2012) for different types of forest and jurisdictions. Adaptation actions can be primarily aimed at reducing vulnerability to increasing threats or shocks from natural disasters or extreme events, or increasing resilience and capacity to respond to progressive change or climate extremes. Adaptation actions can be reactive to changing conditions or planned interventions that anticipate future change. They may involve incremental changes to existing management systems or longer term transformational changes (Stafford Smith et al. 2011). Adaptation actions can also be applied at the stand level or at ownership, estate or national scales (Keskitalo 2011).

Recent research at the stand level in forests in the SE USA showed that forest thinning, often recommended in systems that are likely to experience increased temperature and decreased precipitation as a result of climate change, will need to be more aggressive than traditionally practised to stimulate growth of large residual trees, improve drought resistance and provide greater resilience to future climate-related stress (Kerhoulas et al. 2013).

An analysis of three multi-aged stand-level options in Nova Scotia, Canada, Steenberg et al. (2011) found that leaving sexually immature trees to build stand complexity had the most benefit for timber supply but was least effective in promoting resistance to climate change at the prescribed harvest intensity. Varying the species composition of harvested trees proved the most effective treatment for maximising forest age and old-growth area and for promoting stands composed of climatically suited target species. The combination of all three treatments resulted in an adequate

representation of target species and old forest without overly diminishing the timber supply and was considered most effective in minimising the trade-offs between management values and objectives.

An estate level analysis of Austrian Federal Forests indicated that management to promote mixed stands of species that are likely to be well adapted to emerging environmental conditions, silvicultural techniques fostering complexity and increased management intensity might successfully reduce vulnerability, with the timing of adaptation measures important to sustain supply of forest goods and services (Seidl et al. 2011).

Whilst researchers are analysing different management options, the extent to which they are being implemented in practice is generally limited. For example, in four regions in Germany, strategies for adapting forest management to climate change are in the early stages of development or simply supplement existing strategies relating to general risk reduction or to introduce more 'nature-orientated' forest management (Milad et al. 2013). Guariguata et al. (2012) found that forest managers across the tropics perceived that natural and planted forests are at risk from climate change but were ambivalent about the value of investing in adaptation measures, with climate-related threats to forests ranked below others such as clearing for commercial agriculture and unplanned logging.

Community-based management approaches are often argued to be the most successful approach for adaptation. An analysis of 38 community forestry organisations in British Columbia found that 45 % were researching adaptation and 32 % were integrating adaptation techniques into their work (Furness and Nelson 2012). Whilst these community forest managers appreciated support and advice from government for adaptation, balancing this advice with autonomy for communities to make their own decisions was considered challenging.

In a study of communities impacted by drought in the forest zone of Cameroon, Bele et al. (2013b) identified adaptive strategies such as community-created firebreaks to protect their forests and farms from forest fires, the culture of maize and other vegetables in dried swamps, diversifying income activities or changing food regimes. However, these coping strategies were considered to be incommensurate with the rate and magnitude of change being experienced and therefore no longer seen as useful. Some adaptive actions, whilst effective, were resource inefficient and potentially translate pressure from one sector to another or generated other secondary effects that made them undesirable.

3.2.2 Integrating adaptation and mitigation

In considering responses to climate change, forest managers will generally be looking for solutions that address both mitigation objectives and adaptation. To maintain or increase forest carbon stocks over the long term, the two are obviously inextricably linked (Innes et al. 2009). Whilst there are potentially strong synergies, Locatelli et al. (2011) identified potential trade-offs between actions to address mitigation and the provision of local ecosystem services and those for adaptation. They argued that mitigation projects can facilitate or hinder the adaptation of local people to climate change, whereas adaptation projects can affect ecosystems and their potential to sequester carbon.

Broadly, there has been little integration to date of mitigation and adaptation objectives in climate policy. For example, there is little connection between policies supporting the reducing emissions from deforestation and forest degradation plus (REDD+) initiatives and adaptation. Integrating adaptation into REDD+ can advance climate change mitigation goals and objectives for sustainable forest management (Long 2013). Kant and Wu (2012) considered that adaptation actions in tropical forests (protection against fire and disease, ensuring adequate regeneration and protecting against coastal impacts and desertification) will improve future forest resilience and have significant climate change mitigation value.

3.2.3 Sector-level adaptation

Analyses of climate change impacts and vulnerability at the sector level have been undertaken for some time (Lindner et al. 2002; Johnston and Williamson 2007; Joyce 2007). However, it has recently been argued (Wellstead et al. 2014) that these assessments, which focus on macro system-level variables and relationships, fail to account for the multi-level or polycentric nature of governance and the possibility that policy processes may result in the non-performance of critical tasks required for adaptation.

Joyce et al. (2009) considered that a toolbox of management options for the US National Forests would include the following: practices focused on reducing future climate change effects by building resistance and resilience into current ecosystems and on managing for change by enabling plants, animals and ecosystems to adapt to climate change. Sample et al. (2014) demonstrated the utility of this approach in a coniferous forest management unit in northwestern USA. It provided an effective means for guiding management decisions and an empirical basis for setting budgetary and management priorities. In general, more widespread implementation of already known practices that reduce the impact of existing stressors represents an important 'no regrets' strategy.

Johnston and Hesseln (2012) found that barriers to implementing adaptation across forest sector managers in Canada included inflexible tenure arrangements and regulatory environments which do not support innovation. Echoing calls for wider implementation of SFM as a key adaptation strategy (Innes et al. 2009), they argued that forest certification systems, participating in the Canadian model forest

programme, and adopting criteria and indicators of SFM can support sectoral level adaptation.

Decentralised management approaches are considered to be a more appropriate governance arrangement for forest management, but Rayner et al. (2013) argued that a decentralised forest policy sector in Canada has resulted in limitations where policy, such as adaptation, requires a coherent national response. Climate change adaptation has led to an expansion of departmental mandates that is not being addressed by better coordination of the available policy capacity. Relevant federal agencies are not well represented in information networks, and forest policy workers report lower levels of internal and external networking than workers in related policy subsectors.

Economic diversification can be a valuable strategy to improve resilience to climate-related shocks. This can take a range of forms: developing new industries or different types of forest-based industries based on different goods or services. For the timber sector, the value of diversification as a risk management strategy for communities is open to question. Ince et al. (2011) pointed out that the forest sector operates in an international market and is susceptible to changes in the structure of this market. In the US forest sector, globalization has accelerated structural change, favouring larger and more capital-intensive enterprises and altering historical patterns of resource use. They suggest that future markets for timber will be driven by developments in these larger scale enterprises and may not lead to expansion of opportunities for smaller scale forest enterprises because development of niche markets or customised products is likely to be pursued aggressively by larger globally oriented enterprises to develop branding, product identity and product value. How to best diversify for adaptation therefore remains an open question.

Consequently, whilst policies that support economic diversification will be important, this may involve diversification well beyond traditional sectors. For example, in areas where there is a high probability that forests will be lost in favour of other ecosystems, such as grasslands, managers should recognise early on that their efforts and resources may best be focused outside forests (Innes et al. 2009). These adjustments will involve taking into account the perceptions of climate risk by various stakeholders, including individuals, communities, governments, private institutions and organisations (Adger et al. 2007). Vulnerability assessments and adaptation measures also need to be developed in a framework that takes into account the vulnerabilities and actions in other sectors that are linked to the forest sector, such as food, energy, health and water (Sonwa et al. 2012).

3.3 New approaches to decision making

Climate change presents new challenges for forest managers. Change is likely to happen faster than traditional, empirical approaches can provide evidence to support changes in management. Uncertainties in a range of aspects of future climate may also not be reduced through investment in research. Given that management for activities such as timber production can no longer be based solely on empirically derived growth and yield trajectories and management plans must incorporate uncertainty and the increased probability of extreme events, what types of tools are available to support these approaches? This section presents key points from the literature on decision making under uncertainty, adaptive management and resilience as a guide to future decision making in forest management.

3.3.1 Decision making under uncertainty

The future conditions for forest managers are subject to a high degree of uncertainty, and the future prospects for reducing these large uncertainties are limited. There is uncertainty regarding the trajectory of future increases in atmospheric greenhouse gases, what kind of effects these might have on the climate system and the effects of climatic changes on ecological and social systems and their capacity to adapt (see Fig. 2) (Wilby and Dessai 2010).

Consequently, many forest managers consider that the future situation is too uncertain to support long-term and potentially costly decisions that may be difficult to reverse. Dessai and Hulme (2004) argued that uncertainty per se should not be a reason for inaction. However, the critical issue for managers is deciding the types of actions to take and the timing and conditions under which they should be taken (Ogden and Innes 2007a). A more reactive 'wait and see' approach (or 'purposeful procrastination') might be justified if uncertainty or costs are high relative to the expected impacts and risks, or if it is cheaper to implement interventions by waiting until after a significant disturbance (e.g. replanting an area with more fire- or drought-resistant tree species after a wildfire or drought-induced insect outbreak).

Effective adaptation requires setting clear objectives. Managers and policy makers need to decide whether they are trying to facilitate ecosystem adaptation through changing species composition or forest structure or trying to engineer resistance to change through proactive management strategies (Joyce et al. 2008). Establishing objectives often depends on the integration of the preferences of different stakeholders (Prato 2008), but changing social preferences presents another source of potential uncertainty.

Risk assessment and management provide a foundation for decision making in considering climate change in natural resource management. This approach provides both a qualitative and quantitative framework for evaluating climate change effects and adaptation options. Incorporating risk management approaches into forest management plans can provide

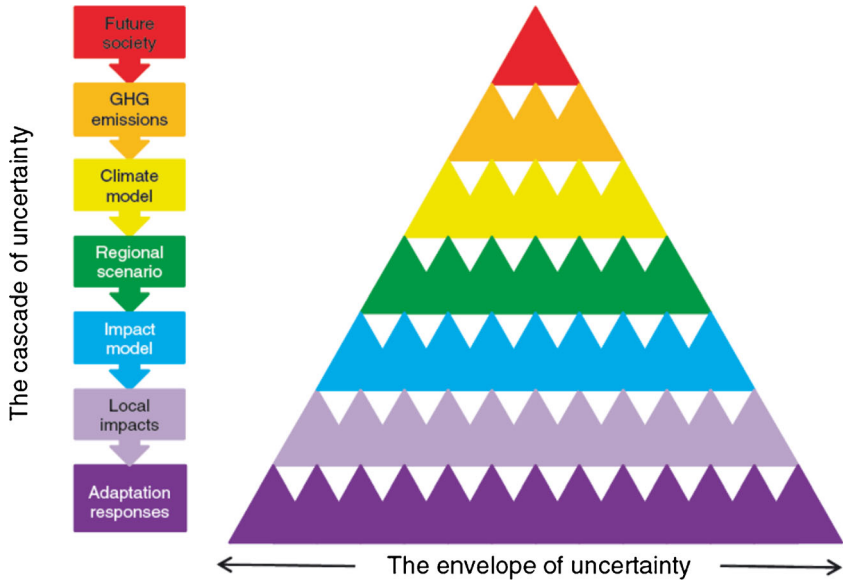


Fig. 2 The cascade of uncertainty (Wilby and Dessai 2010)

a basis for managers to continue to provide forest conditions that meet a range of important values (Day and Perez 2013).

However, risk approaches generally requiring assigning probabilities to future events. In a comprehensive review, Yousefpour et al. (2011) identified a growing body of research literature on decision making under uncertainty, much of which has focused on price uncertainty and variation in timber production but is extending to multiple forest management objectives and other types of risk. They argue that we are actually in a stochastic transition from one known stable (but variable) climate state to a new but largely unknown and likely more rapidly changing set of future conditions.

Decision makers themselves may also not be the rational actors assumed by these models, with their decisions taken according to quite different assumptions, preferences and beliefs (Ananda and Herath 2009; Couture and Reynaud 2008). Therefore, the communication approach will be important in determining whether the information is acted on. In a recent study, Yousefpour et al. (2014) considered that the speed with which decision makers will form firm beliefs about future climate depends on the divergence among climate trajectories, the speed of change and short-term climate variability. Using a Bayesian modelling approach, they found that if a large change in climate occurs, the value of investing in knowledge and taking an adaptive approach would be positive and higher than a non-adaptive approach. In communicating about uncertainty, it may be better to focus discussion on the varying time in the future when things will happen, rather than on whether they will happen at all (Lindner et al. 2014).

Increased investment in climate science and projections or species distribution modelling may not necessarily decrease uncertainty in climate projections or impacts. Climate models are best viewed as heuristic tools rather than as accurate forecasts of the future (Innes et al. 2009). Trajectories of change in many other drivers of forest management (social, political or economic) are also highly uncertain (Keskitalo 2008) and the effects of these on the projected performance of management can be the same order of magnitude, requiring an integrated social-ecological perspective to adaptation (Seidl and Lexer 2013).

In a more 'decision-centred' approach, plausible scenarios of the potential range of future conditions are required. These can be derived from climate models but do not need to be accurate and precise 'predictions' of future climate states (Wilby and Dessai 2010). To support this type of approach, research needs to focus on improved understanding of tree and ecosystem responses and identifying those aspects of climate to which different forest types are most sensitive.

Devising strategies that are able to meet management objectives under a range of future scenarios is likely to be the most robust approach, recognising that these strategies are unlikely to be optimal under all future conditions. In some cases, the effect of different scenarios on forest growth may not be that great and differences in the present value of different management options are relatively small. For example, Eriksson et al. (2011) found that there was limited benefit in attempting to optimise management plans in accordance with future temperature scenarios.

Integration of climate change science and adaptation in forest management planning is considered important for building resilience in forest social and ecological systems (Keskitalo 2011; D'Amato et al. 2011; Chmura et al. 2011; Parks and Bernier 2010; Lindner et al. 2014). Forest restoration is becoming a more prominent aspect of forest management in many parts of the world and restoration approaches will also need to integrate understanding of future climate change to be successful (Stanturf et al. 2014).

3.3.2 Adaptive management, resilience and decisions

Adaptive management provides a mechanism to move forward when faced with future uncertainty (Innes et al. 2009). It can be viewed as a systematic process for continually improving management policies and practices by monitoring and then learning from the outcomes of operational programmes as a basis for incorporating adaptation actions into forest management. Whilst many management initiatives purport to implement these principles, they often lack essential characteristics of the approach (Innes et al. 2009).

However, effective adaptation to changing climate cannot simply involve adaptive management as it is currently understood. The pace of climate change is not likely to allow for the use of management as a tool to learn about the system by implementing methodologies to test hypotheses concerning known uncertainties (Holling 1978). Future climatic conditions may result in system states and dynamics that have never previously existed (Stainforth et al. 2007), so observation of past experience may be a poor guide for future action. Management will need to be more 'forward-looking', considering the range of possible future conditions and planning actions that consider that full range.

How does this translate into the practical guidance forest managers are seeking on how to adapt their current practices and, if necessary, their goals (Blate et al. 2009)? Managers will need to consider trade-offs between different objectives under different conditions. For example, Seidl et al. (2011) showed that, to keep climate vulnerability in an Austrian forest low, Norway spruce will have to be replaced almost entirely by better adapted species. However, indicator weights that favoured timber production over C storage or biodiversity exerted a strong influence on the results. Wider social implications of imposing such drastic changes in forest landscapes will also deserve stronger consideration in decision making.

Ecosystem management will need to be reframed to accommodate the risks of a changing climate. Adaptive strategies, even without specific information on the future climate conditions of a target ecosystem, would enhance social and ecological resilience to address the uncertainties due to changing climate (Mori et al. 2013). These are likely to be more subject to change over the short to medium term, in response to more rapidly changing conditions.

Analysis of ecosystem resilience can provide a framework for these assessments. Resilience can be defined as 'the capacity of ecosystems to absorb disturbance and reorganise so as to retain essentially the same function, structure and feedbacks – to have the same identity' (Walker and Salt 2012). It is a function of the capacity of an ecosystem to resist change, the extent and pace of change and the ability of an ecosystem to reorganise following disturbance. The concept of resilience holds promise for informing future forest management, but Rist and Moen (2013) argue that its contributions are, so far, largely conceptual and offer more in terms of being a problem-framing approach than analytical or practical tools. There may also be trade-offs involved with focusing on resilience through retention of current species composition or using a more adaptation-oriented management approach after disturbances (Buma and Wessman 2013). Complexity theory and concepts can provide an appropriate framework for managing resilience (Messier et al. 2013).

Management decisions will ultimately depend on the costs and benefits of different options, but there are few examples of decision making frameworks that compare the costs of future impacts with the costs of different actions and the efficacy of those actions in reducing impacts. Ogden and Innes (2009) used a structured decision making process to identify and assess 24 adaptation options that managers considered important to achieve their regional goals and objectives of sustainable forest management in light of climate change. In the analysis of options for biodiversity conservation, Wintle et al. (2011) found that the amount of funding available for adaptation was a critical factor in deciding options aimed at minimising species extinctions in the mega-diverse fynbos biome of South Africa. When the available budget is small, fire management was the best strategy. If the budget is increased to an intermediate level, the marginal returns from more fire management were limited and the best strategy was added habitat protection. Above another budget threshold, increased investment should go into more fire management. By integrating ecological predictions in an economic decision framework, they found that making the choice of how much to invest is as important as determining what actions to take.

3.3.3 Adaptation as a social learning process

Whilst adaptation has been defined as 'adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects' (Levina and Tirpak 2006), adaptation is essentially about meeting future human needs (Spittlehouse and Stewart 2003; Hahn and Knoke 2010). Consequently, it is inherently a social process. Forest landscapes are social-ecological systems that involve both nature and society (Innes et al. 2009), and resolving trade-offs between different management objectives to meet the different needs in society is an important element of sustainable forest management. As Kolström et al. (2011) pointed out, some proposed adaptation measures may change the balance between current objectives and stakeholder interests, and it will be important to consider the relative balance of different measures at the stand, management unit and landscape scales.

Those investigating adaptive management also recognise that it goes beyond the focus on scientific methods, statistical designs or analytical rigour favoured by its early proponents and that there is now an expectation of much greater stakeholder involvement, with the concept being renamed by some

as adaptive, collaborative management (Innes et al. 2009). SFM and adaptation are as much about those who inhabit, work in or utilise forests as it is about managing the forest ecosystems themselves (White et al. 2010; Pramova et al. 2012; Fischer et al. 2013).

The choice of adaptation options will thus likely be relatively complex, even in cases where information and policy have been developed, and communication measures for forest management have been well formulated. Making such choices may require considerable knowledge, competence and commitment for implementation at the local level (Keskitalo 2011). Effective adaptation will require much greater cooperation between stakeholders, more flexibility for management actions and commitment of time to develop the social license for action in the absence of conclusive evidence or understanding. This will require venues for sharing perspectives on the nature of the problem (Fig. 3).

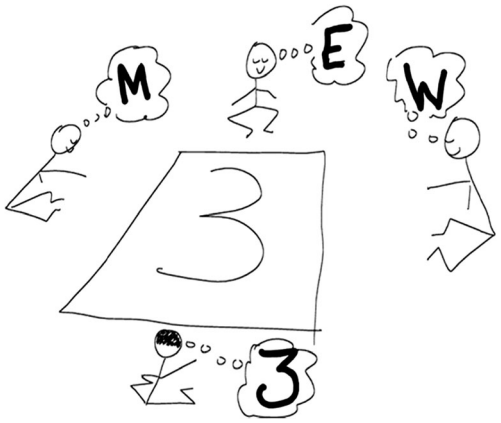


Fig. 3 Adaptation as a social learning process. There is a need to provide situations to share different viewpoints on the nature of the problem as a basis for developing shared solutions (image source: John Rowley, http://ch301.cm.utexas.edu/learn/)

3.3.4 Local and indigenous knowledge

The promotion of community-based forest management may increase local adaptive capacity by putting decisions in the hands of those people who first feel the effects of climate change (Gyampoh et al. 2009). In this context, local knowledge systems based on long-term observation and experience are likely to be of increasing importance in decision making. Adaptation strategies can benefit from combining scientific and indigenous knowledge, especially in developing countries (Gyampoh et al. 2009), with the translation of local forest knowledge into the language of formal forest science being considered an important step towards adaptation (Roberts et al. 2009). However, conservation and natural resource managers in government agencies have often discounted traditional local management systems (Scott 2005), although Spathelf et al. (2014) provided a useful approach for capturing local expert knowledge. Linking this type of knowledge with broader scientific understanding of ecosystem functioning and the global climate system will be a major challenge, requiring consideration of both technical and cultural issues (Caverley 2013), including intellectual property concerns of indigenous people (Lynch et al. 2010).

3.4 Policy arrangements for adaptation

Increasingly, many are arguing that effectively responding to climate change will require polycentric and multi-level governance arrangements (Peel et al. 2012). However, Nilsson et al. (2012) found that institutionalising of knowledge and knowledge exchange regarding climate change adaptation in Sweden was weak and that improved mechanisms are required for feedback from the local to the national level. Recent studies have described stronger relationships between scientific research and forest management to assess trade-offs and synergies, for participatory decision making and for shared learning (Blate et al. 2009; Littell et al. 2012; Klenk et al. 2011).

Many papers emphasised the need for greater flexibility in the policies, cultures and structures of forest management organisations (Brown 2009; von Detten and Faber 2013; Rayner et al. 2013). Because no single community or agency can prepare on their own for future impacts, inter-sectoral policy coordination will be required to ensure that policy developments in related policy sectors are not contradictory or counterproductive. Greater integration of information, knowledge and experience and collaborative projects involving scientists, practitioners and policy makers from multiple policy communities could increase focus on resilience, identify regions of large-scale vulnerability and provide a more rigorous framework for the analysis of vulnerability and adaptation actions (Thomalla et al. 2006).

There is also likely to be a greater need for cross-border implementation of different forest management options, requiring greater coordination between nation states and sub-national governments (Keenan 2012). Policy is the product of both 'top-down' and 'bottom-up' processes and these might sometimes be in conflict. Simply having 'good policy' in place is unlikely to be sufficient, as a great deal of what takes place at 'street level' is not determined by formal aims of central policy (Urwin and Jordan 2008). Having the right policies can send a strong political signal that adaptation needs to be considered seriously but flexibility in policy systems will be required to facilitate adaptive planning.

4 Discussion and conclusions

This broad survey of the literature indicated that, whilst there has been considerable development in research and thinking

about adaptation in forest management over the last 10 years, research is still strongly focused on assessment of future impacts, responses and vulnerability of species and ecosystems (and in some cases communities and forest industries) to climate change. There has been some movement from a static view of climate based on long-term averages to a more detailed understanding of the drivers of different climate systems and how these affect the factors of greatest influence on different forest ecosystems processes, such as variability and extremes in temperature or precipitation or fire disturbance. For example, Guan et al. (2012) demonstrated that quasi-periodic climate variation on an inter-annual (ENSO) to inter-decadal (PDO) time scale can significantly influence tree growth and should be taken into account when assessing the impact of climate changes on forest productivity.

Adaptation is, in essence, about making good decisions for the future, taking into account the implications of climate change. It involves recognising and understanding potential future climate impacts and planning and managing for their consequences, whilst also considering the broader social, economic or other environmental changes that may impact on us, individually or collectively. To effectively provide a role in mitigation, delivering associated ecosystem services and benefits in poverty reduction (Eliasch 2008) forest management will have to adapt to a changing and highly variable climate. In achieving this, the roles and responsibilities of different levels of government, the private sector and different parts of the community are still being defined.

The broader literature emphasises that adaptation is a continuous process, involving a process of 'adapting well' to continuously changing conditions (Tompkins et al. 2010). This requires organisational learning based on past experience, new knowledge and a comprehensive analysis of future options. This can take place through 'learning by doing' or through a process of search and planned modification of routines (Berkhout et al. 2006). However, interpreting climate signals is not easy for organisations, the evidence of change is ambiguous and the stimuli are not often experienced directly within the organisation. For example, many forest managers in Australia currently feel little need to change practices to adapt to climate change, given both weak policy signals and limited perceived immediate evidence of increasing climate impacts (Cockfield et al. 2011). To explain and predict adaptation to climate change, the combination of personal experience and beliefs must be considered (Blennow et al. 2012). 'Climate smart' forest management frameworks can provide an improved basis for managing forested landscapes and maintaining ecosystem health and vitality based on an understanding of landscape vulnerability to future climatic change (Fig. 4) (Nitschke and Innes 2008a).

Many are now asking, do we really need more research to start adapting forest management to climate change? Whilst adaptation is often considered 'knowledge deficit' problem—where scientists provide more information and forest managers will automatically make better decisions—the reality is that the way in which this information is presented and how it is interpreted and received, will play major roles in determining potential responses. Successful adaptation will require dissemination of knowledge of potential climate impacts and suitable adaptation measures to decision makers at both practice and policy levels (Kolström et al. 2011) but it needs to go well beyond that.

Adaptation is, above all, a social learning process. It requires an understanding of sense of place, a capacity for individuals and society to consider potential future changes and what they mean for their circumstances. Leaders in forest management organisations will need to support a greater diversity of inputs into decision making, avoid creating rigid organisational hierarchies that deter innovation, and be inclusive, open and questioning (Konkin and Hopkins 2009). They will need to create more opportunities for interaction between researchers, managers and the community and space for reflection on the implications and the outcomes of management actions and unplanned events. Researchers will need to develop new modes of communication, providing knowledge in forms that are appropriate to the management decision and suitable for digestion by a range of different audiences.

From this analysis, key gaps in knowledge for adaptation may not be improved climate scenarios or better understanding of the biophysical responses of individual tree species or forest ecosystems to future climate. Knowledge gaps lie more in understanding the social and community attitudes and values that drive forest management and the decision making processes of forest managers, in order to work out how 'climate intelligence' can be built in to these processes.

The impacts of changing climate will vary locally. Consequently, managers must be given the flexibility to respond in ways that meet their particular needs and capacity to choose

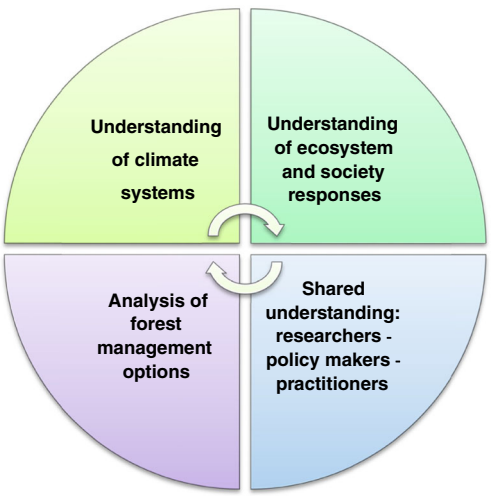


Fig. 4 Components of climate smart forest management (after Nitschke and Innes 2008a, b)

management options that are applicable to the local situation (Innes et al. 2009). This may not be consistent with rigid indicator-driven management assessment processes like forest certification. Whilst policy to support climate change mitigation is primarily a task for national governments and international agreements and processes, responsibility for supporting adaptation will fall more to sub-national and local governments, communities and the private sector. More active management will be required if specific values are to be maintained, particularly for forests in conservation reserves. This will require additional investment, but there has been little analysis to support the business case for investment in adaptation or to determine who should pay, particularly in developing countries.

We need to strengthen the relationship between climate science, forest research, forest managers and the community. Key challenges will include the setting of objectives for desired future conditions and accepting that we may not be able to maintain everything that forests have traditionally provided. It is important to discuss and agree on common goals in order to cope with, or benefit from, the challenges of future climates. Actively managing our forest ecosystems effectively and intelligently, using the best available knowledge and foresight capacity, can make those goals a reality.

Acknowledgments Thanks to Linda Joyce for her comments on an earlier draft of this paper, to a number of anonymous reviewers for their thoughtful suggestions and to many colleagues that I have discussed these ideas with over the past five years.

Open Access This article is distributed under the terms of the Creative Commons Attribution License which permits any use, distribution, and reproduction in any medium, provided the original author(s) and the source are credited.

References

Adams MA (2013) Mega-fires, tipping points and ecosystem services: managing forests and woodlands in an uncertain future. For Ecol Manag 294:250–261. doi:10.1016/j.foreco.2012.11.039

Adger WN, Agrawala S, Mirza MMQ, Conde C, O'Brien K, Pulhin J, Pulwarty R, Smit B, Takahashi K (2007) Assessment of adaptation practices, options, constraints and capacity. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel of Climate Change (IPCC). Cambridge University Press, Cambridge, pp 717–743

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol Appl 1:95–111. doi:10.1111/j.1752-4571.2007.00013.x

Alberto FJ, Aitken SN, Alia R, Gonzalez-Martinez SC, Hanninen H, Kremer A, Lefevre F, Lenormand T, Yeaman S, Whetten R, Savolainen O (2013) Potential for evolutionary responses to climate change evidence from tree populations. Glob Chang Biol 19:1645–1661. doi:10.1111/gcb.12181

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259:660–684. doi:10.1016/j.foreco.2009.09.001

Amraoui M, Liberato MLR, Calado TJ, DaCamara CC, Coelho LP, Trigo RM, Gouveia CM (2013) Fire activity over Mediterranean Europe based on information from Meteosat-8. For Ecol Manag 294:62–75. doi:10.1016/j.foreco.2012.08.032

Ananda J, Herath G (2009) A critical review of multi-criteria decision making methods with special reference to forest management and planning. Ecol Econ 68:2535–2548. doi:10.1016/j.ecolecon.2009.05.010

Andalo C, Beaulieu J, Bousquet J (2005) The impact of climate change on growth of local white spruce populations in Québec, Canada. For Ecol Manag 205:169–182. doi:10.1016/j.foreco.2004.10.045

Anderson JM (1991) The effects of climate change on decomposition processes in grassland and coniferous forests. Ecol Appl 1:326–347. doi:10.2307/1941761

Anderson JT, Panetta AM, Mitchell-Olds T (2012) Evolutionary and ecological responses to anthropogenic climate change. Plant Physiol 160:1728–1740. doi:10.1104/pp. 112.206219

Attorre F, Francesconi F, Scarnati L, De Sanctis M, Alfo M, Bruno F (2008) Predicting the effect of climate change on tree species abundance and distribution at a regional scale. For Biogeosci For 1:132–139. doi:10.3832/ifor0467-0010132

Battaglia M, Bruce J, Brack C, Baker T (2009) Climate change and Australia's plantation estate: analysis of vulnerability and preliminary investigation of adaptation options.

Battaglia M, Sands P, White D, Mummery D (2004) CABALA: a linked carbon, water and nitrogen model of forest growth for silvicultural decision support. For Ecol Manag 193:251–282

Bele MY, Sonwa DJ, Tiani AM (2013a) Supporting local adaptive capacity to climate change in the Congo basin forest of Cameroon a participatory action research approach. Int J Clim Chang Strateg Manag 5:181–197. doi:10.1108/17568691311327587

Bele MY, Tiani AM, Somorin OA, Sonwa DJ (2013b) Exploring vulnerability and adaptation to climate change of communities in the forest zone of Cameroon. Clim Chang 119:875–889. doi:10.1007/s10584-013-0738-z

Berkhout F, Hertin J, Gann D (2006) Learning to adapt: organisational adaptation to climate change impacts. Clim Chang 78:135–156. doi:10.1007/s10584-006-9089-3

Bernier P, Schöne D (2009) Adapting forests and their management to climate change: an overview. Unasylva 60:5–11

Blate GM, Joyce LA, Littell JS, McNulty SG, Millar CI, Moser SC, Neilson RP, O'Halloran K, Peterson DL (2009) Adapting to climate change in United States national forests. Unasylva 60:57–62

Blennow K, Persson J, Tome M, Hanewinkel M (2012) Climate change: believing and seeing implies adapting. PLoS ONE 7:e50182. doi:10.1371/journal.pone.0050182

Boisvenue C, Running SW (2006) Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century. Glob Chang Biol 12:862–882. doi:10.1111/j.1365-2486.2006.01134.x

Bolte A, Eisenhauer DR, Ehrhart HP, Gross J, Hanewinkel M, Kolling C, Profft I, Rohde M, Rohe P, Amereller K (2009) Climate change and forest management—accordances and differences between the German states regarding assessments for needs and strategies towards forest adaptation. Landbauforschung Volkenrode 59:269–278

Bonan GB, Pollard D, Thompson SL (1992) Effects of boreal forest vegetation on global climate. Nature 359:716–718. doi:10.1038/359716a0

Bongers F, Poorter L, Van Rompaey R, Parren MPE (1999) Distribution of twelve moist forest canopy tree species in Liberia and Cote d'Ivoire: response curves to a climatic gradient. J Veg Sci 10:371–382. doi:10.2307/3237066

Booth TH (1990) Mapping regions climatically suitable for particular tree species at the global scale. For Ecol Manag 36:47–60

Booth TH (2013) Eucalypt plantations and climate change. For Ecol Manag 301:28–34. doi:10.1016/j.foreco.2012.04.004

Booth TH, Nix HA, Hutchinson MF, Jovanovic T (1988) Niche analysis and tree species introduction. For Ecol Manag 23:47–59

Bowman DMJS, Williamson GJ, Keenan RJ, Prior LD (2014) A warmer world will reduce tree growth in evergreen broadleaf forests: evidence from Australian temperate and subtropical eucalypt forests. Glob Ecol Biogeogr 23:925–934. doi:10.1111/geb.12171

Brautigam K, Vining KJ, Lafon-Placette C, Fossdal CG, Mirouze M, Marcos JG, Fluch S, Fraga MF, Guevara MA, Abarca D, Johnsen O, Maury S, Strauss SH, Campbell MM, Rohde A, Diaz-Sala C, Cervera MT (2013) Epigenetic regulation of adaptive responses of forest tree species to the environment. Ecol Evol 3:399–415. doi:10.1002/ece3.461

Breed MF, Stead MG, Ottewell KM, Gardner MG, Lowe AJ (2013) Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. Conserv Genet 14:1–10. doi:10.1007/s10592-012-0425-z

Breymeyer A, Melillo JM (1991) Global climate change—the effects of climate change on production and decomposition in coniferous forests and grasslands. Ecol Appl 1:111–111. doi:10.2307/1941804

Brooker RW, Travis JMJ, Clark EJ, Dytham C (2007) Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. J Theor Biol 245:59–65. doi:10.1016/j.jtbi.2006.09.033

Brotak EA, Reifsnyder WE (1977) Predicting major wildland fire occurrence. Fire Manag Notes 38:5–8

Brown HCP (2009) Climate change and Ontario forests: prospects for building institutional adaptive capacity. Mitig Adapt Strateg Glob Chang 14:513–536. doi:10.1007/s11027-009-9183-8

Buma B, Wessman CA (2013) Forest resilience, climate change, and opportunities for adaptation: a specific case of a general problem. For Ecol Manag 306:216–225. doi:10.1016/j.foreco.2013.06.044

Campbell EM, Saunders SC, Coates KD, Meidinger DV, MacKinnon A, O'Neil GA, MacKillop DJ, DeLong SC, Morgan. DG (2009) Ecological resilience and complexity: a theoretical framework for understanding and managing British Columbia's forest ecosystems in a changing climate. B.C. Min. For. Range, For. Sci. Prog., Victoria, B.C.

Cannell MGR, Grace J, Booth A (1989) Possible impacts of climatic warming on trees and forests in the United Kingdom—a review. Forestry 62:337–364. doi:10.1093/forestry/62.4.337

Carvalho A, Flannigan MD, Logan K, Miranda AI, Borrego C (2008) Fire activity in Portugal and its relationship to weather and the Canadian Fire Weather Index System. Int J Wildl Fire 17:328–338. doi:10.1071/WF07014

Castagneri D, Motta R (2010) A research gap in the interactive effects of climate and competition on trees growth. In: Karam WP (ed) Tree growth: influences, layers and types. Nova Science, Hauppauge, pp 93–102

Caverley N (2013) The guardians of Mother Earth: a qualitative study of aboriginal knowledge keepers and their views on climate change adaptation in the South Selkirks region. Nativ Stud Rev 21:125–150

Cheaib A, Badeau V, Boe J, Chuine I, Delire C, Dufrêne E, François C, Gritti ES, Legay M, Pagé C, Thuiller W, Viovy N, Leadley P (2012) Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. Ecol Lett 15:533–544. doi:10.1111/j.1461-0248.2012.01764.x

Chen WJ, Black TA, Yang PC, Barr AG, Neumann HH, Nesic Z, Blanken PD, Novak MD, Eley J, Ketler RJ, Cuenca A (1999) Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. Glob Chang Biol 5:41–53. doi:10.1046/j.1365-2486.1998.00201.x

Chmura DJ, Anderson PD, Howe GT, Harrington CA, Halofsky JE, Peterson DL, Shaw DC, St. Brad Clair J (2011) Forest responses to climate change in the northwestern United States: ecophysiological foundations for adaptive management. For Ecol Manag 261:1121–1142. doi:10.1016/j.foreco.2010.12.040

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG, Jacobsen AL, Lens F, Maherali H, Martinez-Vilalta J, Mayr S, Mencuccini M, Mitchell PJ, Nardini A, Pittermann J, Pratt RB, Sperry JS, Westoby M, Wright IJ, Zanne AE (2012) Global convergence in the vulnerability of forests to drought. Nature 491:752–755

Chuvieco E, Martinez S, Roman MV, Hantson S, Pettinari ML (2014) Integration of ecological and socio-economic factors to assess global vulnerability to wildfire. Glob Ecol Biogeogr 23:245–258. doi:10.1111/geb.12095

Clark DA (2007) Detecting tropical forests' responses to global climatic and atmospheric change: current challenges and a way forward. Biotropica 39:4–19. doi:10.1111/j.1744-7429.2006.00227.x

Clark JS, Bell DM, Hersh MH, Nichols L (2011) Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. Glob Chang Biol 17:1834–1849. doi:10.1111/j.1365-2486.2010.02380.x

Cockfield G, Maraseni T, Buys L, Sommerfeld J, Wilson C, Athukorala W (2011) Socioeconomic implications of climate change with regard to forests and forest management. Contribution of Work Package 3 to the Forest Vulnerability Assessment. National Climate Change Adaptation Research Facility, Gold Coast

Corlett RT (2011) Impacts of warming on tropical lowland rainforests. Trends Ecol Evol 26:606–613

Corlett RT, Westcott DA (2013) Will plant movements keep up with climate change? Trends Ecol Evol 28:482–488. doi:10.1016/j.tree.2013.04.003

Couture S, Reynaud A (2008) Multi-stand forest management under a climatic risk: do time and risk preferences matter? Environ Model Assess 13:181–193

D'Amato AW, Bradford JB, Fraver S, Palik BJ (2011) Forest management for mitigation and adaptation to climate change: insights from long-term silviculture experiments. For Ecol Manag 262:803–816. doi:10.1016/j.foreco.2011.05.014

Daubenmire RF (1978) Plant geography. Academic, New York

Davidar P, Rajagopal B, Mohandass D, Puyravaud JP, Condit R, Wright SJ, Leigh EG (2007) The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. Glob Ecol Biogeogr 16:510–518. doi:10.1111/j.1466-8238.2007.00307.x

Davis MB (1986) Climatic instability, time lags and community disequilibrium. In: Diamond J, Case TJ (eds) Community ecology. Harper and Row, New York, pp 269–284

Day JK, Perez DM (2013) Reducing uncertainty and risk through forest management planning in British Columbia. For Ecol Manag 300:117–124. doi:10.1016/j.foreco.2012.11.035

de Groot WJ, Flannigan MD, Cantin AS (2013) Climate change impacts on future boreal fire regimes. For Ecol Manag 294:35–44. doi:10.1016/j.foreco.2012.09.027

Dessai S, Hulme M (2004) Does climate adaptation policy need probabilities? Clim Pol 4:107–128. doi:10.1080/14693062.2004.9685515

Di Nitto D, Neukermans G, Koedam N, Defever H, Pattyn F, Kairo JG, Dahdouh-Guebas F (2014) Mangroves facing climate change: landward migration potential in response to projected scenarios of sea level rise. Biogeosciences 11:857–871. doi:10.5194/bg-11-857-2014

Dixon RK, Krankina ON, Kobak KI (1996) Global climate change adaptation: examples from Russian boreal forests. Adapting to climate change: an international perspective.

Dobrowski SZ, Abatzoglou J, Swanson AK, Greenberg JA, Mynsberge AR, Holden ZA, Schwartz MK (2013) The climate velocity of the contiguous United States during the 20th century. Glob Chang Biol 19:241–251. doi:10.1111/gcb.12026

Doyle TW, Krauss KW, Conner WH, From AS (2010) Predicting the retreat and migration of tidal forests along the northern Gulf of Mexico under sea-level rise. For Ecol Manag 259:770–777. doi:10.1016/j.foreco.2009.10.023

Eliasch J (2008) Climate change: financing global forests. The Eliasch Review. HMSO

Emanuel WR, Shugart HH, Stevenson MP (1985) Climatic-change and the broad-scale distribution of terrestrial ecosystem complexes. Clim Chang 7:29–43. doi:10.1007/bf00139439

Eriksson LO, Backéus S, Garcia F (2011) Implications of growth uncertainties associated with climate change for stand management. Eur J For Res 131:1199–1209. doi:10.1007/s10342-011-0591-4

Ettl GJ, Peterson DL (1995) Extreme climate and variation in tree growth—individualistic response in sub-alpine fir (*Abies-lasiocarpa*). Glob Chang Biol 1:231–241. doi:10.1111/j.1365-2486.1995.tb00024.x

Feeley KJ, Rehm EM, Machovina B (2012) Perspective: the responses of tropical forest species to global climate change: acclimate, adapt, migrate, or go extinct? Frontiers of Biogeography 4 (2)

Feikema PM, Sherwin CB, Lane PNJ (2013) Influence of climate, fire severity and forest mortality on predictions of long term streamflow: potential effect of the 2009 wildfire on Melbourne's water supply catchments. J Hydrol 488:1–16. doi:10.1016/j.jhydrol.2013.02.001

Fischer AP, Paveglio T, Carroll M, Murphy D, Brenkert-Smith H (2013) Assessing social vulnerability to climate change in human communities near public forests and grasslands: a framework for resource managers and planners. J For 111:357–365. doi:10.5849/jof. 12-091

Fischlin A, Ayres M, Karnosky D, Kellomäki S, Louman B, Ong C, Plattner G-K, Santoso H, Thompson I, Booth TH, Marcar N, Scholes B, Swanston C, Zamolodchikov D (2009) Future environmental impacts and vulnerabilities. In: Seppälä R, Buck A, Katila P (eds) Adaptation of forests and people to climate change: a global assessment report, vol 22. IUFRO World Series, Helsinki, pp 53–100

Franks PJ, Adams MA, Amthor JS, Barbour MM, Berry JA, Ellsworth DS, Farquhar GD, Ghannoum O, Lloyd J, McDowell N, Norby RJ, Tissue DT, von Caemmerer S (2013) Sensitivity of plants to changing atmospheric CO2 concentration: from the geological past to the next century. New Phytol 197:1077–1094. doi:10.1111/nph.12104

Furness E, Nelson H (2012) Community forest organizations and adaptation to climate change in British Columbia. For Chron 88:519–524

Garcia RA, Cabeza M, Rahbek C, Araújo MB (2014) Multiple dimensions of climate change and their implications for biodiversity. Science 344 (6183). doi:10.1126/science.1247579

Gentilli J (1949) Forest influences: the effects of woody vegetation on climatic water, and soil, with applications to the conservation of water and the control of floods and erosion. Geogr Rev 39:164–164. doi:10.2307/211169

Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proc Natl Acad Sci 107:16732–16737. doi:10.1073/pnas.0910275107

Gilman RT, Fabina NS, Abbott KC, Rafferty NE (2012) Evolution of plant–pollinator mutualisms in response to climate change. Evol Appl 5:2–16. doi:10.1111/j.1752-4571.2011.00202.x

Gonzalez ME, Lara A, Urrutia R, Bosnich J (2011) Climatic change and its potential impact on forest fire occurrence in south-central Chile (33 degrees-42 degrees S). Bosque 32:215–219. doi:10.4067/s0717-92002011000300002

Graham RL, Turner MG, Dale VH (1990) How increasing CO2 and climate change affect forests—at many spatial and temporal scales, there will be forest responses that will be affected by human activities. Bioscience 40:575–587. doi:10.2307/1311298

Graumlich LJ (1993) Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great-Lakes region. Can J For Res 23:133–143. doi:10.1139/x93-020

Groffman PM, Rustad LE, Templer PH, Campbell JL, Christenson LM, Lany NK, Socci AM, Vadeboncoeur MA, Schaberg PG, Wilson GF, Driscoll CT, Fahey TJ, Fisk MC, Goodale CL, Green MB, Hamburg SP, Johnson CE, Mitchell MJ, Morse JL, Pardo LH, Rodenhouse NL (2012) Long-term integrated studies show complex and surprising effects of climate change in the northern hardwood forest. Bioscience 62:1056–1066. doi:10.1525/bio.2012.62.12.7

Grubb PJ, Whitmore TC (1966) A comparison of montane and lowland rain forest in Ecuador. 2. Climate and its effects on distribution and physiognomy of forests. J Ecol 54:303. doi:10.2307/2257951

Guan BT, Wright WE, Chung C-H, Chang S-T (2012) ENSO and PDO strongly influence Taiwan spruce height growth. For Ecol Manag 267:50–57. doi:10.1016/j.foreco.2011.11.028

Guardiola-Claramonte M, Troch PA, Breshears DD, Huxman TE, Switanek MB, Durcik M, Cobb NS (2011) Decreased streamflow in semi-arid basins following drought-induced tree die-off: a counter-intuitive and indirect climate impact on hydrology. J Hydrol 406:225–233. doi:10.1016/j.jhydrol.2011.06.017

Guariguata MR (2009) Tropical forest management and climate change adaptation. Rev Estud Soc 32:98–112

Guariguata MR, Cornelius JP, Locatelli B, Forner C, Sánchez-Azofeifa GA (2008) Mitigation needs adaptation: tropical forestry and climate change. Mitig Adapt Strateg Glob Chang 13:793–808. doi:10.1007/s11027-007-9141-2

Guariguata MR, Locatelli B, Haupt F (2012) Adapting tropical production forests to global climate change: risk perceptions and actions. Int For Rev 14:27–38

Gyampoh BA, Amisah S, Idinoba M, Nkem J (2009) Using traditional knowledge to cope with climate change in rural Ghana. Unasylva 60:70–74

Hahn WA, Knoke T (2010) Sustainable development and sustainable forestry: analogies, differences, and the role of flexibility. Eur J For Res 129:787–801. doi:10.1007/s10342-010-0385-0

Hamrick JL (2004) Response of forest trees to global environmental changes. For Ecol Manag 197:323–335. doi:10.1016/j.foreco.2004.05.023

Hansenbristow KJ, Ives JD, Wilson JP (1988) Climatic variability and tree response within the forest alpine tundra ecotone. Ann Assoc Am Geogr 78:505–519. doi:10.1111/j.1467-8306.1988.tb00221.x

Harper RJ, Smettem KRJ, Carter JO, McGrath JF (2009) Drought deaths in Eucalyptus globulus (Labill.) plantations in relation to soils, geomorphology and climate. Plant Soil 324:199–207. doi:10.1007/s11104-009-9944-x

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol Conserv 142:14–32. doi:10.1016/j.biocon.2008.10.006

Hennessy K, Lucas C, Nicholls N, Bathols J, Suppiah R, Ricketts J (2005) Climate change impacts on fire-weather in south-east Australia. CSIRO Division of Marine and Atmospheric Research, Aspendale

Holling CS (1978) Adaptive environmental assessment and management. Wiley, Chichester

Hughes L, Cawsey EM, Westoby M (1996) Climatic range sizes of Eucalyptus species in relation to future climate change. Glob Ecol Biogeogr Lett 5:23–29. doi:10.2307/2997467

Huntingford C, Zelazowski P, Galbraith D, Mercado LM, Sitch S, Fisher R, Lomas M, Walker AP, Jones CD, Booth BBB, Malhi Y, Hemming D, Kay G, Good P, Lewis SL, Phillips OL, Atkin OK, Lloyd J, Gloor E, Zaragoza-Castells J, Meir P, Betts R, Harris PP,

Nobre C, Marengo J, Cox PM (2013) Simulated resilience of tropical rainforests to CO2-induced climate change. Nat Geosci 6: 268–273

Huntley B (1990) European postglacial forests—compositional changes in response to climatic-change. J Veg Sci 1:507–518. doi:10.2307/3235785

Ince PJ, Kramp AD, Skog KE, Yoo DI, Sample VA (2011) Modeling future U.S. forest sector market and trade impacts of expansion in wood energy consumption. J For Econ 17:142–156. doi:10.1016/j.jfe.2011.02.007

Innes J, Joyce LA, Kellomäki S, Louman B, Ogden A, Parrotta J, Thompson I, Ayres M, Ong C, Santoso H, Sohngen B, Wreford A (2009) Management for adaptation. In: Seppälä R, Buck A, Katila P (eds) Adaptation of forests and people to climate change: a global assessment report, vol World Series Volume 22. IUFRO Helsinki, pp 135–186

IPCC (2013) Climate Change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge, United Kingdom and New York, NY, USA

IUCN (2008) Ecosystem-based adaptation: an approach for building resilience and reducing risk for local communities and ecosystems. Submission to the Chair of the AWG-LCA with respect to the Shared Vision and Enhanced Action on Adaptation. International Union for the Conservation of Nature,

Iverson LR, Schwartz MW, Prasad AM (2004) How fast and far might tree species migrate in the eastern United States due to climate change? Glob Ecol Biogeogr 13:209–219

Johnson G, Sorensen FC, St Clair JB, Cronn RC (2004) Pacific Northwest forest tree seed zones: a template for native plants? Nativ Plants J 5:131–140

Johnston M, Hesseln H (2012) Climate change adaptive capacity of the Canadian forest sector. For Policy Econ 24:29–34. doi:10.1016/j.forpol.2012.06.001

Johnston M, Lindner M, Parrotta J, Giessen L (2012) Adaptation and mitigation options for forests and forest management in a changing climate. For Policy Econ 24:1–2. doi:10.1016/j.forpol.2012.09.007

Johnston M, Williamson T (2007) A framework for assessing climate change vulnerability of the Canadian forest sector. For Chron 83: 358–361

Joyce LA (2007) The impacts of climate change on forestry. In: Adams DM, Haynes RW (eds) Resource and market projections for forest policy development: twenty-five years of experience with the US RPA Timber Assessment, vol 14. Managing Forest Ecosystems. pp 449–488

Joyce LA, Blate GM, Littell JS, McNulty SG, Millar CI, Moser SC, Neilson RP, O'Halloran K, Peterson DL (2008) National forests. Preliminary review of adaptation options for climate-sensitive ecosystems and resources. A report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. US Environmental Protection Agency, Washington, DC

Joyce LA, Blate GM, McNulty SG, Millar CI, Moser S, Neilson RP, Peterson DL (2009) Managing for multiple resources under climate change: national forests. Environ Manag 44:1022–1032. doi:10.1007/s00267-009-9324-6

Joyce LA, Mills JR, Heath LS, McGuire AD, Haynes RW, Birdsey RA (1995) Forest sector impacts from changes in forest productivity under climate change. J Biogeogr 22:703–713. doi:10.2307/2845973

Kalame FB, Luukkanen O, Kanninen M (2011) Making the National Adaptation Programme of Action (NAPA) more responsive to the livelihood needs of tree planting farmers, drawing on previous experience in dryland Sudan. Forests 2:948–960. doi:10.3390/f2040948

Kallarackal J, Roby TJ (2012) Responses of trees to elevated carbon dioxide and climate change. Biodivers Conserv 21:1327–1342. doi:10.1007/s10531-012-0254-x

Kant P, Wu S (2012) Should adaptation to climate change be given priority over mitigation in tropical forests? Carbon Manag 3:303–311. doi:10.4155/cmt.12.29

Karjalainen T, Pussinen A, Liski J, Nabuurs GJ, Eggers T, Lapvetelainen T, Kaipainen T (2003) Scenario analysis of the impacts of forest management and climate change on the European forest sector carbon budget. For Policy Econ 5:141–155. doi:10.1016/s1389-9341(03)00021-2

Keenan RJ (2012) Adaptation of forests and forest management to climate change: an editorial. Forests 3:75–82. doi:10.3390/f3010075

Kellomaki S, Peltola H, Nuutinen T, Korhonen KT, Strandman H (2008) Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. Phil Trans R Soc B 363:2341–2351. doi:10.1098/rstb.2007.2204

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proc Natl Acad Sci 105:11823–11826. doi:10.1073/pnas.0802891105

Kerhoulas LP, Kolb TE, Hurteau MD, Koch GW (2013) Managing climate change adaptation in forests: a case study from the US Southwest. J Appl Ecol 50:1311–1320. doi:10.1111/1365-2664.12139

Keskitalo EC (2008) Vulnerability and adaptive capacity in forestry in northern Europe: a Swedish case study. Clim Chang 87:219–234. doi:10.1007/s10584-007-9337-1

Keskitalo ECH (2011) How can forest management adapt to climate change? Possibilities in different forestry systems. Forests 2:415–430. doi:10.3390/f2010415

Kienast F, Brzeziecki B, Wildi O (1996) Long-term adaptation potential of Central European mountain forests to climate change: a GIS-assisted sensitivity assessment. For Ecol Manag 80:133–153. doi:10.1016/0378-1127(95)03633-4

Kimmins JP (2002) Future shock in forestry—where have we come from; where are we going; is there a "right way" to manage forests? Lessons from Thoreau, Leopold, Toffler, Botkin and Nature. For Chron 78:263–271

Kimmins JP (2008) From science to stewardship: harnessing forest ecology in the service of society. For Ecol Manag 256:1625–1635. doi:10.1016/j.foreco.2008.02.057

Kimmins JP, Blanco JA, Seely B, Welham C, Scoullar K (2008) Complexity in modelling forest ecosystems: how much is enough? For Ecol Manag 256:1646–1658. doi:10.1016/j.foreco.2008.03.011

Kimmins JP, Mailly D, Seely B (1999) Modelling forest ecosystem net primary production: the hybrid simulation approach used in forecast. Ecol Model 122:195–224

Kint V, Aertsen W, Campioli M, Vansteenkiste D, Delcloo A, Muys B (2012) Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901–2008. Clim Chang 115:343–363. doi:10.1007/s10584-012-0465-x

Kirschbaum MUF, Watt MS, Tait A, Ausseil A-GE (2012) Future wood productivity of Pinus radiata in New Zealand under expected climatic changes. Glob Chang Biol 18:1342–1356. doi:10.1111/j.1365-2486.2011.02625.x

Klenk NL, Adams BW, Bull GQ, Innes JL, Cohen SJ, Larson BC (2011) Climate change adaptation and sustainable forest management: a proposed reflexive research agenda. For Chron 87:351–357

Kobak KI, Turchinovich IY, Kondrasheva NY, Schulze ED, Schulze W, Koch H, Vygodskaya NN (1996) Vulnerability and adaptation of the larch forest in eastern Siberia to climate change. Water Air Soil Pollut 92:119–127

Kolström M, Lindner M, Vilén T, Maroschek M, Seidl R, Lexer MJ, Netherer S, Kremer A, Delzon S, Barbati A, Marchetti M, Corona P (2011) Reviewing the science and Implementation of climate change

adaptation measures in European forestry. Forests 2:961–982. doi:10.3390/f2040961
Konkin D, Hopkins K (2009) Learning to deal with climate change and catastrophic forest disturbances. Unasylva 60:17–23
Kremer A, Ronce O, Robledo-Arnuncio JJ, Guillaume F, Bohrer G, Nathan R, Bridle JR, Gomulkiewicz R, Klein EK, Ritland K, Kuparinen A, Gerber S, Schueler S (2012) Long-distance gene flow and adaptation of forest trees to rapid climate change. Ecol Lett 15: 378–392. doi:10.1111/j.1461-0248.2012.01746.x
Kuparinen A, Savolainen O, Schurr FM (2010) Increased mortality can promote evolutionary adaptation of forest trees to climate change. For Ecol Manag 259:1003–1008. doi:10.1016/j.foreco.2009.12.006
Lal R, Cummings DJ (1979) Clearing a tropical forest. 1. Effects on soil and micro-climate. Field Crop Res 2:91–107. doi:10.1016/0378-4290(79)90012-1
Leites LP, Rehfeldt GE, Robinson AP, Crookston NL, Jaquish B (2012) Possibilities and limitations of using historic provenance tests to infer forest species growth responses to climate change. Nat Resour Model 25:409–433. doi:10.1111/j.1939-7445.2012.00129.x
Lenoir J, Gegout JC, Dupouey JL, Bert D, Svenning JC (2010) Forest plant community changes during 1989–2007 in response to climate warming in the Jura Mountains (France and Switzerland). J Veg Sci 21:949–964. doi:10.1111/j.1654-1103.2010.01201.x
Leuzinger S, Luo Y, Beier C, Dieleman W, Vicca S, Körner C (2011) Do global change experiments overestimate impacts on terrestrial ecosystems? Trends Ecol Evol 26:236–241
Levina E, Tirpak D (2006) Adaptation to climate change: key terms. OECD/IEA, Paris
Lin BB, Petersen B (2013) Resilience, regime shifts, and guided transition under climate change: examining the practical difficulties of managing continually changing systems. Ecology and Society 18 (1). doi:10.5751/es-05128-180128
Lindner M (2000) Developing adaptive forest management strategies to cope with climate change. Tree Physiol 20:299–307
Lindner M, Fitzgerald JB, Zimmermann NE, Reyer C, Delzon S, van der Maaten E, Schelhaas MJ, Lasch P, Eggers J, van der Maaten-Theunissen M, Suckow F, Psomas A, Poulter B, Hanewinkel M (2014) Climate change and European forests: what do we know, what are the uncertainties, and what are the implications for forest management? J Environ Manag 146:69–83. doi:10.1016/j.jenvman.2014.07.030
Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolström M, Lexer MJ, Marchetti M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For Ecol Manag 259: 698–709. doi:10.1016/j.foreco.2009.09.023
Lindner M, Sohngen B, Joyce LA, Price DT, Bernier PY, Karjalainen T (2002) Integrated forestry assessments for climate change impacts. For Ecol Manag 162:117–136. doi:10.1016/S0378-1127(02)00054-3
Littell JS, Peterson DL, Millar CI, O'Halloran KA (2012) U.S. national forests adapt to climate change through science-management partnerships. Clim Chang 110:269–296. doi:10.1007/s10584-011-0066-0
Liu Y, Stanturf J, Goodrick S (2010) Trends in global wildfire potential in a changing climate. For Ecol Manag 259:685–697. doi:10.1016/j.foreco.2009.09.002
Locatelli B, Evans V, Wardell A, Andrade A, Vignola R (2011) Forests and climate change in Latin America: linking adaptation and mitigation. Forests 2:431–450. doi:10.3390/f2010431
Loehman RA, Clark JA, Keane RE (2011) Modeling effects of climate change and fire management on Western White Pine (Pinus monticola) in the Northern Rocky Mountains, USA. Forests 2: 832–860. doi:10.3390/f2040832
Long A (2013) REDD plus, adaptation, and sustainable forest management: toward effective polycentric global forest governance. Trop Conserv Sci 6:384–408
Lucier A, Ayres M, Karnosky D, Thompson I, Loehle C, Percy K, Sohngen B (2009) Forest responses and vulnerabilities to recent climate change. In: Seppälä R, Buck A, Katila P (eds) Adaptation of forests and people to climate change: a global assessment report, vol World Series Volume 22. IUFRO Helsinki, pp 29–52
Lynch AJJ, Fell DG, McIntyre-Tamwoy S (2010) Incorporating Indigenous values with 'Western' conservation values in sustainable biodiversity management. Aust J Environ Manag 17:244–255
Macdonald GM, Edwards TWD, Moser KA, Pienitz R, Smol JP (1993) Rapid response of treeline vegetation and lakes to past climate warming. Nature 361:243–246. doi:10.1038/361243a0
Mahat V, Anderson A (2013) Impacts of climate and catastrophic forest changes on streamflow and water balance in a mountainous headwater stream in Southern Alberta. Hydrol Earth Syst Sci 17:4941–4956. doi:10.5194/hess-17-4941-2013
Malcolm JR, Markham A, Neilson RP, Garaci M (2002) Estimated migration rates under scenarios of global climate change. J Biogeogr 29:835–849. doi:10.1046/j.1365-2699.2002.00702.x
Matthews SN, Iverson LR, Prasad AM, Peters MP (2011) Changes in potential habitat of 147 North American breeding bird species in response to redistribution of trees and climate following predicted climate change. Ecography 34:933–945. doi:10.1111/j.1600-0587.2011.06803.x
McEvoy D, Fünfgeld H, Bosomworth K (2013) Resilience and climate change adaptation: the importance of framing. Plan Pract Res 28: 280–293. doi:10.1080/02697459.2013.787710
Medlyn B, Zeppel M, Brouwers N, Howard K, O'Gara E, Hardy G, Lyons T, Li L, Evans B (2011) Biophysical impacts of climate change on Australia's forests. Contribution of Work Package 2 to the Forest Vulnerability Assessment. National Climate Change Adaptation Research Facility, Gold Coast
Messier C, Puettmann K, Coates DJ (2013) Managing forests as complex adaptive systems: building resilience to the challenge of global change. Earthscan, London
Michelot A, Breda N, Damesin C, Dufrene E (2012) Differing growth responses to climatic variations and soil water deficits of Fagus sylvatica, Quercus petraea and Pinus sylvestris in a temperate forest. For Ecol Manag 265:161–171. doi:10.1016/j.foreco.2011.10.024
Milad M, Schaich H, Konold W (2013) How is adaptation to climate change reflected in current practice of forest management and conservation? A case study from Germany. Biodivers Conserv 22: 1181–1202. doi:10.1007/s10531-012-0337-8
Miles L, Grainger A, Phillips O (2004) The impact of global climate change on tropical forest biodiversity in Amazonia. Glob Ecol Biogeogr 13:553–565. doi:10.1111/j.1466-822X.2004.00105.x
Mok H-F, Arndt SK, Nitschke CR (2012) Modelling the potential impact of climate variability and change on species regeneration potential in the temperate forests of South-Eastern Australia. Glob Chang Biol 18:1053–1072. doi:10.1111/j.1365-2486.2011.02591.x
Mori AS, Spies TA, Sudmeier-Rieux K, Andrade A (2013) Reframing ecosystem management in the era of climate change: issues and knowledge from forests. Biol Conserv 165:115–127. doi:10.1016/j.biocon.2013.05.020
Namkoong G (2001) Forest genetics: pattern and complexity. Can J For Res 31:623–632. doi:10.1139/cjfr-31-4-623
Neukum C, Azzam R (2012) Impact of climate change on groundwater recharge in a small catchment in the Black Forest, Germany. Hydrogeol J 20:547–560. doi:10.1007/s10040-011-0827-x
Nilsson AE, Gerger Swartling Å, Eckerberg K (2012) Knowledge for local climate change adaptation in Sweden: challenges of multilevel governance. Local Environ 17:751–767. doi:10.1080/13549839.2012.678316
Nitschke CR, Innes JL (2008a) Integrating climate change into forest management in South-Central British Columbia: an assessment of landscape vulnerability and development of a climate-smart

framework. For Ecol Manag 256:313–327. doi:10.1016/j.foreco.2008.04.026
Nitschke CR, Innes JL (2008b) A tree and climate assessment tool for modelling ecosystem response to climate change. Ecol Model 210:263–277. doi:10.1016/j.ecolmodel.2007.07.026
Nkem J, Kalame FB, Idinoba M, Somorin OA, Ndoye O, Awono A (2010) Shaping forest safety nets with markets: adaptation to climate change under changing roles of tropical forests in Congo Basin. Environ Sci Pol 13:498–508. doi:10.1016/j.envsci.2010.06.004
Ogden AE, Innes J (2007a) Incorporating climate change adaptation considerations into forest management planning in the boreal forest. Int For Rev 9:713–733. doi:10.1505/ifor.9.3.713
Ogden AE, Innes JL (2007b) Perspectives of forest practitioners on climate change adaptation in the Yukon and Northwest Territories of Canada. For Chron 83:557–569
Ogden AE, Innes JL (2009) Application of structured decision making to an assessment of climate change vulnerabilities and adaptation options for sustainable forest management. Ecology and Society 14 (1). doi:11
Ohlson DW, McKinnon GA, Hirsch KG (2005) A structured decision-making approach to climate change adaptation in the forest sector. For Chron 81:97–103
Otterman J, Chou MD, Arking A (1984) Effects of nontropical forest cover on climate. J Clim Appl Meteorol 23:762–767. doi:10.1175/1520-0450(1984)023<0762:eonfco>2.0.co;2
Parks CG, Bernier P (2010) Adaptation of forests and forest management to changing climate with emphasis on forest health: a review of science, policies and practices. For Ecol Manag 259:657–659. doi:10.1016/s0378-1127(09)00903-7
Pastor J, Post WM (1988) Response of northern forests to CO2-induced climate change. Nature 334:55–58. doi:10.1038/334055a0
Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr 12:361–371. doi:10.1046/j.1466-822X.2003.00042.x
Peel J, Godden L, Keenan RJ (2012) Climate change law in an era of multi-level governance. Transl Environ Law 1:245–280. doi:10.1017/S2047102512000052
Peters EB, Wythers KR, Zhang SX, Bradford JB, Reich PB (2013) Potential climate change impacts on temperate forest ecosystem processes. Can J For Res 43:939–950. doi:10.1139/cjfr-2013-0013
Peterson DL, Millar CI, Joyce LA, Furniss MJ, Halofsky JE, Neilson RP, Morelli TL (2011) Responding to climate change in national forests: a guidebook for developing adaptation options. General Technical Report. USDA Forest Service, Pacific Northwest Research Station
Phillips OL, Lewis SL, Baker TR, Chao K-J, Higuchi N (2008) The changing Amazon forest. Phil Trans R Soc B 363:1819–1827. doi:10.1098/rstb.2007.0033
Pinkard EA, Battaglia M, Bruce J, Leriche A, Kriticos DJ (2010) Process-based modelling of the severity and impact of foliar pest attack on eucalypt plantation productivity under current and future climates. For Ecol Manag 259:839–847. doi:10.1016/j.foreco.2009.06.027
Pojar J, Klinka K, Meidinger DV (1987) Biogeoclimatic ecosystem classification in British Columbia. For Ecol Manag 22:119–154
Pramova E, Locatelli B, Djoudi H, Somorin OA (2012) Forests and trees for social adaptation to climate variability and change. Wiley Interdiscip Rev Clim Chang 3:581–596. doi:10.1002/wcc.195
Prato T (2008) Conceptual framework for assessment and management of ecosystem impacts of climate change. Ecol Complex 5:329–338
Pretzsch H, Biber P, Schütze G, Uhl E, Rötzer T (2014) Forest stand growth dynamics in Central Europe have accelerated since 1870. Nat Commun 5. doi:10.1038/ncomms5967
Rastetter EB, Ryan MG, Shaver GR, Melillo JM, Nadelhoffer KJ, Hobbie JE, Aber JD (1991) A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO2, climate, and N deposition. Tree Physiol 9:101–126
Rayner J, McNutt K, Wellstead A (2013) Dispersed capacity and weak coordination: the challenge of climate change adaptation in Canada's forest policy sector. Rev Policy Res 30:66–90. doi:10.1111/ropr.12003
Regniere J (2009) Predicting insect continental distributions from species physiology. Unasylva 60:37–42
Reyer C, Lasch-Born P, Suckow F, Gutsch M, Murawski A, Pilz T (2014) Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide. Ann For Sci 71:211–225. doi:10.1007/s13595-013-0306-8
Rigling A, Bigler C, Eilmann B, Feldmeyer-Christe E, Gimmi U, Ginzler C, Graf U, Mayer P, Vacchiano G, Weber P, Wohlgemuth T, Zweifel R, Dobbertin M (2013) Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Glob Chang Biol 19:229–240. doi:10.1111/gcb.12038
Rist L, Moen J (2013) Sustainability in forest management and a new role for resilience thinking. For Ecol Manag 310:416–427. doi:10.1016/j.foreco.2013.08.033
Roberts G, Parrotta J, Wreford A (2009) Current adaptation measures and policies. In: Seppälä R, Buck A, Katila P (eds) Adaptation of forests and people to climate change: a global assessment report, vol World Series Volume 22. IUFRO Helsinki, pp 123–134
Ruiz-Labourdette D, Schmitz MF, Pineda FD (2013) Changes in tree species composition in Mediterranean mountains under climate change: indicators for conservation planning. Ecol Indic 24:310–323. doi:10.1016/j.ecolind.2012.06.021
Running SW, Nemani RR (1991) Regional hydrologic and carbon balance responses of forests resulting from potential climate change. Clim Chang 19:349–368. doi:10.1007/bf00151173
Sample VA, Halofsky JE, Peterson DL (2014) US strategy for forest management adaptation to climate change: building a framework for decision making. Ann For Sci 71:125–130. doi:10.1007/s13595-013-0288-6
Schaich H, Milad M (2013) Forest biodiversity in a changing climate: which logic for conservation strategies? Biodivers Conserv 22:1107–1114. doi:10.1007/s10531-013-0491-7
Schoene DHF, Bernier PY (2012) Adapting forestry and forests to climate change: a challenge to change the paradigm. For Policy Econ 24:12–19. doi:10.1016/j.forpol.2011.04.007
Schwartz MW, Dolanc CR, Gao H, Strauss SY, Schwartz AC, Williams JN, Tang Y (2013) Forest structure, stand composition, and climate-growth response in montane forests of Jiuzhaigou National Nature Reserve, China. Plos One 8 (8). doi:10.1371/journal.pone.0071559
Scott D (2005) Integrating climate change into Canada's National Parks System. In: Lovejoy T, Hannah L (eds) Climate change and biodiversity. Yale University Press, New Haven, pp 343–345
Seidl R, Lexer MJ (2013) Forest management under climatic and social uncertainty: trade-offs between reducing climate change impacts and fostering adaptive capacity. J Environ Manag 114:461–469. doi:10.1016/j.jenvman.2012.09.028
Seidl R, Rammer W, Lexer MJ (2011) Adaptation options to reduce climate change vulnerability of sustainable forest management in the Austrian Alps. Can J For Res 41:694–706. doi:10.1139/x10-235
Seppala R (2009) A global assessment on adaptation of forests to climate change. Scand J For Res 24:469–472. doi:10.1080/02827580903378626
Seppälä R, Buck A, Katila P (2009) Adaptation of forests and people to climate change: a global assessment report, vol World Series Volume 22. Helsinki, IUFRO
Six DL (2009) Climate change and mutualism. Nat Rev Microbiol 7:686–686
Somorin OA, Brown HCP, Visseren-Hamakers IJ, Sonwa DJ, Arts B, Nkem J (2012) The Congo Basin forests in a changing climate: Policy discourses on adaptation and mitigation (REDD+). Glob Environ Chang 22:288–298. doi:10.1016/j.gloenvcha.2011.08.001

Sonwa DJ, Somorin OA, Jum C, Bele MY, Nkem JN (2012) Vulnerability, forest-related sectors and climate change adaptation: the case of Cameroon. For Policy Econ 23:1–9. doi:10.1016/j.forpol.2012.06.009

Sork VL, Aitken SN, Dyer RJ, Eckert AJ, Legendre P, Neale DB (2013) Putting the landscape into the genomics of trees: approaches for understanding local adaptation and population responses to changing climate. Tree Genet Genome 9:901–911. doi:10.1007/s11295-013-0596-x

Spathelf P, van der Maaten E, van der Maaten-Theunissen M, Campioli M, Dobrowolska D (2014) Climate change impacts in European forests: the expert views of local observers. Ann For Sci 71:131–137. doi:10.1007/s13595-013-0280-1

Spies TA, Giesen TW, Swanson FJ, Franklin JF, Lach D, Johnson KN (2010) Climate change adaptation strategies for federal forests of the Pacific Northwest, USA: ecological, policy, and socio-economic perspectives. Landsc Ecol 25:1185–1199. doi:10.1007/s10980-010-9483-0

Spittlehouse DL (2005) Integrating climate change adaptation into forest management. For Chron 81:691–695

Spittlehouse DL, Stewart RB (2003) Adaption to climate change in forest management. BCJ Ecosyst Manag 4:1–11

Stafford Smith M, Horrocks L, Harvey A, Hamilton C (2011) Rethinking adaptation for a 4 degrees C world. Philos Transact A Math Phys Eng Sci 369:196–216

Stainforth DA, Allen MR, Tredger ER, Smith LA (2007) Confidence, uncertainty and decision-support relevance in climate predictions. Philos Trans R Soc A Math Phys Eng Sci 365:2145–2161. doi:10.1098/rsta.2007.2074

Stanturf JA, Palik BJ, Dumroese RK (2014) Contemporary forest restoration: a review emphasizing function. For Ecol Manag 331:292–323

Steenberg JWN, Duinker PN, Bush PG (2011) Exploring adaptation to climate change in the forests of central Nova Scotia, Canada. For Ecol Manag 262:2316–2327. doi:10.1016/j.foreco.2011.08.027

Stephens M, Pinkard L, Keenan RJ (2012) Plantation forest industry climate change adaptation handbook. Australian Forest Products Association, Canberra

Tacconi L, Moore PF, Kaimowitz D (2007) Fires in tropical forests—what is really the problem? Lessons from Indonesia. Mitig Adapt Strateg Glob Chang 12:55–66. doi:10.1007/s11027-006-9040-y

Temperli C, Bugmann H, Elkin C (2012) Adaptive management for competing forest goods and services under climate change. Ecol Appl 22:2065–2077

Thackway R, Cresswell ID (1992) Environmental regionalisations of Australia: a user-oriented approach. Environmental Resources Information Network, Canberra

Thomalla F, Downing T, Spanger-Siegfried E, Han GY, Rockstrom J (2006) Reducing hazard vulnerability: towards a common approach between disaster risk reduction and climate adaptation. Disasters 30:39–48. doi:10.1111/j.1467-9523.2006.00305.x

Thomson-Reuters (2014) Web of Science. http://thomsonreuters.com/thomson-reuters-web-of-science/. Accessed 21 Aug 2014

Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE (2008) Predicting global change impacts on plant species' distributions: future challenges. Perspect Plant Ecol Evol Syst 9:137–152. doi:10.1016/j.ppees.2007.09.004

Toffler A (1970) Future shock. Bantam, Toronto

Tompkins EL, Adger WN, Boyd E, Nicholson-Cole S, Weatherhead K, Arnell N (2010) Observed adaptation to climate change: UK evidence of transition to a well-adapting society. Glob Environ Chang Hum Policy Dimens 20:627–635. doi:10.1016/j.gloenvcha.2010.05.001

Urwin K, Jordan A (2008) Does public policy support or undermine climate change adaptation? Exploring policy interplay across different scales of governance. Glob Environ Chang Hum Policy Dimens 18:180–191. doi:10.1016/j.gloenvcha.2007.08.002

Van Damme L (2008) Can the forest sector adapt to climate change? For Chron 84:633–634

van Dijk AIJM, Keenan RJ (2007) Planted forests and water in perspective. For Ecol Manag 251:1–9. doi:10.1016/j.foreco.2007.06.010

Versini PA, Velasco M, Cabello A, Sempere-Torres D (2013) Hydrological impact of forest fires and climate change in a Mediterranean basin. Nat Hazards 66:609–628. doi:10.1007/s11069-012-0503-z

Vignola R, Locatelli B, Martinez C, Imbach P (2009) Ecosystem-based adaptation to climate change: what role for policy-makers, society and scientists? Mitig Adapt Strateg Glob Chang 14:691–696. doi:10.1007/s11027-009-9193-6

Vihervaara P, D'Amato D, Forsius M, Angelstam P, Baessler C, Balvanera P, Boldgiv B, Bourgeron P, Dick J, Kanka R, Klotz S, Maass M, Melecis V, Petrik P, Shibata H, Tang JW, Thompson J, Zacharias S (2013) Using long-term ecosystem service and biodiversity data to study the impacts and adaptation options in response to climate change: insights from the global ILTER sites network. Curr Opin Environ Sustain 5:53–66. doi:10.1016/j.cosust.2012.11.002

von Detten R, Faber F (2013) Organizational decision-making by German state-owned forest companies concerning climate change adaptation measures. For Policy Econ 35:57–65. doi:10.1016/j.forpol.2013.06.009

Walker B, Meyers JA (2004) Thresholds in ecological and social-ecological systems: a developing database. Ecology and Society 9 (2)

Walker B, Salt D (2012) Resilience practice: engaging the sources of our sustainability. Island Press, Washington, DC

Wang T, Campbell EM, O'Neill GA, Aitken SN (2012) Projecting future distributions of ecosystem climate niches: uncertainties and management applications. For Ecol Manag 279:128–140. doi:10.1016/j.foreco.2012.05.034

Wellstead A, Rayner J, Howlett M (2014) Beyond the black box: forest sector vulnerability assessments and adaptation to climate change in North America. Environ Sci Pol 35:109–116. doi:10.1016/j.envsci.2013.04.002

Westerling AL, Gershunov A, Cayan DR, Barnett TP (2002) Long lead statistical forecasts of area burned in western US wildfires by ecosystem province. Int J Wildl Fire 11:257–266. doi:10.1071/wf02009

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940–943. doi:10.1126/science.1128834

White A, Hatcher J, Khare A, Liddle M, Molnar A, Sunderlin WD (2010) Seeing people through the trees and the carbon: mitigating and adapting to climate change without undermining rights and livelihoods. Social dimensions of climate change: equity and vulnerability in a warming world: 277–301

Wilby RL, Dessai S (2010) Robust adaptation to climate change. Weather 65:180–185. doi:10.1002/wea.543

Williams J (2013) Exploring the onset of high-impact mega-fires through a forest land management prism. For Ecol Manag 294:4–10. doi:10.1016/j.foreco.2012.06.030

Williams JE (2000) The biodiversity crisis and adaptation to climate change: a case study from Australia's forests. Environ Monit Assess 61:65–74. doi:10.1023/a:1006361917359

Williams JT (2004) Managing fire-dependent ecosystems: we need a public lands policy debate. Fire Manag Today 64:6–11

Wintle BA, Bekessy SA, Keith DA, van Wilgen BW, Cabeza M, Schroder B, Carvalho SB, Falcucci A, Maiorano L, Regan TJ, Rondinini C, Boitani L, Possingham HP (2011) Ecological-economic optimization of biodiversity conservation under climate change. Nat Clim Chang 1:355–359. doi:10.1038/nclimate1227

Wu HX, Ying CC (2004) Geographic pattern of local optimality in natural populations of lodgepole pine. For Ecol Manag 194:177–198. doi:10.1016/j.foreco.2004.02.017

Yousefpour R, Jacobsen JB, Meilby H, Thorsen BJ (2014) Knowledge update in adaptive management of forest resources under climate change: a Bayesian simulation approach. Ann For Sci 71:301–312. doi:10.1007/s13595-013-0320-x

Yousefpour R, Jacobsen JB, Thorsen BJ, Meilby H, Hanewinkel M, Oehler K (2011) A review of decision-making approaches to handle uncertainty and risk in adaptive forest management under climate change. Ann For Sci 69:1–15. doi:10.1007/s13595-011-0153-4

Zhao D, Wu S, Yin Y (2013) Responses of terrestrial ecosystems' net primary productivity to future regional climate change in China. PLoS ONE 8:e60849. doi:10.1371/journal.pone.0060849

Zhou GY, Wei XH, Wu YP, Liu SG, Huang YH, Yan JH, Zhang DQ, Zhang QM, Liu JX, Meng Z, Wang CL, Chu GW, Liu SZ, Tang XL, Liu XD (2011) Quantifying the hydrological responses to climate change in an intact forested small watershed in Southern China. Glob Chang Biol 17: 3736–3746. doi:10.1111/j.1365-2486.2011.02499.x

Zimmermann NE, Yoccoz NG, Edwards TC, Meier ES, Thuiller W, Guisan A, Schmatz DR, Pearman PB (2009) Climatic extremes improve predictions of spatial patterns of tree species. Proc Natl Acad Sci 106:19723–19728. doi:10.1073/pnas.0901643106

ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/285728799

Maintaining the Mosaic: The role of indigenous burning in land management

Article *in* Journal of Forestry · November 2001

DOI: 10.1093/jof/99.11.36

CITATIONS
311

READS
7,351

2 authors:



Robin Kimmerer
SUNY College of Environmental Science and Forestry
32 PUBLICATIONS **2,013** CITATIONS

SEE PROFILE



Frank K. Lake
US Forest Service
38 PUBLICATIONS **1,460** CITATIONS

SEE PROFILE

All content following this page was uploaded by Frank K. Lake on 21 August 2018.

The user has requested enhancement of the downloaded file.

The Role of Indigenous Burning in Land Management

Robin Wall Kimmerer and Frank Kanawha Lake

ABSTRACT

This article highlights the findings of the literature on aboriginal fire from the human- and the land-centered disciplines, and suggests that the traditional knowledge of indigenous peoples be incorporated into plans for reintroducing fire to the nation's forests. Traditional knowledge represents the outcome of long experimentation with application of fire by indigenous people, which can inform contemporary policy discussions.

Keywords: biodiversity; fire; history; policy; traditional knowledge

Every landscape reflects the history and culture of the people who inhabit it. The worldview of a society is often written more truthfully on the land than in its documents. The current American landscape represents the historical legacy of one worldview superimposed on another, the colonial overlaying the indigenous. Nowhere is this history more apparent than in the attitudes toward fire, attitudes made manifest on the landscape.

Euro-Americans arrived in North America bearing their folk knowledge that held fire in forests to be destructive and hazardous to humans (Arno 1985; Lewis 1982). This view contrasted sharply with the traditional knowledge of the indigenous inhabitants, who embraced the benefits of burning and were skilled in application of fire technology.

Fire suppression began soon after colonization, and its effects followed the expansion of the frontier westward. Anthropogenic fire all but disappeared from eastern forests by the early 1700s and from the West by 1899 (Arno 1985). The consequences of suppression are written on the landscape today, creating what former Secretary of Interior Bruce Babbitt (1997) called "a crisis in forest health." Fire suppression was a "catastrophic disturbance for those ecosystems which had been influenced by anthropogenic fire throughout their development" (Packard 1993).

The results of fire suppression have been well documented for ecosystems throughout North America (e.g., Botkin 1990; Wilson 1992; Pyne 1995; Williams 2000a). Parklands were replaced by dense forests (Biswell 1989; Lewis 1993), prairies and savannas disappeared (Lewis 1993), and re-

generation patterns were dramatically altered. Fire suppression has promoted stand homogeneity and the associated problems of insects and disease, disrupting the age-class mosaic that was historically maintained by burning (Barrett 2000).

The loss of fire in the American landscape is inextricably linked with the history of federal Indian policy that removed tribal people and, therefore, indigenous land management. In the words of Williams (2000a),

> The basis for much of our forest health crisis nationwide lies in the almost complete cessation of burning by Indians in fire-adapted ecosystems. The crisis is commonly attributed to the advent of systematic fire suppression and the Smokey Bear mentality of the 20th century. To fully come to grips with our forest health crisis today, we must go back to much earlier land management decisions that ended thousands of years of Indian interactions with the land, especially through the use of fire.

Policymakers are struggling with the outcome of that history and trying to develop new management policy to restore forest health and biodiversity. The policy pendulum has now swung back from fire suppression to recognition that fire regimes are an important part of ecosystem health. However, the role of humans in a "natural" fire regime continues to be debated (Kilgore 1985).

National forest policy now calls for managers to recreate forests of the presettlement type. Babbitt (1997) proposed that fire be reintroduced for restoration of ecosystem health and productivity. If we are to manage forests with the intent of restoration of the presettlement condition, then it is imperative that we understand the role of indigenous practices in shaping the landscape (Kimmerer 2000).

Every ecosystem in North America has been affected in some way by a fire regime (Pyne 1982; Gruell 1985; Williams 2000a) manipulated by indigenous people. Much forest science, including ecological classifications of vegetation types, arose from observation of forests that were essentially in transition from conditions of indigenous fire management to post-colonial fire suppression. Our understanding of forest processes may thus be based on an anomalous, transitional landscape (Phillips 1985). "Humans have been a part of the ecosystem over the past ten centuries of major climatic change, so that all forests have developed under some kind of human influence. This influence must be accounted for as an important part of any study of forest structure and dynamics" (Russell 1997). Further, Anderson (1997) suggests that

> a full understanding of wild plant production will be achieved only through the development of a better rapprochement between the social, historical and biological sciences. It would require the sustained and cooperative efforts of scholars using both human- and land-centered avenues of research.

Extent of Indigenous Burning

In contrast to the romanticized view of native peoples living with minimal impact on unspoiled nature (Botkin 1990; Martinez 1998), the presettlement landscape was strongly influenced by indigenous land management to enhance productivity (Botkin 1992; Wilson 1992; Blackburn and Anderson 1993; Pyne 1995). The most powerful tool for landscape manipulation was fire. Fire was used by indigenous people throughout North America (Kilgore 1985; Williams 2000a), and its presence or absence strongly shaped the presettlement vegetation. For example, evidence suggests that the dominance of oak and chestnut in Appalachian forests was enhanced by vigorous resprouting after indigenous burning (Abrams 1986, 1992; Delcourt and Delcourt 1997). The extent of tallgrass prairie of the Midwest is thought to be largely a result of Indian fires (e.g., Axelrod 1985).

Western forests, often thought to be shaped primarily by wildfire, may be more the product of indigenous burning than previously thought. For example, the distribution and historical dominance of sugar pine cannot be explained by frequency of "natural" lightning ignition alone. Cultural data provide evidence that sugar pine stands were managed by tribal groups who took "ownership" of individual stands and applied fire to reduce encroachment by competing species (Schenk and Gifford 1952). Dated fire scars on sugar pine offer the best evidence of heightened aboriginal fire frequency in the Sierra Nevada (Lewis 1993), which altered the distribution and abundance of numerous species.

So ubiquitous was Indian burning that its absence also shaped forest composition. The coastal forests of the Pacific Northwest have a very low incidence of lightning fire. Williams (2000a) notes that coastal redwood forests were little affected by burning, although small clearings were made. He argues that fire was less prominent among peoples who relied primarily on marine resources for food and materials. However, a few miles inland even the coastal redwoods contained patches of prairie "too numerous to mention" which

> if left to themselves would doubtless soon have produced forest, but the Indians were accustomed to burn them annually so as to gather seeds. These prairies were of incalculable value to the Indians, not alone for their vegetable products, but for the game found upon them (Loud [1918] quoted in Lewis 1993).

Resource-rich patches in the old-growth coastal forests were created by indigenous manipulation of the fire return interval.

Goals of Indigenous Burning

Fires were intentionally ignited to fulfill a wide variety of purposes, from clearing village sites (Brown 2000) to long-distance signaling. Lewis (1993) documents more than 70 uses of fire, including treefelling, clearing travel corridors, fireproofing settlements, and hunting. Burning also was used to reduce pest populations, including rodents and biting insects, as well as for collecting edible insects such as Pandora moths and grasshoppers. Burning

in oak woodlands reduced the population levels of acorn weevils and yielded a more abundant acorn crop, which was easier to harvest after burning (McCarthy 1993). Riparian areas commonly were burned to attract game animals to the new grass and tree sprouts (Williams 2000a). Fire still is widely used in management of basketry plants, to provide a consistent crop of straight, slender shoots and roots (Ortiz 1993). From crop management to range management, fire was a ubiquitous tool.

Indigenous people used fire to modify the environment for their own survival. The most important outcome of fire use was the intentional creation of a mosaic of habitat patches that promoted food security by ensuring a diverse and productive landscape (Lewis 1985; Williams 2000a). Producing such a mosaic promoted stability in the food supply by creating multiple resource patches. Maintaining a diversity of habitats buffers the impact of natural fluctuation in a single food species and increases overall productivity. For example, fire was used to create prairies which would attract elk, deer, and other game. Indigenous people skillfully modified the fire regime to create a range of forest openings in many different stages of postfire succession, which enhanced the diversity and yield of game, berries, root crops, edible seeds, and medicinal plants. In contrast, fire was often used by the colonists with a different intent—uniformity, such as production of pastures, cropland, and plantations (Williams 2000a).

Philosophy

The policy of fire suppression in Western society arises from the myth that nature can be controlled. Ironically, trying to control nature through fire suppression has led to greater unpredictability. The indigenous worldview emphasizes the dual nature, creative and destructive, of all forces. Fire can be a force for good as it warms homes and stimulates grasses, but it can also be immensely destructive. The role of humans is not to control nature, but to maintain a balance between these opposing forces.

This balance is based on recognition of reciprocal relationships between human and nonhuman members of the ecological community. As coequals, humans are dependent on nonhumans, and the reverse is also true (Pierotti and Wildcat 2000). Human application of fire is part of that interdependence. The ethic of reciprocal responsibility underlies the indigenous use of fire, an adaptive symbiosis in which humans and nonhumans both benefit from burning. For example, indigenous people of the Northwest routinely burned grasslands and savannas to increase the yield of root crops, such as camas and other geophytes. The people realized a direct benefit from burning, and so did the plants, as the fire frequency and extent produced expansion in the patch size and population density of the geophyte species (Anderson 1997).

Meeting the responsibility for reciprocity among members of the ecosystem is understood to be simultaneously pragmatic and spiritual. Application of fire is viewed by many indigenous groups as a spiritual responsibility to the land, a tool that was given to people to fulfill the caregiving responsibilities for the land (Martinez 1998) and to promote world renewal (Krober and Gifford 1949). The Karuk people of northern California burn ritually in New Year ceremonies. Silas Whitman of the Nez Perce tribe states, "We burn because it is good for the land; fire brings more life." For example, the prairies of Walpole Island First Nation have been ritually burned since time immemorial by the Potawatomi, Ojibwe, and Ottawa peoples who accept this as their responsibility and name themselves the "keepers of the fire." The prairies of Walpole Island are renowned among ecologists for their species richness, which far exceeds the diversity where the indigenous fire regime has been interrupted.

Evidence

Sophisticated application of fire technology has been a major component of indigenous land management for millennia. The landscape encountered by colonists was largely shaped by indigenous burning, yet until recently, few people acknowledged that Indian fire use had an impact on the land (Pyne 1995; Williams 2000a). A forestry textbook published as recently as 1973 portrayed the view that "no habitual or systematic burning was carried out by the Indians" (Williams 2000a). This marginalization of traditional knowledge arose partly out of ignorance and prejudice, but also because of the fragmentary nature of the evidence (Williams 2000a). Accounts of aboriginal burning are found in notes, journals, and the oral tradition. These are qualitative, anecdotal sources that are not readily accepted by Western scientists whose training is usually limited to interpretation of quantitative data. Much traditional knowledge has been lost to time and forced assimilation, but much persists in the oral tradition and practices of contemporary native communities, who are only rarely consulted as equal partners in land management.

The correspondence between traditional ecological knowledge of fire response and later scientific evidence is very strong. Examination of traditional knowledge offers an opportunity for crosscultural verification of scientific hypotheses concerning fire management. There is an increasing body of evidence noted by Brown (2000) that validates the oral tradition, through data collected from historical documents, dendrochronology, charcoal profiles, archeological evidence, and statistical analysis of land survey records. Paleoecological data also support interpretation of widespread Indian burning and its effects on vegetation composition (e.g., Clark and Royall 1996; Delcourt and Delcourt 1997). However, it must be acknowledged that there are many pitfalls in the interpretation of such indirect evidence (Williams 2000a). The widespread significance of indigenous burning is by no means universally accepted. Kilgore (1985) summarizes the arguments critical of the importance of aboriginal burning, which focus primarily on issues of scale.

The main impediment to scientific acceptance of the wide impact of aboriginal burning arises from a lack of understanding of the cultural context in which it took place. For many peoples, manipulation of the landscape through

skillful application of fire was critical to cultural survival, and enhanced food productivity made agriculture unnecessary (Biswell 1989).The material culture of many tribal peoples simply could not have been sustained without extensive use of fire (Blackburn and Anderson 1993). In terms of energy efficiency, fire was the most potent land management tool available to indigenous people. Millennia of experimentation and detailed empirical observations led to a sophisticated application of fire technology. Coupled with a worldview that emphasizes the role of humans as active participants in nature, fire was integral to many cultures.

The Practice

A careful examination of the philosophy and practice of Indian burning reveals that it differs from a nonanthropogenic fire regime (i.e., wildfire) in five important respects: seasonality, frequency, extent, site, and outcome (Williams 2000a).

Seasonality of burning varied with the tribe and the ecosystem in question, but in general fire was applied at a carefully considered time that would minimize its destructive nature while harnessing its creative power. Numerous studies confirm that the timing of indigenous burns differs significantly from the seasonality of natural lightning ignitions (Barrett 1980; Barrett and Arno 1982; Lewis 1982; Arno 1985; Brown 2000; Williams 2000a). Lightning fires are most abundant in the late summer, but indigenous fires were set in seasons less conducive to wildfire. For example, in the boreal forests of northern Alberta, fire was applied in the early spring when the grass was dry but the soil was still moist and the surrounding forests were too wet to carry a fire. The small-scale, low-intensity burns created openings in the forest where regrowth was accelerated on the newly blackened earth, extending the growing season in this harsh environment by several weeks and attracting abundant game (Lewis 1982).

The season of burning also depended on the desired outcome. For example, people in the Southwest would burn the chaparral in the fall to increase forage for deer. The lower temperatures and increased soil moisture favored vigorous resprouting, which was beneficial in attracting deer in the winter. In contrast, if the intent was to clear land for tobacco cultivation, the chaparral was ignited in the spring, when a hotter burn would discourage resprouting and prepare a suitable seedbed. In the Great Plains, Indians rotated the seasonality of burning as a tool to influence seasonal movement of bison, in synchrony with their own semi-nomadic movements. In the mosaic of tallgrass prairie and aspen parkland, the prairie was burned in the fall, forcing bison into the parklands that the people inhabited during the winter. In spring, the parklands were burned, which stimulated movement of the bison out onto the open prairies (Lewis 1982). This sophisticated application of fire required extensive knowledge of the vegetation response, the life history of herbivores, and their interactions with predators.

Williams (2000a) reports an exception to the general pattern of burning in the spring or fall, when fire intensity would be reduced. In northern California and in the Willamette Valley of Oregon, Kalapuya people burned the grasslands in the summer, when fire might be expected to be more intense and potentially destructive. This unusual midsummer burn created a second flush of growth in the fall when the rains returned, a dual cropping system that maintained local herbivore populations. However, the intensity of the summer burns was quite low because of their high frequency, which reduced fuel accumulation. Appropriate season of burn was thus understood in interaction with fire frequency.

Frequency. Most wildfires are started by lightning strikes; however, scholars of aboriginal fire agree that anthropogenic fire far exceeded the frequency of natural lightning strikes. "Lightning in fire-adapted ecosystems does not usually cause fires. Lightning tends to strike … high rocky points, individual trees, or other places where no ignition occurs. Most snag fires are soon extinguished by the rain that usually accompanies lightning" (Williams 2000b). Indigenous people enhanced fire frequency not only with more ignitions but in creating fuel piles so that areas would burn that ordinarily might not carry a fire. Several studies of fire return intervals (Barrett 1980; Blackburn and Anderson 1993; Brown 2000; Williams 2000b) indicate that fire scars are much more abundant in areas of Indian habitation than in comparable regions not managed by indigenous people.

Ironically, trying to control nature through fire suppression has led to greater unpredictability.

The frequency of fire application generally was based on the management goal. Land was burned annually if the intent was to increase game by providing new grass forage. Berry patches were maintained by burning on a cycle of three to five years, depending on the ecology of the target species. A 10- to 12-year fire interval was typically observed around beaver ponds to maximize regeneration of aspen and willows to feed beaver (Lewis 1982; Williams 2000a). The result of altered fire frequency was to create a mosaic of successional patches, varying in species composition and age structure, which ensured a diversity of plant foods, medicines, game, and materials for the subsistence of the people.

Extent. Aboriginal burning also differs from wildfire in its extent. Most burns were of a modest scale, designed to maintain small successional patches. Large-scale burns could be viewed as maladaptive, disrupting the diverse mosaic, disrupting ecotones, and decreasing productivity and stability of the food supply (Lewis 1993). Extent of fires was controlled by careful timing, increased fire frequency and reduced fuel load, and the use of natural fire breaks. The mosaic of patches differing in successional age and flammability would itself limit the extent of fires.

Without doubt, fire control was not uniformly effective, just as we experience today, and some fires escaped, with unintended consequences. One notable exception to the general pattern of small-scale burning is the huge conflagrations traditionally set by peoples of the northern Great Plains. Prairie fires would extend for miles and were used to influence the distribution of buffalo. This large scale of burning reflects the very different ways of Plains peoples, whose food security arose not from a mosaic of diverse patches in a local area, but from maximizing productivity of a single species, the buffalo. A broad range of effects is seen, depending on the resource needs of the people and the flammability of their landscape.

Site. Indian fires also differ from lightning-ignited wildfires in the sites at which they occur. For example, riparian areas that might not burn without assistance were regularly ignited to improve waterfowl habitat and encourage growth of basketry materials and certain medicines. Locations of fires might reflect annual migrations along the elevational gradient, which enabled people to take advantage of seasonally available foods. By understanding differential burning conditions, Indians were able to restrict fires to certain areas, matching the fire regime to the ecological conditions and life history of the target species and thus enhancing productivity.

Application to Current Goals

Aboriginal use of fire to create and maintain a landscape mosaic is an ancient practice that can be a key to meeting contemporary land-use goals. Fire was used as a pragmatic tool to meet the goals of indigenous practitioners, to increase the yield and diversity of subsistence foods. These practical goals were also coupled to a spiritual responsibility to carefully use fire to multiply life. The "natural" fire regime was manipulated to produce a richly diverse mosaic of vegetation types differing in successional age and species composition.

The intent of contemporary forest management is no longer to support the subsistence economy of human beings but to enhance ecosystem health, productivity, and biodiversity. It is in this capacity that indigenous knowledge of fire is an invaluable resource for forest managers. The same indigenous strategy that was used to increase biodiversity and productivity for subsistence can also be used to enhance and maintain biodiversity for goals of ecosystem health.

For example, indigenous Kalapuya people of Oregon's Willamette Valley routinely burned savannas and meadows to increase the yield of food plants such as camas and tarweed (Williams 2000b). Other postfire species increased as well, among them the Kincaids Lupine, a legume that is vital to the life cycle of the Fenders blue butterfly (Schulz and Crone 1998). At least 24 species of butterflies once inhabited these meadows; since cessation of indigenous burning, seven have become extinct and six, including the Fenders blue, are listed as endangered species (Schulz and Crone 1998). Restoration of the indigenous fire regime and the mosaic it created can have significant impacts on biodiversity.

Restoration of indigenous-style burning is not a panacea for problems of fuel accumulation and structural changes that have accompanied a century of fire suppression, but it should be part of the strategy for restoration of forest health. Pyne (1995) states that

> to restore natural conditions without the Indians and the things they did, including burning, is to construct an artificial landscape that is historically and ecologically incomplete. The reason for reinstating fire is not to try and restore pre-Columbian vistas, but because we cannot sustain the landscape we value without it.

The suppression of traditional caregiving practices has contributed to the current state of forest health; resumption of human responsibility for fire can be part of the solution. Indigenous practice and philosophy offer us an alternative view of the "natural" fire regime, in which humans regain their role as "keepers of the fire" and the symbiotic relationship between humans, forests, and fire is reestablished for mutual benefit.

Literature Cited

ABRAMS, M. 1986. Historical development of gallery forests in northeast Kansas. *Vegetatio* 65:29–37.

———. 1992. Fire and the development of oak forests. *BioScience* 42:346–53.

ANDERSON, M.K. 1997. From tillage to table: The indigenous cultivation of geophytes for food in California. *Journal of Ethnobiology* 17:149–69.

ARNO, S.F. 1985. Ecological effects and management implications of Indian fires. In *Proceedings: Symposium and workshop on wilderness fire;* tech. coords. J.E. Lotan et al., 81–86. General Technical Report INT-182. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station.

AXELROD, D.I. 1985. Rise of the grassland biome, central North America. *Botanical Review* 51:163–201.

BABBITT, B. 1997. A coordinated campaign: Fight fire with fire by treating fuel, through thinning and prescribed burns, we can restore our wildlands to their former health and character. Remarks of US Secretary of the Interior Bruce Babbit at Boise State University, February 11.

BARRETT, S.W. 1980. Indians and fire. *Western Wildlands* 6:17–21.

———. 2000. Fire history along the ancient Lolo Trail. *Fire Management Today* 60:21–28.

BARRETT, S.W., and S.F. ARNO. 1982. Indian fires as an ecological influence in the northern Rockies. *Journal of Forestry* 80:647–50.

BISWELL, H. 1989. *Prescribed burning in California wildlands vegetation management.* Berkeley: University of California Press.

BLACKBURN T.C., and M.K. ANDERSON. 1993. Introduction. In *Before the wilderness: Native Californians as environmental managers,* eds. T.C. Blackburn and K. Anderson, 15–25. Menlo Park, CA: Ballena Press.

BOTKIN, D.B. 1990. *Discordant harmonies: A new ecology for the 21st century.* New York: Oxford University Press.

———. 1992. A natural myth. *Nature Conservancy* 42:38.

BROWN, H. 2000. Wildland burning by American Indians in Virginia. *Fire Management Today* 60:29–39.

CLARK, J.S., and P.D. ROYALL. 1996. Local and regional sediment charcoal evidence for fire regimes in presettlement north-eastern North America. *Journal of Ecology* 84:365–82.

DELCOURT, H.R., and P.A. DELCOURT. 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. *Conservation Biology* 11: 1010–14.

GRUELL, G.E. 1985. Indian fires in the Interior West: A widespread influence. In *Proceedings: Symposium and workshop on wilderness fire;* tech. coords. J.E. Lotan et al., 68–74. General Technical Report INT-182. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station.

KILGORE, B.M. 1985. What is "natural" in wilderness fire management? In *Proceedings: Symposium and workshop on wilderness fire;* tech. coords. J.E. Lotan et al., 57–67. General Technical Report INT-182. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station.

KIMMERER, R.W. 2000. Native knowledge for native ecosystems. *Journal of Forestry* 98(8):4–9.

KROBER, A., and GIFFORD, E. 1949. World renewal: A cult system of native Northwest California. *University of California Anthropological Records* 13:1–155.

LEWIS, H.T. 1982. Fire technology and resource management in aboriginal North America and Australia. Chapter 2 in *AAAS #67: Resource managers: North American and Australian hunter and gatherers,* eds. N.M. Williams and E.S. Hunn. Washington, DC:

American Association for the Advancement of Science.
LEWIS, H.T. 1985. Why Indians burned: Specific versus general reasons. In *Proceedings: Symposium and workshop on wilderness fire;* tech. coords. J.E. Lotan et al., 75–80. General Technical Report INT-182. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station.
———. 1993. Patterns of Indian burning in California: Ecology and ethnohistory. In *Before the wilderness: Native Californians as environmental managers,* eds. T.C. Blackburn and K. Anderson, 55–116. Menlo Park, CA: Ballena Press.
MARTINEZ, D. 1998. Wilderness with or without you. *Earth First!* 18(5):1, 13.
MCCARTHY, H. 1993. Managing oaks and the acorn crop. In *Before the wilderness: Native Californians as environmental managers,* eds. T.C. Blackburn and K.Anderson, 213–28. Menlo Park, CA: Ballena Press.
ORTIZ, B. 1993. Contemporary California Indian basketweavers and the environment. In *Before the wilderness: Native Californians as environmental managers,* eds. T.C. Blackburn and K. Anderson, 196–211. Menlo Park, CA: Ballena Press.
PACKARD, S. 1993. Restoring oak ecosystems. *Restoration and Management Notes* 1:5–16.
PHILLIPS, C.B. 1985. The relevance of past Indian fires to current management programs. In *Proceedings: Symposium and workshop on wilderness fire;* tech. coords. J.E. Lotan et al., 87–92. General Technical Report INT-182. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station.
PIEROTTI, R., and D. WILDCAT. 2000. Traditional ecological knowledge: The third alternative (commentary). *Ecological Applications* 10:1333–40.
PYNE, S.J. 1982. *Fire in America: A cultural history of wildland and rural fire.* Princeton, NJ: Princeton University Press.
———. 1995. *World fire: The culture of fire on Earth.* New York: Henry Holt and Co.
RUSSELL, E.W.B. 1997. *People and the land through time: Linking ecology and history.* New Haven, CT: Yale University Press.
SCHENK, S.M., and E.W. GIFFORD. 1952. Karok ethnobotany. *Anthropological Record* 13:377–92.
SCHULZ, C.B., and E.E. CRONE. 1998. Burning prairie to restore butterfly habitat: A modeling approach to management tradeoffs for the Fender's Blue. *Restoration Ecology* 6:244–52.
WILLIAMS, G.W. 2000a. Introduction to aboriginal fire use in North America. *Fire Management Today* 60:8–11.
———. 2000b. Early fire use in Oregon. *Fire Management Today* 60:13–20.
WILSON, S.M. 1992. "That unmanned wild countrey": Native Americans both conserved and transformed New World environments. *Natural History* 110:16–17.

Robin Wall Kimmerer (Potawatomi) (rwkimmer@syr.edu) is associate professor, SUNY College of Environmental Science and Forestry, One Forestry Drive, Syracuse, NY 13210-2778; Frank Kanawha Lake is graduate research assistant, Pacific Traditional Ecological Knowledge Program, Intertribal Programs Office, College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis.

View publication stats

CSIRO PUBLISHING

www.publish.csiro.au/journals/ijwf *International Journal of Wildland Fire*, 2006, **15**, 37–45

Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest*

Eric E. Knapp[A,C] *and Jon E. Keeley*[B]

[A]US Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA.
[B]US Geological Survey, Western Ecological Research Center, Sequoia and Kings Canyon Field Station, HCR 89 Box 4, Three Rivers, CA 93271, USA.
[C]Corresponding author. Email: eknapp@fs.fed.us

Abstract. Structural heterogeneity in forests of the Sierra Nevada was historically produced through variation in fire regimes and local environmental factors. The amount of heterogeneity that prescription burning can achieve might now be more limited owing to high fuel loads and increased fuel continuity. Topography, woody fuel loading, and vegetative composition were quantified in plots within replicated early and late season burn units. Two indices of fire severity were evaluated in the same plots after the burns. Scorch height ranged from 2.8 to 25.4 m in early season plots and 3.1 to 38.5 m in late season plots, whereas percentage of ground surface burned ranged from 24 to 96% in early season plots and from 47 to 100% in late season plots. Scorch height was greatest in areas with steeper slopes, higher basal area of live trees, high percentage of basal area composed of pine, and more small woody fuel. Percentage of area burned was greatest in areas with less bare ground and rock cover (more fuel continuity), steeper slopes, and units burned in the fall (lower fuel moisture). Thus topographic and biotic factors still contribute to the abundant heterogeneity in fire severity with prescribed burning, even under the current high fuel loading conditions. Burning areas with high fuel loads in early season when fuels are moister may lead to patterns of heterogeneity in fire effects that more closely approximate the expected patchiness of historical fires.

Additional keywords: fire ecology; landscape heterogeneity; prescribed fire; season of burning.

Introduction

Prior to European settlement and modern-day fire exclusion, vegetation in the mixed-conifer zone of the Sierra Nevada was likely a complex mosaic of early and late successional stages, ranging from montane chaparral to old-growth forest (Bonnicksen and Stone 1982; Chang 1996; Russell *et al*. 1998; Nagle and Taylor 2005). Patch size was typically very small, ranging from a fraction of a hectare to several hectares (Franklin and Fites-Kaufmann 1996). This within-stand heterogeneity is believed to have been produced by and maintained through spatial and temporal variation in fire regime (including severity, frequency, and size), as well as local environmental and topographic variability (Kilgore 1973; Agee 1993; Chang 1996; Skinner and Chang 1996; Taylor and Skinner 1998; Beaty and Taylor 2001).

Spatial heterogeneity is a vital component of forests, promoting a greater diversity of flora (Martin and Sapsis 1992; Halpern and Spies 1995) and fauna (Chang 1996). Gaps within the forest canopy allow shade-intolerant species such as ponderosa pine (*Pinus ponderosa* Laws.) and giant sequoia (*Sequoiadendron giganteum* [Lindley] Bucholtz) to become established (Harvey *et al*. 1980). Survival and rate of growth of newly germinating tree seedlings is often especially pronounced in areas that burn with the greatest intensity (Harvey and Shellhammer 1991; Stephenson *et al*. 1991; Stephenson 1994). However, fires cannot be uniformly intense over large spatial scales, or the ability of the forest to regenerate would be reduced. The matrix of mature forest surrounding gaps is vital for recruitment, because the majority of seeds are typically dispersed in relatively close proximity to the parent trees (Nathan *et al*. 2000). Once seedlings become established, growing in gaps may allow these young trees to escape mortality from subsequent fires. Deposition of litter and woody surface fuels is reduced in gaps due to lack of an overstory fuel source. By the time trees are large enough to produce enough ground fuel to carry fire, they are also more likely to be large enough to survive fire (Cooper 1960, 1961; Kilgore 1973; Keeley and Stephenson 2000).

* This article was written and prepared by US Government employees on official time and is therefore in the public domain and not subject to copyright.

10.1071/WF04068 1049-8001/06/010037

Dramatic changes to forest structure and pattern have occurred in the Sierra Nevada mixed-conifer forest as a result of reduced fire frequency. In areas without a history of logging, the amount of forested area occupied by younger, early successional patches has declined and the amount of forested area occupied by dense intermediate-aged patches has increased (Bonnicksen and Stone 1982). Shade-tolerant tree species such as firs (*Abies* sp.) and incense cedar (*Calocedrus decurrens* [Torrey] Florin) have become more abundant at the expense of shade-intolerant species such as ponderosa pine and black oak (*Quercus kelloggii* Newb.), and the overall tree density is higher (Kilgore 1973; Vankat and Major 1978; Parsons and DeBenedetti 1979; Ansley and Battles 1998). In the absence of fire, forests may have become more structurally homogeneous (Bonnicksen and Stone 1980; Skinner 1995; Chappell and Agee 1996; Taylor 2000).

Another impact of the reduction in fire frequency in the mixed-conifer zone of the Sierra Nevada has been a substantial accumulation of surface fuels (Biswell *et al*. 1968; van Wagtendonk 1985) and greater fuel continuity (Miller and Urban 2000), both of which can increase the probability of large, high-intensity wildfires (van Wagtendonk 1985; Stephens 1998). Historically, frequent fires are believed to have resulted in low fuel loads and a patchy pattern of fire spread (Swetnam 1993). These fires burned predominantly at low-to-moderate intensity with patchy high intensity (Kilgore 1973; Stephenson *et al*. 1991; Stephenson 1999). Most overstory canopy trees survived in areas with lower-intensity fire, but groups of canopy trees were killed locally within a matrix of surviving trees in the higher-intensity areas (Stephenson 1999). This variability in fire behavior helped to maintain a patchy mosaic of vegetation and fuels. The size of high-severity patches produced when fire is reintroduced to the landscape may now be greater than it was historically (Keeley and Stephenson 2000).

The best means of reducing fuels and restoring a forest structure similar to the historical conditions is a source of debate (Bonnicksen and Stone 1985; Parsons *et al*. 1986; Stephenson 1999; Weatherspoon 2000). Bonnicksen and Stone (1985) have argued that prescription burning under the current fuel conditions could result in a more uniformly intense fire that is less likely to restore the desired landscape mosaic. This argument assumes that fuel loading and fuel continuity are the primary drivers of variability in fire severity in these forests and that both have become more homogeneous with fire exclusion. If other factors such as vegetation pattern, weather, topography, and ignition pattern also play an important role in generating variability in fire effects, prescribed fire alone may produce considerable forest heterogeneity, even under the current fuel conditions. Our understanding of patterns of landscape heterogeneity produced by prescribed fire and how this heterogeneity is affected by season of burning remains incomplete.

In the pre-Euro American Sierra Nevada, much of the area that burned did so during the dry late summer to early fall period (Caprio and Swetnam 1995). Most prescribed burning in Sequoia and Kings Canyon National Parks has, up to now, been done during the latter part of this same time period. However, because of poor air quality in the adjacent Central Valley, burning opportunities at this time of year are increasingly limited. As a result, only a fraction of the area necessary to maintain historical fire return intervals typically gets burned. Atmospheric conditions conducive to smoke dispersal are often more common during the spring to early summer period and expanding the burn window to include prescribed fire at this time of year allows more of the landscape to be treated.

Fuel moisture levels are typically higher in the spring and early summer than later in the season, which can strongly influence fire behavior and effects. Both the amount of heat generated and spread of fires is reduced at higher fuel moisture levels, owing to the energy required to vaporize water (DeBano *et al*. 1998; Nelson 2001). Computer models have shown fuel connectivity to be less at high fuel moisture levels (Miller and Urban 2000), and the depth of the forest floor fuel layer must be greater in order for combustion to propagate in moist duff (Miyanishi and Johnson 2002). Thus, early season burns in these mixed-conifer forests often consume less of the available fuel (Kauffman and Martin 1989; Knapp *et al*. 2005) and produce a patchier and less complete burn pattern (Knapp *et al*. 2005).

The purpose of the present study was to describe within-stand heterogeneity in fire severity resulting from early season and late season prescribed fire treatments, and to identify the relative importance of different topographic and biotic variables associated with this heterogeneity. Two components of fire severity were investigated: (1) scorch height; and (2) the percentage of the burnable ground surface that did burn.

Materials and methods

Study site description

Three early and three late season prescribed burn units were established, along with three control units, in an old-growth mixed-conifer forest within the watershed of the Marble Fork of the Kaweah River in Sequoia National Park. Each unit was 15–20 ha in size with irregular boundaries established along topographic features in accordance with National Park Service fire management concerns. The three control units were installed as part of another study and only the six burn units were used for the research reported in this paper. A map of the burn and control units is shown in Knapp *et al*. (2005).

Elevation in the study area ranged from 1900 to 2150 m above sea level and aspect was generally NW, although there was substantial micro-topographic variation. Tree species, in order of abundance, were white fir (*Abies concolor* [Gordon & Glend.] Lindley), sugar pine (*Pinus lambertiana*

Douglas), incense cedar, Shasta red fir (*A. magnifica* var. *shastensis* Lemmon), Jeffrey pine (*P. jeffreyi* Grev. & Balf.), ponderosa pine, mountain dogwood (*Cornus nuttallii* Audubon), and California black oak. The historical fire return interval in the study area was 27.4 years, but much of the study area had not burned since 1879 (A. C. Caprio and E. E. Knapp, unpublished data).

Pretreatment data collection

Ten 50 × 20 m (0.1 ha) plots were established within each of the six burn units (two treatments [early and late season burns] × three replicates [units] × 10 plots/unit = 60 plots total), in reference to a system of 36 permanent points on a 50-m grid. Plots were assigned randomly to 10 grid points and the direction of the plot was also random (one of four cardinal directions [0°, 90°, 180°, 270°]). Within each plot, diameter at breast height (dbh) was measured for all trees (dbh > 10 cm), and species and status (alive or dead) noted. Cover of herbaceous species, bare ground, and rock within the 0.1-ha plots was estimated by averaging the visual scores for twenty 1 × 1 m subplots systematically located within each plot. Cover was scored on the following scale: 1 = 0–1%; 2 = 2–10%; 3 = 11–25%; 4 = 26–50%; 5 = 51–75%; 6 = 76–100%. Cover scores were later converted back to a percentage, using the mean of each cover class range. Total herbaceous species cover was the sum of the cover of individual species.

Loading of woody fuels was estimated retrospectively using digital photographs taken of each plot from the midpoint of each 20-m side prior to the prescribed burns. Both small woody fuels (roughly including 1 h [<0.6 cm diameter], 10 h [0.6–2.54 cm diameter], and 100 h fuels [2.54–7.6 cm diameter]) and large woody fuels (1000 h [>7.6 cm diameter]) were visually scored (scale = 1–5, with 5 being the greatest amount of fuel) in all plots by seven different observers, and scores averaged. For an approximation of the actual fuel mass, the lowest small woody fuel score was similar to photo 1-PP-4 in a photo series depicting fuel loadings with different tree composition and size classes in the northern Sierra Nevada and southern Cascades (Blonski and Schramel 1981), whereas the highest small woody fuel score was similar to photo 2-MF-4. The large woody fuel scores approximated fuel mass values associated with photos 1-MF-4 to 5-MF-4 in the same photo series. Loading of litter and duff fuels could not be estimated from photographs, but both should be highly correlated with the basal area of trees within the plot.

Slope and aspect of each plot were calculated by overlaying the spatial coordinates of the nearest gridpoints with a 10-m-resolution digital elevation model in a geographic information system (GIS). Slope and aspect enabled an index of the potential total yearly heat load for each plot to be estimated, using equation 3 of McCune and Keon (2002). Potential total yearly heat load is proportional to the amount of direct incident solar radiation intercepted by a given aspect and slope, corrected for the fact that aspects with afternoon sun will have higher maximum temperatures than aspects with morning sun. Heating as a result of solar radiation will influence the amount of moisture contained within fuels (Byram and Jemison 1943), and variability in the potential heat load within the burn units may therefore be predictive of variability in fuel moisture at the same scale.

Prescribed burns

Early season burns were conducted on 20 and 27 June 2002, and late season burns were conducted on 28 September, 17 October, and 28 October 2001. Whereas the early season burns occurred approximately 6 weeks following the end of snow melt, the late season burns were preceded by over 4 months of mainly dry summer and early fall weather. Weather conditions and fuel moisture levels were very similar for burns within the same burning season treatment. One estimate of fuel moisture was made per unit immediately prior to ignition. Fuels were sampled widely outside of the plots in order to limit influence on fire behavior and effects resulting from disturbance of the fuel bed within the plots. Fuel moisture was significantly higher for the early season than the late season burns (Knapp *et al*. 2005). Average temperature, relative humidity, and maximum wind speed during the ignition period were 20°C, 52%, and 3 km h^{-1}, respectively, for the early season burns, and 15°C, 44%, and 3 km h^{-1}, respectively, for the late season burns. Using drip torches, strip head fires spaced ~10–15 m apart were ignited progressively from higher to lower elevations. With the exception of occasional single small trees that torched, fire was predominantly on the surface. Flame lengths were generally less than 1 m, except in areas with an abundance of large downed logs.

Post-treatment data collection

Scorch height, defined as the maximum height of complete needle kill, was measured on all trees within plots 2–9 months post burn, using a laser rangefinder. Scorch height often varied on different sides of a tree and was therefore measured at both the point of maximum height above ground and on the side of the tree opposite of where the maximum scorch height occurred. The two values were then averaged. Scorch height was not determined for trees that were completely scorched or trees with a base of live crown located above the scorching level. Percentage of the ground surface containing fuel that burned (hereafter referred to as 'percentage of area burned' for ease of explanation) was quantified for each plot as the average of visual scores within twenty 1 × 1 m subplots systematically located in each plot, to the nearest 10%. We felt that this was more accurate than making one visual estimate of percentage of area burned for the entire plot, because whether or not an area burned could often be determined only by close observation. Rocks were not considered in the visual estimates and the percentage of bare ground prior to the burns was subtracted from the field values; the percentage

of area burned variable was therefore the percentage of the area burned that contained fuel and potentially could have burned.

Percentage of area burned was evaluated during the first full growing season following completion of the prescribed burn in that unit. This was the earliest time at which the late season units could be entered owing to snow cover (snow began falling within days after completion of the burns). The early season burn units were evaluated the same way for consistency. More measurement error is likely associated with the early season than the late season percentage area burned estimates, owing to a heavy rainstorm in November 2002, which caused some soil erosion and made the boundaries between burned and unburned patches more difficult to distinguish.

Data analysis

Frequency histograms for scorch height and percentage of area burned were constructed to demonstrate the variation among plots in these two variables. Significance of differences between treatments was determined with one-way analyses of variance. Levene's test was performed on the residuals to determine if differences in the amount of among-plot variability existed. The Kolmogorov–Smirnoff goodness-of-fit test was used to evaluate the significance of differences in frequency histograms between treatments.

Mixed model analyses of variance (PROC MIXED; SAS Institute, Cary, NC, USA) were used to investigate factors most closely associated with scorch height and percentage of area burned. Slope, potential annual heat load, small woody fuel score, large woody fuel score, tree basal area, percentage of tree basal area composed of pine, herbaceous species cover, and bare ground or rock cover were fixed effects, whereas burn unit was random.

Slope affects flame length and rate of spread. Other variables that influence fire behavior directly, such as fuel moisture, fuel loading, and fuel bulk density, are more difficult to obtain accurate estimates of at the plot scale, but differences in these variables may have been captured by variables that were easier to measure. For example, potential heat load may be predictive of fuel moisture, because fuel moisture is expected to be lowest on SW-facing aspects and slopes perpendicular to the sun angle, where heat load is the greatest. Basal area of trees does not influence fire behavior directly because live trees in this system typically do not act as fuel, but basal area may be correlated with among-plot differences in fuel moisture, owing to the influence of shading by the canopy. Basal area also indirectly influences how much litter, duff, and small woody fuel is potentially deposited on the forest floor – the greater the tree volume, the more litter, duff, and small woody fuel production is expected. The percentage of basal area composed of pine may be an indicator of litter flammability because the lower bulk density of pine litter causes it to burn more readily than fir and other short-needled litter (Agee *et al*. 1978; van Wagtendonk *et al*. 1998). In addition, lower bulk density litter dries faster to the point where combustion is possible (Stephens 2001). The herbaceous species cover variable was possibly a predictor of fine-scale soil and fuel moisture differences because the presence of understory vegetation was generally highest in moister microsites. Most abundant herb species included bracken fern (*Pteridium aquilinum* [L.] Kuhn var. *pubescens* L. Underw.), hawkweed *Hieracium albiflorum* Hook., and violet draperia (*Draperia systyla* [A. Gray] Torrey), which in total comprised 56% of the herbaceous cover (E. E. Knapp, D. W. Schwilk, J. M. Kane and J. E. Keeley, unpublished data). The amount of bare ground and rock was a predictor of how much area lacked fuel and potentially provided quantification of the degree of fuel continuity.

The scorch height variable approximated a normal distribution and did not require transformation. The percentage of area burned variable was arcsine square root transformed prior to analysis to improve normality.

Results

Scorch height

Scorch height did not differ between burn season treatments (early = 11.1 m; late = 13.5 m; $F = 1.41$, $P = 0.240$), but was highly variable among plots, ranging from 2.8 to 25.4 m in the early season burns, and from 3.1 to 38.5 m in the late season burns (Table 1, Fig. 1). Analysis of variance conducted on the absolute value of the residuals (Levene's test) indicated that the amount of variability in scorch height generated by the burns also did not differ between the burn season treatments ($P = 0.181$). In addition, the scorch height frequency distributions for the two seasons (Fig. 1) were very similar (Kolmogorov–Smirnov test, $P = 0.995$).

Factors associated with variation in scorch height

When analyzed together in a mixed-model ANOVA, the variables most strongly associated with scorch height were slope, tree basal area, percentage of basal area composed of pine, and small woody fuel score, in order of significance (Table 2). Scorch height was greatest in plots on steeper slopes, plots containing more tree basal area, plots with a higher percentage of pine relative to short-needled species such as fir and incense cedar, and plots with abundant small woody fuel. The burn season variable approached significance ($P = 0.134$).

The large number of main effects made it impossible to analyze all possible two-way interactions without sacrificing most of the statistical power of the model. Therefore analysis of interactions was conducted in an exploratory manner, including only the two-way interactions among the four significant ($P < 0.05$) main effects in a separate mixed-model ANOVA. Of these, only slope × percentage of basal area composed of pine was significant ($P = 0.043$). When the non-significant interactions were removed, and the model

Table 1. Means and ranges for independent and dependent variables measured within early season and late season burn treatment units

Variable	Early season burn		Late season burn	
	Average	Range	Average	Range
Slope (degrees)	16.5	9.0–29.5	18.7	10.6–31.8
Heat load index[A]	0.99	0.84–1.07	0.93	0.71–1.07
Small woody fuel score (scale = 1 to 5)	3.09	1.79–4.38	2.75	1.31–4.19
Large woody fuel score (scale = 1 to 5)	2.24	1.10–3.79	2.14	1.24–4.57
Basal area (m^2/ha)	69.5	25.6–117.9	67.8	31.3–115.2
Pine basal area (%)	26.0	0–73.1	25.7	0–80.2
Herbaceous cover (%)	7.7	0–24.4	17.4	1.6–51.8
Bare ground/rock cover (%)	6.7	0–43.9	5.1	0–21.9
Scorch height (m)	11.1	2.8–25.4	13.5	3.1–38.5
Plot area burned (%)	70	15–96	88	48–100

[A]Calculated using formula #3 of McCune and Keon (2002).

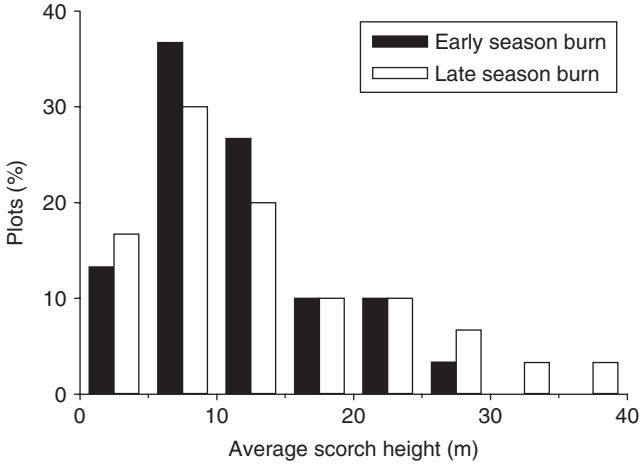


Fig. 1. Percentage of plots within different average scorch height (m) categories in both early season ($n = 30$) and late season ($n = 30$) prescribed burning treatments.

Table 2. Significance of fixed effects in a mixed-model analysis of variance of average scorch height for prescribed burns conducted in early and late season

The random effect (unit) was not significant ($P = 0.351$). Denominator degrees of freedom (d.d.f.) are based on Satterthwaite's approximation. n.d.f., numerator degrees of freedom

Fixed effect	n.d.f.	d.d.f.	*F*	*P*
Burn season	1	3.23	3.96	0.134
Slope	1	22	10.79	0.003
Head load	1	16.2	1.21	0.287
Small woody fuel score	1	48.5	4.82	0.033
Large woody fuel score	1	49	0.55	0.460
Basal area	1	46.8	7.82	0.008
Pine basal area (% of total)	1	47.8	7.16	0.010
Canopy closure	1	48.1	0.50	0.484
Herbaceous cover	1	20.4	0.28	0.606
Bare ground and rock cover	1	45.6	1.37	0.248

containing all main effects and the one significant interaction was run again, explanatory power, as expressed by Aikake's Information Criterion (AIC), was reduced relative to the model containing only the main effects. The mixed-model ANOVA including the slope × percentage of basal area composed of pine interaction is therefore not shown.

Percentage of area burned

The percentage of area burned varied substantially among plots, ranging from 15 to 96% in the early season burn units and from 47 to 100% in the late season burn units (Table 1, Fig. 2). Overall, significantly less area burned in the early season than in the late season (early season mean = 70%; late season mean = 88%; $F = 24.66$, $P < 0.001$). (The actual total plot area that burned was somewhat less because an average of 6% of the study area contained bare ground and rock prior to the burns, and this was factored out of the percentage of area burned estimates.) Variance in the percentage of area burned tended to be greater in the early season than the late season (Levine's test, $P = 0.080$). The difference in frequency distribution of percentage of area burned between seasons was strongly significant (Kolmogorov–Smirnov test, $P < 0.001$) (Fig. 2).

Factors associated with variation in percentage of area burned

When analyzed together in a mixed-model ANOVA, the variables most strongly associated with percentage of area burned were cover of bare ground and rock, burn season, and slope, in order of significance (Table 3). Percentage of area burned was greatest in plots containing less bare ground and rock, in plots burned in the fall, and in plots on steeper slopes. Percentage of basal area composed of pine and small woody fuel score approached significance ($P = 0.118$, $P = 0.097$, respectively), with a tendency for greater percentage of area burning in plots with a higher percentage of pine and in plots where loading of small woody fuels was high.

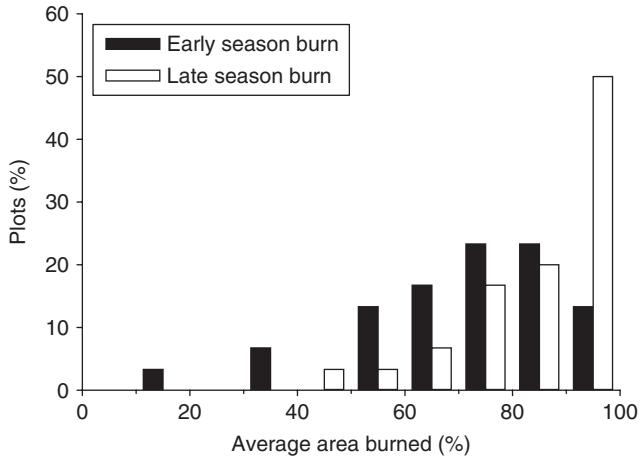


Fig. 2. Percentage of plots within different average percentage of area burned categories in both early season ($n = 30$) and late season ($n = 30$) prescribed burning treatments.

Table 3. Significance of fixed effects in a mixed-model analysis of variance of percentage of area burned for prescribed burns conducted in early and late season

The random effect (unit) was not significant ($P = 0.496$). Percentage of ground surface area burned was arcsine square root transformed prior to analysis. Denominator degrees of freedom are based on Satterthwaite's approximation

Fixed effect	n.d.f.	d.d.f.	*F*	*P*
Burn season	1	3.57	18.97	0.016
Slope	1	13.4	5.50	0.035
Head load	1	11.3	0.88	0.368
Small woody fuel score	1	49	2.66	0.110
Large woody fuel score	1	48.6	0.35	0.554
Basal area	1	47.6	0.12	0.735
Pine basal area (% of total)	1	48.6	2.38	0.129
Canopy closure	1	45.9	0.00	0.945
Herbaceous cover	1	17.3	0.01	0.924
Bare ground and rock cover	1	39.6	8.54	0.006

A separate exploratory mixed-model ANOVA was run to investigate possible two-way interactions among the three significant ($P < 0.05$) main effects. None of these interactions were found to be significant or add to the explanatory power of the model as expressed by AIC. The final model presented in Table 3 therefore includes only the main effects.

Discussion

The abundance of fuels that have accumulated in many forested areas has led to a concern that fire effects generated by prescription burning might now overwhelm mechanisms that historically generated heterogeneity in fire severity, leading to greater than desired landscape uniformity. Our results illustrate that substantial variation in two measures of fire severity – scorch height and percentage of area burned – can be produced by both early season and late season prescribed burns, even after over a century of fire suppression. Whereas several of the independent variables significant in the ANOVAs of scorch height were direct or indirect measures of fuel loading (small woody fuel score, tree basal area), other topographic and biotic factors also likely contributed to this heterogeneity. The importance of slope, the independent variable with the strongest significance, was expected because rate of fire spread increases with slope steepness (Agee 1993), and fireline intensity is higher when more fuel is consumed per unit time. In addition, hot air is more readily convectively lifted into tree crowns on slopes, contributing to greater scorching. Percentage basal area composed of pine was also important in explaining variation in scorch height, likely because fire in pine litter produces greater flame lengths than fire in the more compact litter of shorter-needled conifer species (Fonda *et al*. 1998). This relationship between proportional abundance of pines and height of crown scorching has been noted with wildfire as well (Weatherspoon and Skinner 1995).

Most of the independent variables significant in the ANOVA of percentage of area burned were more strongly related, either directly or indirectly, to fuel continuity rather than fuel loading. Less of the burnable area was burned in plots containing more bare ground and rock, presumably because these barriers can limit fire spread. Significance of burn season was likely largely the result of greater fuel moisture in the early season. Effective fuel continuity is less at higher fuel moisture levels (Miller and Urban 2000) because the likelihood that adjacent fuel particles will become heated to the point of combustion is reduced (Nelson 2001), limiting fire spread. Our finding of greater burn patchiness with prescribed fires conducted under higher fuel moisture conditions is consistent with other studies (e.g. Slocum *et al*. 2003).

The third significant independent variable, slope, was positively associated with the amount of area burned, presumably because fuels are exposed to greater convective and radiant heat on slopes, making preheating more effective (Rothermel 1972). The variables 'amount of small woody fuel' and 'percentage basal area composed of pine' both approached statistical significance and may have also influenced the percentage of area burned. Fuel continuity was expected to be greater in areas with more fine fuels and a higher proportion of long-needled conifers such as pine. Fire carries more readily in pine litter than in the litter of shorter-needled species, owing to lower bulk density of the pine litter (Agee *et al*. 1978; van Wagtendonk *et al*. 1998; Stephens *et al*. 2004). Miller and Urban (2000) reported that bulk density, in addition to fuel moisture, played a role in controlling area burned in fire spread models. High bulk density litter of short-needled conifer species dries more slowly to the point where combustion is possible after snows melt, potentially resulting in a shorter burning season (Stephens 2001). Agee *et al*. (1978) noted that pine fuels could be effectively reduced by burning

in the spring, summer, or fall, but white fir and other short-needled fuels required drier conditions in the summer and fall.

Other factors besides those included in the ANOVA models, such as weather and how fire was applied during the prescription burn, also likely contributed to the observed heterogeneity in fire severity. The number of igniters applying fire at one time, the horizontal distance between igniters, and the time between passes were variable and all can strongly influence fire severity. In addition, some breaks in ignition occurred when fire crews were preoccupied with burning snags or spot fires. Plots that burned during these times may have experienced reduced fire intensity (more backing fire, less heading fire). It was not possible to quantify these ignition factors at the plot scale, owing to operational constraints. Because weather conditions were mild and relatively consistent during all of the burns, variation in fire severity was probably less strongly influenced by weather than by ignition patterns. Still, variability in relative humidity and wind speed were likely sufficient to exert some influence on fire behavior. Although weather variables were recorded hourly during the burns, they were not included in the ANOVA models because it was difficult to determine exactly when each plot burned and to match weather conditions at that time. Another factor we did not quantify – proximity to water courses – has been shown to exert a strong influence on fire effects, presumably because of species composition and fuel moisture differences (Russell and McBride 2001; Skinner 2003). However, most water courses within the units in the present study were ephemeral and did not contain water at the time of the burns.

It is not known how the relative contribution of fuel loading-related and non-fuel loading-related factors for generating variation in fire severity compared to historical fires, but the role of non-fuel loading variables in generating heterogeneity under current conditions is perhaps under appreciated. The strong positive association between percentage of basal area composed of pine and scorch height (and to a lesser extent, percentage of area burned) suggests that some of the capacity of prescribed fires to generate a heterogeneous post-burn landscape might be jeopardized in the future by shifts in species composition away from pine. Whereas shade-tolerant species with less flammable and more compact litter have always been part of the mixed-conifer forest, they have become more abundant as a result of fire suppression and shade-intolerant species with more flammable litter, such as ponderosa pine and Jeffrey pine, have become less abundant. In addition, sugar pine is in decline, due in part to white pine blister rust, and may play a lesser role in forests of the future (van Mantgem *et al*. 2004). Loss of pines may be reducing the extent of the historical mosaic of long-needled and short-needled species.

Forest gap models parameterized with data from the Sierra Nevada predict that surface fire regimes should increase the fine-scale spatial heterogeneity in some components of forest structure, over that found in the absence of fire (Miller and Urban 1999). Of interest to resource managers is whether the heterogeneity produced by prescribed burns is comparable to the heterogeneity that was produced historically by natural fires. To modulate fire behavior and aid in control, prescribed fires are often ignited in strips and also conducted within a relatively narrow range of weather and fuel moisture conditions compared with historical fires. All potentially reduce heterogeneity in the burning pattern. However, the weather and fuel conditions under which prescribed fires are conducted may also be what maximize heterogeneity in burn patterns produced by other mechanisms. Model outputs of Miller and Urban (2000) indicate that connectivity of fuels influences fire spread under moderate weather conditions, but that this relationship diminishes under dry and windy conditions. Dry, windy conditions can lead to intense fire and uniform fire coverage over large areas, despite heterogeneity in the arrangement of fuels. In addition, fuel connectivity is a function of fuel moisture mainly at intermediate fuel moisture levels (Miller and Urban 2000). Model outputs of Miller and Urban (2000) predict that at low fuel moisture levels, much of the area will burn regardless of patterns of fuel connectivity. At high fuel moisture levels, little of the area burns. Both of the latter situations limit the amount of heterogeneity potentially produced by fire. Thus the heterogeneity in fire severity that results from conducting prescribed burns within a relatively narrow window of weather and fuel moisture conditions may to some extent compensate for the heterogeneity historically generated by variability in weather that natural fires burned under.

Heterogeneity in fire severity may play an important ecological role. Unburned or less severely burned patches provide refugia for plant and animal species and propagules for recolonizing more severely burned areas. Such patchiness can also slow erosion and increase infiltration of run-off (Martin and Sapsis 1992). Whereas both early and late season prescribed burns in the present study produced abundant heterogeneity in fire severity, patchiness in the percentage of area burned in the early season may be more similar to the patchiness of historical fires that typically burned under lower fuel moisture conditions but when fuel loading was not as high, or fuels as continuous. Even with the abundance of fuel in many forested areas today, variability in other factors may still be sufficient for prescribed fires conducted under moderate weather and fuel moisture conditions to produce a highly heterogeneous post-burn landscape.

Acknowledgements

We wish to thank Sequoia National Park Fire Management for conducting the prescribed burns, Nathan Stephenson for intellectual insights and his early involvement with the project, Tony Caprio for fire history information, Julie Yee and Jim Baldwin for statistical advice, Kyle Merriam for

assistance with GIS analyses, and members of the field crews (Anni Ala, Clara Arndt, Liz Ballenger, Tess Brennan, Lea Condon, Todd Erdody, Eric Fabio, Eric Groth, Shauna Hee, Jeffrey Kane, Dan Lieberman, Hanna Mershman, Katie Panichelle, Dorothy Wallace-Senft, Katie Vinzant, Kelly Wengronowitz and Upekala Wijayratne) for assistance with data collection. The paper benefited from comments by Teresa Brennan, Tony Caprio, Scott Ferrenberg, Kyle Merriam, Monique Rocca, Carl Skinner, Nathan Stephenson, Steven Schwarzbach, Phil van Mantgem, and two anonymous reviewers. This is contribution number 95 of the National Fire and Fire Surrogate Project (FFS-99S1), funded by the USA Joint Fire Science Program.

References

Agee JK (1993) 'Fire Ecology of Pacific Northwest Forests.' (Island Press: Covelo, CA)

Agee JK, Wakimoto RH, Biswell HH (1978) Fire and fuel dynamics of Sierra Nevada conifers. *Forest Ecology and Management* **1**, 255–265. doi:10.1016/0378-1127(76)90030-X

Ansley JS, Battles JJ (1998) Forest composition, structure, and change in an old-growth mixed conifer forest in the northern Sierra Nevada. *The Journal of the Torrey Botanical Society* **125**, 297–308.

Beaty RM, Taylor AH (2001) Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA. *Journal of Biogeography* **28**, 955–966. doi:10.1046/J.1365-2699.2001.00591.X

Biswell HH, Gibbens RP, Buchanan H (1968) Fuel conditions and fire hazard reduction costs in giant sequoia forests. *California Agriculture* **22**, 2–4.

Blonski KS, Schramel JL (1981) 'Photo series for quantifying natural forest residues: southern Cascades and northern Sierra Nevada.' USDA Forest Service Pacific Southwest Research Station, General Technical Report PSW-56. Pacific Southwest Forest and Range Experiment Station. (Berkeley, CA)

Bonnicksen TM, Stone EC (1980) The giant sequoia–mixed conifer forest community characterized through pattern analysis as a mosaic of aggregations. *Forest Ecology and Management* **3**, 307–328. doi:10.1016/0378-1127(80)90031-6

Bonnicksen TM, Stone EC (1982) Reconstruction of a presettlement giant sequoia–mixed conifer forest community using the aggregation approach. *Ecology* **63**, 1134–1148.

Bonnicksen TM, Stone EC (1985) Restoring naturalness to National Parks. *Environmental Management* **9**, 479–486. doi:10.1007/BF01867322

Byram GM, Jemison GM (1943) Solar radiation and forest fuel moisture. *Journal of Agricultural Research* **67**, 149–176.

Caprio AC, Swetnam TW (1995) Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. In 'Proceedings, Symposium on fire in wilderness and park management'. (Tech. coords JK Brown, RW Mutch, CW Spoon, RH Wakimoto) pp. 173–179. USDA Forest Service GTR INT-320. (Missoula, MT)

Chang C (1996) Ecosystem responses to fire and variations in fire regimes. In 'Sierra Nevada Ecosystem Project, Final report to Congress, Vol. II, Assessments and scientific basis for management options'. pp. 1071–1099. (Centers for Water and Wildland Resources, University of California Davis: Davis, CA)

Chappell CB, Agee JK (1996) Fire severity and tree seedling establishment in *Abies magnifica* forests, southern Cascades, Oregon. *Ecological Applications* **6**, 628–640.

Cooper CF (1960) Changes in vegetation, structure, and growth of southwest pine forests since white settlement. *Ecological Monographs* **30**, 129–164.

Cooper CF (1961) The ecology of fire. *Scientific American* **204**, 150–160.

DeBano LF, Neary DG, Ffolliott PF (1998) 'Fire's effects on ecosystems.' (John Wiley and Sons: New York)

Fonda RW, Belanger LA, Burley LL (1998) Burning characteristics of western conifer needles. *Northwest Science* **72**, 1–9.

Franklin JF, Fites-Kaufmann J (1996) Assessment of late-successional forests of the Sierra Nevada. In 'Sierra Nevada Ecosystem Project, Final report to Congress, Vol. II, Assessments and scientific basis for management options'. pp. 627–662. (Centers for Water and Wildland Resources, University of California Davis: Davis, CA)

Halpern CB, Spies TA (1995) Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications* **5**, 913–934.

Harvey HT, Shellhammer HS (1991) Survivorship and growth of giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchh.) after fire. *Madroño* **38**, 14–20.

Harvey HT, Shellhammer HS, Stecker RE (1980) 'Giant sequoia ecology, fire and reproduction.' Science Monograph Series No. 12. (National Park Service: Washington, DC)

Kauffman JB, Martin RE (1989) Fire behavior, fuel consumption, and forest-floor changes following prescribed understory fires in Sierra Nevada mixed conifer forests. *Canadian Journal of Forest Research* **19**, 455–462.

Keeley JE, Stephenson HL (2000) Restoring fire regimes to the Sierra Nevada in an era of global climate change. In 'Proceedings of the wilderness science in a time of change conference'. (Eds DN Cole, SF McCool, WT Borrie, J McLoughlin) pp. 255–265. USDA Forest Service, Rocky Mountain Research Station, RMRS-P-15, Vol. 5. (Ogden, UT)

Kilgore BM (1973) The ecological role of fire in Sierran conifer forests: Its application to National Park management. *Quaternary Research* **3**, 496–513. doi:10.1016/0033-5894(73)90010-0

Knapp EE, Keeley JE, Ballenger EA, Brennan TJ (2005) Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fire in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* **208**, 383–397. doi:10.1016/J.FORECO.2005.01.016

Martin RE, Sapsis DB (1992) Fires as agents of biodiversity: pyrodiversity promotes biodiversity. In 'Proceedings of the symposium on biodiversity of northwestern California, 28–30 October 1991, Santa Rosa, CA'. Report No. 29. (Tech. coords RR Harris, DC Erman; Ed. HM Kerner) pp. 150–157. (University of California, Wildland Resources Center: Berkeley, CA)

McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* **13**, 603–606.

Miller C, Urban DL (1999) Interactions between forest heterogeneity and surface fire regimes in the southern Sierra Nevada. *Canadian Journal of Forest Research* **29**, 202–212. doi:10.1139/CJFR-29-2-202

Miller C, Urban DL (2000) Connectivity of forest fuels and surface fire regimes. *Landscape Ecology* **15**, 145–154. doi:10.1023/A:1008181313360

Miyanishi K, Johnson EA (2002) Process and patterns of duff consumption in the mixedwood boreal forest. *Canadian Journal of Forest Research* **32**, 1285–1295. doi:10.1139/X02-051

Nagle TA, Taylor AH (2005) Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California. *The Journal of the Torrey Botanical Society* **132**, 442–457.

Nathan R, Safriel UN, Noy-Meir I, Schiller G (2000) Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. *Ecology* **81**, 2156–2169.

Nelson RM Jr (2001) Water relations in forest fuels. In 'Forest fires: behavior and ecological effects'. (Eds EA Johnson, K Miyanishi) pp. 79–149. (Academic Press: San Diego, CA)

Parsons DJ, DeBenedetti SH (1979) Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management* **2**, 21–33. doi:10.1016/0378-1127(79)90034-3

Parsons DJ, Graber DM, Agee DK, van Wagtendonk JW (1986) Natural fire management in National Parks. *Environmental Management* **10**, 21–24. doi:10.1007/BF01866414

Rothermel RC (1972) 'A mathematical model for predicting fire spread in wildland fuels.' USDA Forest Service. Intermountain Forest and Range Experiment Station Research Paper INT-115. (Ogden, UT)

Russell WH, McBride JR (2001) The relative importance of fire and watercourse proximity in determining stand composition in mixed conifer riparian forests. *Forest Ecology and Management* **150**, 259–265. doi:10.1016/S0378-1127(00)00586-7

Russell WH, McBride J, Rowntree R (1998) Revegetation after four stand-replacing fires in the Lake Tahoe basin. *Madroño* **45**, 40–46.

Skinner CN (1995) Change in spatial characteristics of forest openings in the Klamath Mountains of northwestern California, USA. *Landscape Ecology* **10**, 219–228. doi:10.1007/BF00129256

Skinner CN (2003) A tree-ring based fire history of riparian reserves in the Klamath Mountains. In 'Californian riparian systems: processes and floodplain management, ecology, and restoration'. (Ed. PM Faber) pp. 116–119. (Riparian Habitat Joint Venture: Sacramento, CA)

Skinner CN, Chang C (1996) Fire regimes, past and present. In 'Sierra Nevada Ecosystem Project, Final report to Congress, Vol. II, Assessments and scientific basis for management options'. pp. 1041–1069. (Centers for Water and Wildland Resources, University of California Davis: Davis, CA)

Slocum MG, Platt WJ, Cooley HC (2003) Effects of differences in prescribed fire regimes on patchiness and intensity of fires in subtropical savannas of Everglades National Park, Florida. *Restoration Ecology* **11**, 91–102. doi:10.1046/J.1526-100X.2003.00115.X

Stephens SL (1998) Evaluation of the effects of silvicultural and fuels treatments on potential fire behavior in Sierra Nevada mixed conifer forests. *Forest Ecology and Management* **105**, 21–35. doi:10.1016/S0378-1127(97)00293-4

Stephens SL (2001) Fire history differences in adjacent Jeffrey pine and upper montane forests in the eastern Sierra Nevada. *International Journal of Wildland Fire* **10**, 161–167. doi:10.1071/WF01008

Stephens SL, Finney MA, Shantz H (2004) Bulk density and fuel loads of ponderosa pine and white fir forest floors: impacts of leaf morphology. *Northwest Science* **78**, 93–100.

Stephenson NL (1994) Long-term dynamics of giant sequoia populations: implications for managing a pioneer species. In 'Proceedings of the symposium on giant sequoias: Their place in the ecosystem and society'. (Tech. coord. P Aune) pp. 56–63. USDA Forest Service General Technical Report PSW-151. Pacific Southwest Forest and Range Experiment Station. (Albany, CA)

Stephenson NL (1999) Reference conditions for giant Sequoia forest restoration: structure, process, and precision. *Ecological Applications* **9**, 1253–1265.

Stephenson NL, Parsons DJ, Swetnam TW (1991) Restoring natural fire to the Sequoia–mixed conifer forest: should intense fire play a role? In 'Proceedings 17th Tall Timbers Fire Ecology Conference, High Intensity Fire in Wildlands: Management Challenges and Options'. pp. 321–337. (Tall Timbers Research Station: Tallahassee, FL)

Swetnam TW (1993) Fire history and climate change in giant sequoia groves. *Science* **262**, 885–889.

Taylor AH (2000) Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, USA. *Journal of Biogeography* **27**, 87–104. doi:10.1046/J.1365-2699.2000.00353.X

Taylor AH, Skinner CN (1998) Fire history and landscape dynamics in a late-successional reserve, Klamath mountains, California, USA. *Forest Ecology and Management* **111**, 285–301. doi:10.1016/S0378-1127(98)00342-9

Vankat JL, Major J (1978) Vegetation changes in Sequoia National Park, California. *Journal of Biogeography* **5**, 377–402.

van Mantgem PJ, Stephenson NL, Keifer M, Keeley JE (2004) Effects of an introduced pathogen and fire exclusion on the demography of sugar pine. *Ecological Applications* **14**, 1590–1602.

van Wagtendonk JW (1985) Fire suppression effects on fuels and succession in short-fire-interval wilderness ecosystems. In 'Proceedings, symposium and workshop on wilderness fire'. pp. 119–126. USDA Forest Service, Intermountain Research Station General Technical Report INT-182. (Ogden, UT)

van Wagtendonk JW, Benedict JM, Sydoriak WM (1998) Fuel bed characteristics of Sierra Nevada conifers. *Western Journal of Applied Forestry* **13**, 73–84.

Weatherspoon CP (2000) A proposed long-term national study of the consequences of fire and fire-surrogate treatments. In 'Proceedings of the joint fire science conference and workshop – Crossing the millenium: Integrating spatial technologies and ecological principles for a new age in fire management', Boise, ID, 15–17 June 1999. (Eds LF Neuenschwander, KC Ryan, GE Goldberg) pp. 117–126. (University of Idaho Press: Moscow, ID)

Weatherspoon CP, Skinner CN (1995) An assessment of factors associated with damage to tree crowns from the 1987 wildfires in Northern California. *Forest Science* **41**, 430–451.

nature communications

Article

https://doi.org/10.1038/s41467-024-46702-0

Fire suppression makes wildfires more severe and accentuates impacts of climate change and fuel accumulation

Received: 14 June 2023

Accepted: 7 March 2024

Published online: 25 March 2024

Check for updates

Mark R. Kreider[1] ✉, Philip E. Higuera[2], Sean A. Parks[3], William L. Rice[4], Nadia White[5] & Andrew J. Larson[1,6]

Fire suppression is the primary management response to wildfires in many areas globally. By removing less-extreme wildfires, this approach ensures that remaining wildfires burn under more extreme conditions. Here, we term this the "suppression bias" and use a simulation model to highlight how this bias fundamentally impacts wildfire activity, independent of fuel accumulation and climate change. We illustrate how attempting to suppress all wildfires necessarily means that fires will burn with more severe and less diverse ecological impacts, with burned area increasing at faster rates than expected from fuel accumulation or climate change. Over a human lifespan, the modeled impacts of the suppression bias exceed those from fuel accumulation or climate change alone, suggesting that suppression may exert a significant and underappreciated influence on patterns of fire globally. Managing wildfires to safely burn under low and moderate conditions is thus a critical tool to address the growing wildfire crisis.

Wildfires are becoming more destructive and deadly around the world[1–4]. The societal and ecological impacts of fires[5,6] are in our collective consciousness—from Australia's 2019–2020 megafires[7], to destructive wildfires in the Mediterranean[8], to beloved giant sequoias killed by fire in California[9]—prompting widespread calls to address the wildfire crisis[8,10–14]. We understand the broad drivers of increasing fire activity: changes in climate[1,15,16], vegetation and fuel accumulation[8,17,18], and ignition patterns[19]. However, humans also play a direct role in modifying fire activity across much of the globe by engaging with fires minutes to hours after ignition (i.e., initial attack[20,21]), and subsequent suppression of escaped fires[22–24]. While weather, fuels, topography, and ignitions determine how fires might burn, humans strongly shape this into when, where, and how fires do burn (Fig. 1).

Wildfires only burn if they are not extinguished through suppression. Thus, suppression is a "filter" that allows certain types of fire to pass through while removing other types of fire (Fig. 1b). In some locations (e.g., a remote wilderness area) this filter may be relatively porous, and many fires may burn with only minimal suppression[25]. In most landscapes, however, aggressive suppression of fire is a cultural expectation, and the suppression filter is much less permeable, with only the most extreme fires escaping (e.g., Maximum suppression in Fig. 1)[20,21]. Intentional fires (i.e., prescribed fires and cultural burning) are the only types of fires that do not pass through the suppression filter, as they are allowed to burn unimpeded if they are within prescription (Fig. 1a). Area that does not burn because it was "removed" through suppression, results in fuel accumulation and ultimately increases the likelihood and intensity of future fires[26,27] (Fig. 1a). This well-known consequence has been termed the "fire suppression paradox"[28,29]: by putting out a fire today, we make fires harder to put out in the future[26,30–32] (Table 1).

Suppressing wildfires also has an additional and poorly quantified consequence that we define as the "suppression bias":

[1]Department of Forest Management, University of Montana, Missoula, MT 59812, USA. [2]Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA. [3]Aldo Leopold Wilderness Research Institute, Rocky Mountain Research Station, USDA Forest Service, Missoula, MT 59801, USA. [4]Department of Society and Conservation, University of Montana, Missoula, MT 59812, USA. [5]Environmental Science and Natural Resource Journalism, University of Montana, Missoula, MT 59812, USA. [6]Wilderness Institute, University of Montana, Missoula, MT 59812, USA.
✉e-mail: mark.kreider@umontana.edu

https://doi.org/10.1038/s41467-024-46702-0

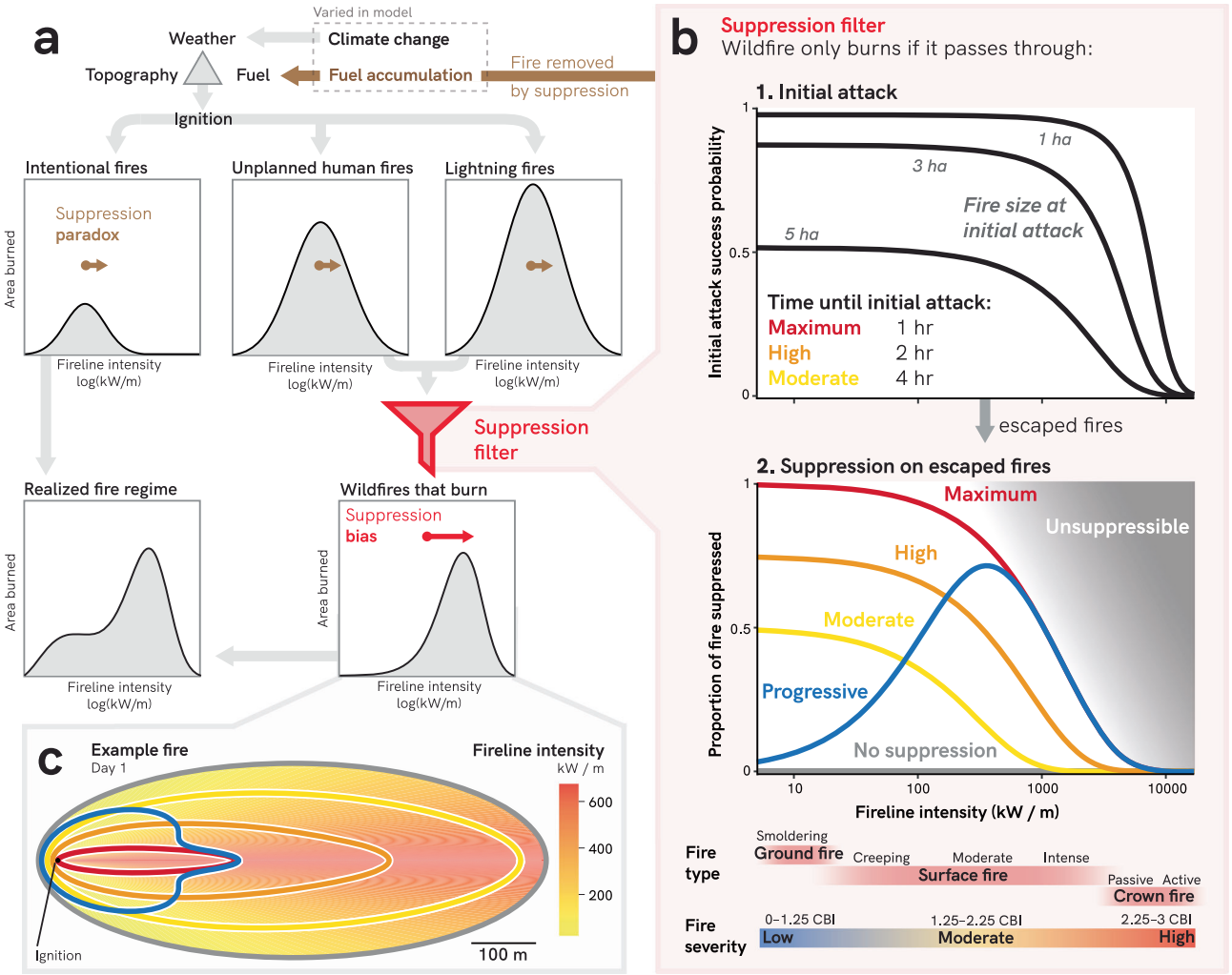


Fig. 1 | Conceptual diagram of how suppression influences fire. a Potential fire behavior depends on the fire triangle (topography, weather, fuel) and ignitions. Intentional ignitions (i.e., prescribed fires and cultural burning) do not pass through the suppression filter, as they are allowed to burn unimpeded if within prescription. Unplanned human ignitions and lightning ignitions only burn if they successfully pass through the "suppression filter." Fire "removed" by the suppression filter leads to fuel accumulation, influencing fires from all ignition types (suppression paradox, brown color). Wildfires that do burn are biased toward the fire that was not removed (suppression bias, red). These wildfires, together with intentional fires, form the realized fire regime with the suppression paradox and suppression bias inherently incorporated. **b** The suppression filter. 1) Initial attack success probability as a function of fireline intensity and fire size at initial attack (from Hirsch et al.[69]); 2) Proportion of escaped fire suppressed as a function of fire intensity. Suppression becomes increasingly impossible at high fire intensities. Colors depict the suppression scenarios used in the simulation. **c** Fire perimeters (viewed from overhead) after the first day of burning for an example ignition. Colors correspond to suppression scenarios shown in panel **b**. Fire intensity of the burned area is displayed with a color ramp.

Table 1 | Comparison of the fire suppression paradox and bias

Term	Definition	Mechanism	Impact	Time lag
Fire suppression paradox	By suppressing fire today, we increase fuel loads, making fires harder to suppress in the future	Fuel accumulation	Indirect	Future
Fire suppression bias	By suppressing some fire types more than others, the remainder reflects a biased representation of fire types	Differential suppression filter	Direct	Immediate

fire suppression extinguishes some types of fire (e.g., surface fire) more than others (e.g., crown fire), and thus skews the resulting fire activity toward those types less likely to be removed (Table 1). In contemporary fire management, which easily suppresses and removes low-intensity fire, this bias is inevitably toward higher-intensity burning occurring under extreme weather[20,21,33–35]. Thus, the fires which ecosystems, species, and people experience are skewed towards the most severe and destructive.

We define management approaches that suppress lower-intensity fire more heavily than higher-intensity fire as "regressive suppression," borrowing language from economics (e.g., a regressive tax rate decreases as taxable income increases) (Table 2). In some instances, however, management could contain and suppress relatively higher-intensity fire more heavily than lower-intensity fire, an approach we term "progressive suppression" (e.g., a progressive tax rate increases as taxable income increases) (Table 2). Both regressive and progressive suppression are subject to the same upper limit, above which fires are

Table 2 | How the type of suppression influences the resulting suppression bias

Type of suppression	Definition	Direction of suppression bias
Regressive suppression	Suppresses lower-intensity fire more heavily than higher-intensity fire	Toward higher-intensity fires, more extreme fires
Progressive suppression	Suppresses higher-intensity fire more heavily than lower-intensity fire	Toward lower-intensity fires, more moderate fires

simply too intense to suppress (Fig. 1b)[36]; however, within the domain where suppression is possible, regressive and progressive approaches can have profoundly different impacts (i.e., biases) on the way fires burn.

Although the fire suppression bias has been referenced tangentially in the literature[8,28,33,37–39], the emergent impacts of the suppression bias have not been assessed. This is largely due to the difficulty of isolating the impact of suppression with empirical data. Suppression is so ubiquitous that we have virtually no control landscapes where fire is completely unsuppressed; even in remote wilderness areas, some fires are still suppressed[40]. Furthermore, it is difficult to measure the magnitude of suppression efforts because even relatively direct proxies such as suppression cost are confounded by other factors, including terrain accessibility, human infrastructure at risk, and availability of suppression resources[41]. Finally, data on suppression efforts are generally only available for larger fires[42], obscuring the many ignitions that are quickly and easily suppressed during initial attack[20,21]. To overcome these constraints, we used a simulation approach to assess and quantify the magnitude of the fire suppression bias on fire behavior and ecological impacts, relative to the influence of climate change and fuel accumulation.

Our modeling framework simulates fundamental components of fires: weather and fuel moisture; ignitions; fire growth; fire suppression (through initial attack and containment of escaped fires); and ecological effects. To isolate the effect of fire suppression, we simulated thousands of fires with identical biophysical conditions, but which differed only in their suppression scenario, including three "regressive suppression" scenarios (Moderate, High, and Maximum; Fig. 1b), one "progressive suppression" scenario (Progressive; Fig. 1b), and a control scenario with no suppression. For each fire, we calculated the proportion burned at high severity, average fire severity, daily and total fire size, and the diversity of fire severity[43]. To compare the influence of suppression to that of climate change and fuel accumulation, we simulated fires across a range of plausible current and future fuel aridity (vapor pressure deficit; VPD) and fuel loading conditions in forest ecosystems in North America. These ranges represent a 240-year time period of modeled increases (e.g., increased VPD based on RCP 8.5 climate scenario[44]; fuel loading rates based on historical fuel modeling[45]).

Using this modeling framework, we show how the suppression bias directly influences fire activity and subsequent fire effects. Specifically, we asked: 1) How does fire suppression influence patterns of area burned, ecological impacts (i.e., fire severity), and the diversity of both factors over space and time? 2) How does the magnitude of this influence compare to that from climate change and fuel accumulation?

Results

Regressive fire suppression makes fires more severe

Across the simulated range of fuel aridity, regressive suppression scenarios (Moderate, High, and Maximum) increased the ecological impacts of wildfire, as reflected by higher fire severity metrics. We simulated fire severity by linking fire intensity to the Composite Burn Index (CBI), which runs from zero (unburned) to three (maximum fire severity), with values above 2.25 considered high-severity[46]. Under the Maximum fire suppression scenario, a greater proportion of each wildfire burned at high severity (Fig. 2a, b). On average, wildfires burning under the Maximum suppression scenario had over twice as high proportion that burned at high severity, compared to fires burning with no suppression. Across all fuel aridity simulations, Maximum suppression increased mean fire severity by an average of 0.21 CBI units, relative to fires with no suppression (Fig. 2c). This increase in fire severity is equivalent to the cumulative effects of 102 years of increased fuel aridity from climate change alone, under the no-suppression scenario (i.e., an increase in mean summer VPD of +0.85 kPa) (Fig. 2c inset). Similarly, across the simulated range of fuel loading values, Maximum suppression increased mean fire severity by an average of 0.22 CBI units, relative to control scenarios (Fig. 2d). This increase is equivalent to the effect of 102 years of additional fuel accumulation under no fire suppression (i.e., an increase in 100-h surface fuel loading of +3.7 Mg ha^{-1}) (Fig. 2d inset).

In contrast, Progressive suppression reduced the proportion of each wildfire that burned at high severity, for most levels of fuel aridity and fuel loading (Fig. 2a, b). Compared to fires burning with no suppression, wildfires burning under the Progressive suppression scenario had an average of 17% (across fuel aridity gradient) and 15% (across fuel loading gradient) less proportion that burned at high severity. Mean fire severity was also lower under the Progressive fire suppression scenario, across most of the simulated range of fuel aridity and loading, with an average reduction of 0.04 and 0.03 CBI units, respectively (Fig. 2c, d). Given modeled rates of fuel aridity and fuel loading change, these differences are equivalent to burning under scenarios of no suppression from 17 and 14 years in the past (i.e., changes of −0.15 kPa VPD and −0.49 Mg ha^{-1}), respectively (Fig. 2c, d insets).

Regressive fire suppression accentuates trends of increasing area burned

While increasing fuel aridity and fuel loading led to a rise in area burned for wildfires under all scenarios (i.e., suppression or not), fires under the regressive suppression scenarios displayed higher sensitivity to increasing fuel aridity and fuel loading (Fig. 3). Across the gradient of increasing fuel aridity, area burned under the Maximum suppression scenario increased by 5.0% per year, compared to only 1.8% per year for wildfires under the no-suppression scenario. Thus, across the 240-year range of increased fuel aridity, yearly burned area doubled nearly three times as fast under Maximum fire suppression, compared to scenarios without fire suppression (i.e., 14 vs. 39 years). This difference was even more marked under increasing fuel loading: area burned under the Maximum suppression scenario increased by 3.7% per year, compared to only 0.7% per year for wildfires that were not suppressed (Fig. 3). Thus, across the 240-year range of increased fuel loading, yearly burned area doubled over five times faster under Maximum suppression, compared to scenarios without fire suppression (i.e., 19 vs. 94 years). Fires simulated under the Progressive suppression scenario had the lowest sensitivity to increasing fuel aridity and fuel loading of any suppression strategy, including no suppression. Yearly burned area doubled every 44 years across the simulated increases in fuel aridity, and only every 133 years across the simulated gradient of fuel accumulation. Patterns were similar for area burned at high severity, with regressive scenarios leading to faster proportional increases in area burned and the Progressive scenario maintaining the slowest increase in area burned (Supplementary Fig. S1).

Regressive fire suppression decreases the diversity of fire effects

Relative to unsuppressed fires, regressive suppression decreased the diversity of fire effects (i.e., diversity of burn severity) at all levels of fuel aridity and fuel loading values (Fig. 4). In the Maximum

https://doi.org/10.1038/s41467-024-46702-0

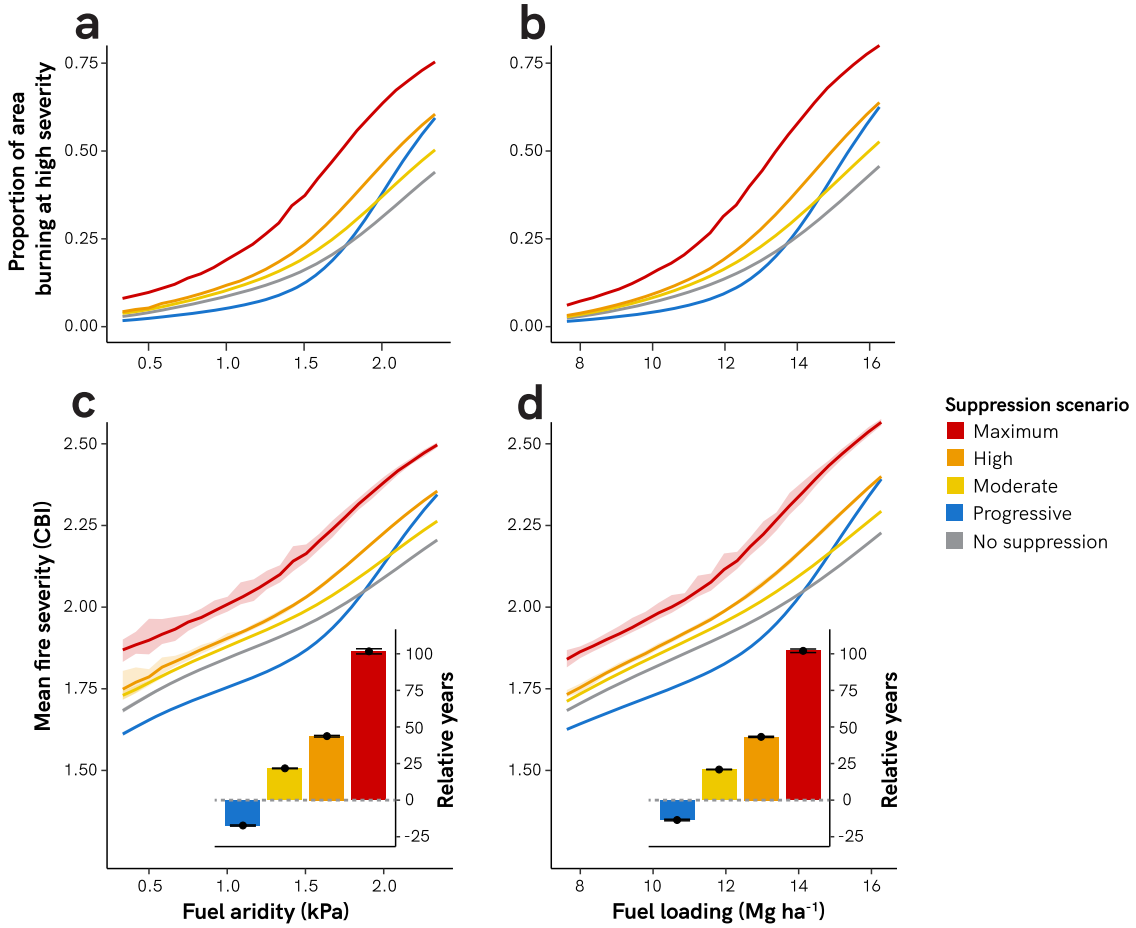


Fig. 2 | Effects of fire suppression on fire severity. Panels **a** and **b** show the proportion of high-severity fire (CBI > 2.25) across ranges of fuel aridity and fuel loading. Panels **c** and **d** show mean fire severity across ranges of fuel aridity and fuel loading. Insets show the average number of years of modeled climate change (vapor pressure deficit increase of 0.008 kPa yr^{-1}) or fuel accumulation (100-h fuel accumulation rate of 0.036 Mg ha^{-1} yr^{-1}) to yield the difference in fire severity between suppressed and unsuppressed fires. Variability across the 40 simulation replications is shown with 95% confidence intervals (too small to see for some) or error bars (insets on **c** and **d**). Fuel loading in panel **b** and **d** depicts 100-h surface fuel loading values. Simulations across the fuel aridity range were run at a constant 100-h surface fuel loading of 11.23 Mg ha^{-1}; simulations across the fuel loading range were run at constant mean fire season vapor pressure deficit of 1.17 kPa.

suppression scenario, 97–99% of fires were contained under 121 ha (300 ac) for all but the most extreme levels of fuel aridity and loading (Supplementary Fig. S2). Under the regressive fire suppression scenarios, a higher proportion of area burned came from a small proportion of extreme fires (Fig. 4c). For example, under the Maximum suppression scenario, 91% of the area burned came from the largest 1% of fires, compared to only 4% of the area burned that came from the largest 1% of fires under the scenario of no fire suppression. In contrast, under the Progressive fire suppression scenario, fires had the highest diversity of fire effects across the entire range of fuel aridity and fuel loading values, with especially pronounced increases in diversity under more extreme conditions. Progressive suppression also led to fires with the most even distribution of area burned across fires of any suppression scenario (Fig. 4c).

Discussion

We show with a simulation experiment how decades of regressive fire suppression have likely contributed to observed rates of increased burned area and high-severity area burned, independent of climate change and fuel accumulation. While some wildfires have always burned under extreme conditions and at high severity, the fire suppression bias magnifies the proportional representation of these fires by removing fires that would have burned with low or moderate severity (Supplementary Fig. S3). The result is akin to the over-prescription of antibiotics: in our attempt to eliminate all fires, we have only eliminated the less intense fires (that may best align with management objectives such as fuel reduction[47]) and instead selected for primarily the most extreme events (suppression bias) and created higher fuel loads and more "suppression-resistant" fires (suppression paradox). Through regressive fire suppression, we are effectively bringing a more severe future to the present—experiencing average fire severities that would not otherwise happen for a century. Our findings suggest that the abnormally high proportions of high-severity fire witnessed in many areas globally (e.g. refs. 48–51), is due, in part, to the influence of the suppression bias itself.

The suppression bias also has profound impacts on society and social perceptions of fire. By disproportionately removing fires with desirable impacts[47], regressive fire suppression ensures that most people interact with wildfires that burn during extreme events. This in turn makes it less likely for individuals to value the beneficial aspects of less-extreme fires, and less likely to support or desire active fire management[52], further exacerbating the suppression bias[10].

Though regressive suppression keeps many fires at small sizes (Supplementary Fig. S2) and reduces the absolute amount of burned area (relative to a world with no suppression), in the face of climate change and fuel accumulation, it counter-intuitively leads to a higher relative rate of increasing area burned over time. This is because regressive suppression amplifies the difference between the amount of fire that burns under less fire-conducive climates (e.g., in the recent past) and how much will burn despite heavy suppression under more

https://doi.org/10.1038/s41467-024-46702-0

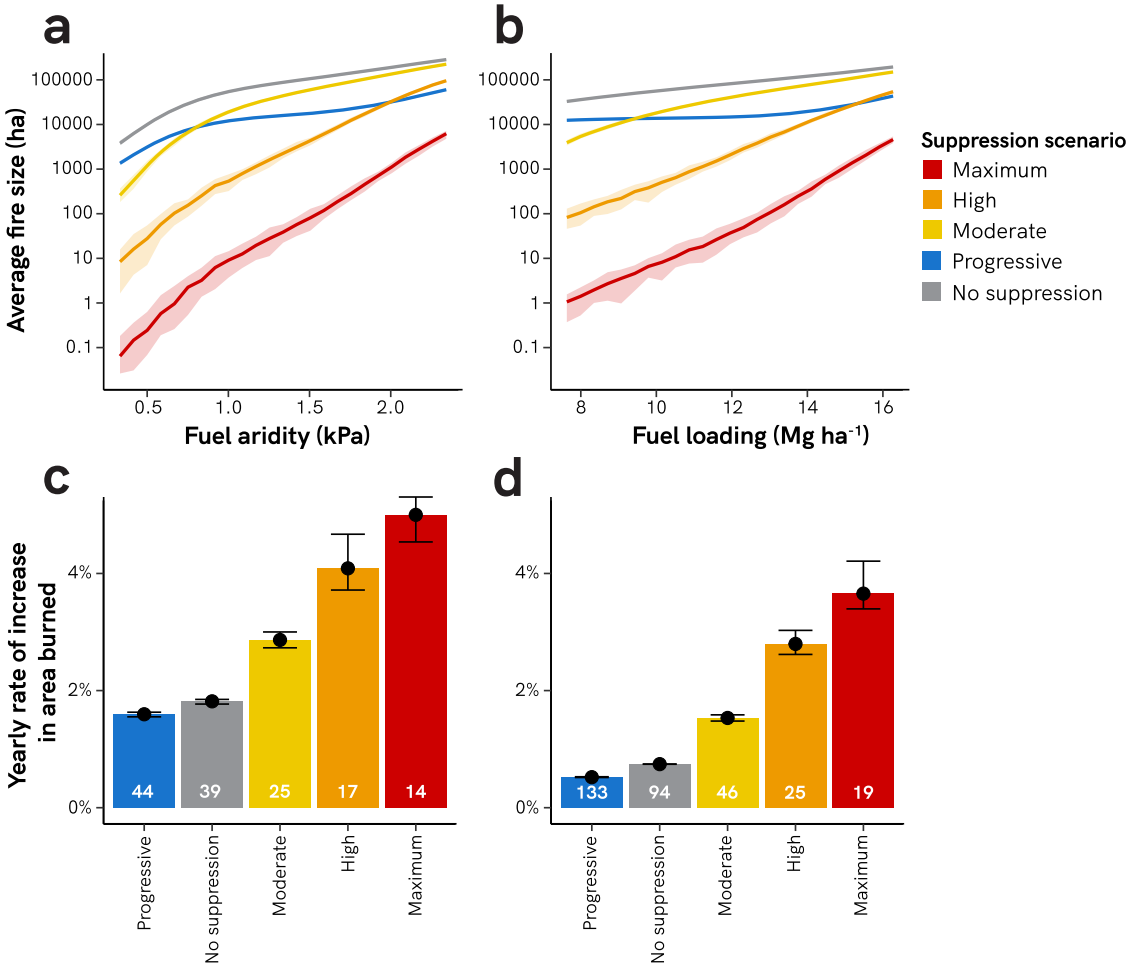


Fig. 3 | Effects of fire suppression on burned area increase. Panels **a** and **b** show trends in average fire size across ranges of fuel aridity and fuel loading. Fuel loading in panel **b** depicts 100-h surface fuel loading values. Yearly rates of increase in panels **c** and **d** are calculated with a yearly increase in fuel aridity of 0.008 kPa yr^{-1} or a yearly increase in fuel accumulation (100-h fuel accumulation rate) of 0.036 Mg ha^{-1} yr^{-1}, respectively. White numbers at the base of bars are the doubling time, in years, of burned area. Variability across the 40 simulation replications is shown with 95% confidence intervals (**a** and **b**; too small to see on some curves) or error bars (**c** and **d**). Simulations across the fuel aridity range were run at a constant 100-h surface fuel loading of 11.23 Mg ha^{-1}; simulations across the fuel loading range were run at constant mean fire season vapor pressure deficit of 1.17 kPa.

fire-conducive future climates. For example, across simulated climate change, area burned doubled nearly twice as quickly under regressive suppression, compared to not suppressing fires at all. Our work thus suggests that observed high rates of increasing area burned around the world (e.g. refs. 3,53) are at least partially driven by the suppression bias. People and societies are adapted to what they experience to be "normal," and deviations from this baseline require adaptation; by causing the baseline to shift at an even faster rate, regressive suppression further heightens the stress on societies responding to changing conditions[54,55].

The fire suppression bias also has fundamental effects on the longstanding ecological and evolutionary role of fire in terrestrial ecosystems[56]. Fire suppression not only reduces how often plants and animals are exposed to fire, which is detrimental to fire-dependent organisms[57], but it also guarantees that a greater proportion of these encounters are with high-intensity fire. By preferentially removing low-intensity fire through regressive suppression, we have likely shifted the selective pressures of natural selection, unintentionally favoring traits that confer resistance or resilience to high-intensity fire over traits supporting persistence through lower-intensity fire. Fire is also an important catalyst for community reorganization and adaptation in the face of changing environmental conditions such as global warming[58]. However, by reducing the prevalence of fire, suppression limits opportunities for reorganization; instead, ecosystems accumulate inertia from the current species composition and structure, which may not be well-aligned to future conditions[59–61]. Furthermore, because regressive suppression biases fire toward more severe conditions, with decreased seed and propagule availability and more stressful post-fire climatic environments, any reorganization that does occur is more likely to lead to state-shifts[61–64].

We demonstrate that progressive suppression leads to less extreme simulated fire behavior and effects. Indeed, empirical data from protected areas (which tend to have lower rates of suppression[65] and may represent the closest existing examples to progressive suppression) show lower fire severities[66,67] and a greater diversity of fire effects[43], consistent with our conclusions. In our simulations, fires under the Progressive suppression scenario had equivalent fire severity to unsuppressed fires burning under less fire-conducive conditions—in other words, effectively reversing the impacts of climate change or fuel accumulation by one to nearly two decades. Area burned under the Progressive suppression scenario also doubled much slower in response to climate change, compared to regressive suppression scenarios. A society living under progressive suppression would be less stressed by climate change, as their perceived "normal"

https://doi.org/10.1038/s41467-024-46702-0

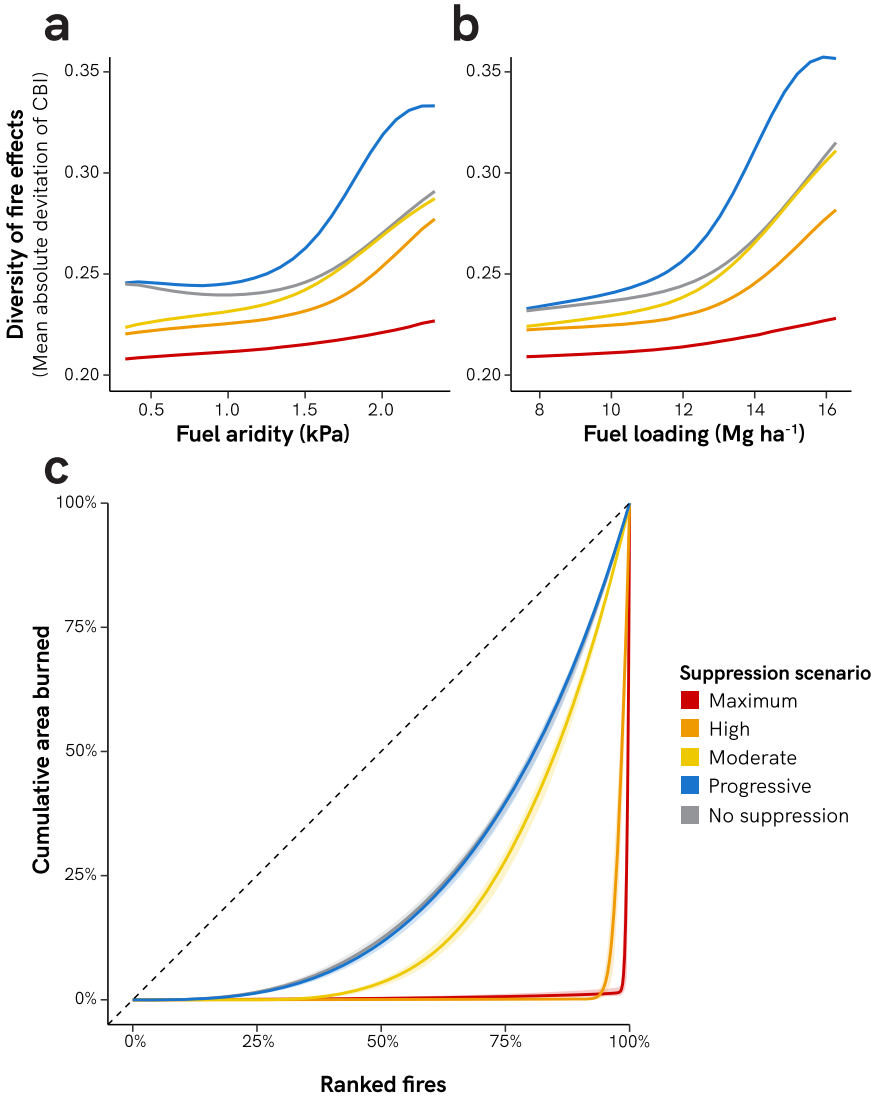


Fig. 4 | Effects of fire suppression on diversity of fire effects. Panels **a** and **b** show the effects of fire suppression on the diversity of fire effects across ranges of fuel aridity and fuel loading. Diversity of fire effects is calculated as the mean absolute deviation of fire severity (CBI) sensu Steel and colleagues[43]. Fuel loading in panel **b** depicts 100-h surface fuel loading values. Simulations across the fuel aridity range were run at a constant 100-h surface fuel loading of 11.23 Mg ha^{-1}; simulations across the fuel loading range were run at constant mean fire season vapor pressure deficit of 1.17 kPa. **c** Lorenz curves for each suppression scenario; fires are ranked by increasing area burned. Simulations run at mean seasonal vapor pressure deficit of 1.17 kPa and fuel loading of 11.23 Mg ha^{-1} (100-h fuel load). The dashed line represents hypothetical fire activity where the area burned is spread equally across all fire days. Variability across the 40 simulation replications is shown with 95% confidence intervals but which are too small to see for some curves.

conditions would change half as fast. By allowing more lower-intensity fire, progressive suppression could buy time, helping societies and ecosystems adapt to climate change[54].

Our simulations are grounded in fundamental physical aspects of fire behavior[68] and reveal important and underappreciated consequences of fire suppression; however, our model is not intended to predict fine-scale fire behavior. For example, we did not incorporate spatial variability in topography, wind direction, or fuel loading within any individual fire. Additionally, each modeled fire is unaffected by fires that have occurred in prior years (i.e., the model does not incorporate the effects of the fire suppression paradox; Table 1). This may make our results a conservative estimate of the total impact of regressive suppression, since landscapes under regressive suppression would accumulate fuel faster than those with no suppression, further heightening the difference in fire intensity.

While our model includes practical implementations of suppression[36,69], it does not incorporate dynamic resource allocation as the number of fires increase across a landscape. This means it does not explicitly account for scenarios where suppression resources are depleted from numerous fires burning simultaneously, such as during National Wildland Fire Preparedness Level 5 in the U.S.[41,70]. Consequently, the simulation may overestimate suppression effectiveness and underestimate suppressed fire sizes in these conditions. However, the model assumes near-complete ineffectiveness of suppression during extreme weather events when fire intensity is high (Fig. 1b), effectively incorporating resource scarcity. Regardless, in conditions when fire suppression is effective, our results show that it inherently biases resulting fire patterns.

Our model generates patterns of fire behavior that align with empirical data. For example, burned area patterns under Maximum suppression (e.g., nearly all fires contained before reaching 121 ha (300 ac); 1% of fires accounting for 91% of area burned) closely resemble long-term trends observed in the U.S. (97–99% of fires contained before reaching 121 ha (300 ac); 1% of fires accounting for 98% of area

burned[71]). Thus, our results reveal important general expectations of the impacts of fire suppression, relevant to any flammable location worldwide where suppression is used. Future empirical work can test these expected impacts across a variety of ecological and cultural settings.

Although safely allowing low- and moderate-intensity fire is essential for learning to co-exist with wildfire[72], implementing progressive suppression faces a range of challenges that span social-ecological systems[41]. Numerous land management agencies have ingrained cultures and policies that incentivize regressive fire suppression[8,10,33], and shifts in management may be hampered by a lack of trust and support from the public[73], in addition to the widespread public expectation that all wildfires should be suppressed[74]. Progressive suppression would let low-intensity fire spread relatively unencumbered, while more strongly suppressing higher-intensity fire −a management approach that may not always be practical, safe, or possible. Additionally, the operating space for progressive suppression (i.e., maintaining a gradient where higher-intensity fire is more heavily suppressed than lower-intensity fire) is increasingly constrained as conditions become more fire-conducive (Supplementary Fig. S4), and as more valued human resources are built in flammable environments[5]. Finally, while lower- and moderate-intensity fires can reduce the smoke-related health impacts of large, high-intensity wildfires[75], moving toward progressive suppression would likely increase the frequency of low-level smoke emissions, much like the increased use of prescribed fire[75,76]. As such, paradigm shifts in fire management would necessitate public health interventions at all levels: from individual behavioral strategies to public policies and community resources (e.g., facilitating the use of publicly available air-quality data, subsidizing or providing high efficiency particulate air [HEPA] air filters, and creating publicly accessible clean-air spaces)[4,77].

Even when and where progressive suppression is infeasible, our results show that less aggressive implementations of regressive suppression (e.g., moving from Maximum to Moderate suppression, analogous to calls for increased fire use[10]) can dramatically reduce the suppression bias. Adaptive management frameworks that facilitate risk-informed differences in management approaches (e.g., the PODs framework[78]) could likewise help lessen the impact of the suppression bias. For example, such fire management could implement regressive suppression approaches when necessary (e.g., near human infrastructure) and progressive or no suppression approaches when and where more feasible. Finally, intentional fires (i.e., prescribed fires and cultural burning; Fig. 1) also play an important role in tandem with progressive suppression[10,79,80]. While these practices support a range of values on their own[47], they also facilitate the implementation of progressive suppression strategies by introducing low-intensity fire and creating landscape heterogeneity.

We demonstrate that the suppression bias is a major driver of fire activity and ecological impacts. While the negative impacts of fuel accumulation are commonly recognized as an indirect consequence of fire suppression, integrating the impacts of the suppression bias would improve our understanding of fire-human relationships, and ongoing changes in fire activity. Part of the solution to coexisting with wildfire now and into the future requires developing and applying technologies and approaches that allow us to safely manage wildfires under moderate burning conditions. Arguably, this will be as effective as other needed interventions, such as mitigating global warming, minimizing unintentional human-related ignitions, and modifying forest structure to reduce fire severity when fires occur.

Methods

Our model simulates individual fire events independently, and it is not intended to represent a specific real-world landscape. All models are tradeoffs between fine-scale precision and large-scale generalizability[81], and we designed our simulation approach to be generalizable while incorporating fundamental physical aspects of fire behavior. We use a wide range of fuel loading and climate parameters, to both demonstrate the global applicability of our results and address the variability and uncertainty inherent in complex real-world environments[82] and demonstrate that the consequences of the suppression bias are not unique to a specific biophysical setting (i.e., a fire regime). The parameters and simulations described below are generally informed by variables and ranges of variability representing forest ecosystems in western North America. Full details are provided in the Supplementary Information (Supplementary Methods).

Simulating ignitions & fire spread

For each fire, we randomly chose an ignition day from a hypothetical 150-day fire season. Ignitions could smolder for up to three days, during which fire spread would occur if the daily fuel moisture was less than the moisture of extinction (25%). If fuel moisture never fell below 25% during this three-day period, the ignition was assumed to be extinguished naturally.

We assumed elliptical fire shape[83] and modeled daily fire growth based on Huygens' principle[84], which assumes that the growth of each point on the fire perimeter can be independently modeled as an expanding ellipse. The shape of this ellipse becomes longer and narrower at higher wind speeds[83] (Supplementary Fig. S5). We modeled daily heading-direction fire spread rate, using the rothermel function in the R package firebehavioR[85], which incorporates potential transitions to crown fire spread[86,87] (Supplementary Fig. S5). We converted the modeled heading-direction fire spread rates to elliptical expansion factors and distances at any angle from the ignition (Supplementary Methods). We calculated two metrics of fire intensity−fireline intensity and flame length−using equations from the rothermel function in the R package firebehavioR[85] and extended them to elliptical fireline intensity using equations of Catchpole and colleagues[88]. We estimated fire severity by linking flame length to estimated tree mortality from mixed-conifer ecosystems[89] and finally to Composite Burn Index (CBI), a measure of fire-caused vegetation mortality and soil organic matter consumption[46].

Simulating suppression

We tested several different suppression scenarios: three regressive suppression scenarios (Moderate, High, Maximum), one progressive suppression scenario (Progressive), and one control scenario (No suppression). We simulated suppression of fires with a two-step process: 1) initial attack, and 2) subsequent suppression of fires that escape initial attack[23,24]. To simulate initial attack success, we used a modeled relationship from Hirsch and colleagues[69] that estimates the probability of escape as a function of heading fireline intensity and fire size at the time of initial engagement. For regressive suppression scenarios, we stochastically simulated whether initial attack was successful (i.e., the fire was fully contained) using different times of initial engagement, and thus fire size (Moderate = 4 h; High = 2 h; Maximum = 1 h). For the progressive suppression scenario, we assumed ignitions were managed without any initial attack but with subsequent suppression. For fires where initial attack was not successful, we modeled subsequent suppression using suppression functions to relate fireline intensity to the expected proportion of fire suppressed (Fig. 1b). The Maximum suppression filter roughly equates to the maximum possible effectiveness of on-the-ground fire suppression efforts, where suppression becomes virtually impossible above a certain fireline intensity[36].

We calculated daily elliptical distance burned under each suppression scenario as the unsuppressed distance burned (with the assumption that fire actively spread for half of the day length) multiplied by the proportion of fire remaining after suppression. Points on the ellipse were considered permanently extinguished if the daily

distance burned was less than 5 m. Other points on the ellipse could continue burning, and a fire was not considered extinguished until points at all angles were extinguished or until after the 150th day of the fire season. Supplementary Fig. S6 shows the daily fire weather and progression of burning for an example ignition, across all suppression scenarios.

Fire behavior model inputs

For each ignition, we simulated daily fire weather: windspeed and temporally autocorrelated live and dead fuel moistures. We modeled daily windspeeds as arising from a Weibull distribution, with a single wind direction for each fire event. We simulated canopy fuel moisture as varying temporally across a sinusoidal seasonal trend. We also simulated daily live and dead surface fuel moisture (i.e., 1-, 10-, and 100-h fuel moisture, live woody and herbaceous fuel moisture) using a sinusoidal seasonal trend around a mean seasonal fuel aridity value, with random variation in amplitude and daily, temporally autocorrelated fluctuations. For a given ignition, we assumed a terrain slope of 40% (20.8°) and uniform and continuous fuel loading, meaning that simulated fires never experienced fuel breaks and would continue burning as long as weather conditions allowed for fire spread.

We ran simulations across ranges of mean fuel aridity and fuel loading to emulate changes in both time (i.e., climate change, fuel accumulation) and space (i.e., moving from one climatic region or forest type to another). Fuel aridity and fuel loading ranges spanned 240 years of modeled climate change or fuel accumulation in the Western U.S., respectively. To estimate a rate of yearly fuel aridity change under an RCP 8.5 climate change scenario, we used Ficklin & Novick's[44] projected median increase in summer vapor pressure deficit (VPD) of 0.72 kPa for the continental U.S. from the historical period (1979–2013; midpoint 1996) to the future period (2065–2099; midpoint 2082) to calculate a mean annual increase between midpoint years of 0.00837 kPa yr^{-1}. Because fire spread models are input with fuel moisture, we converted VPD to dead fuel moisture, using a statistical relationship parameterized with gridMET data[90] from across Western U.S. temperate conifer forests. To estimate plausible yearly increases in fuel loading, we estimated the slope of modeled dead wood carbon accumulation (i.e., the difference in fuel loads between suppressed and unsuppressed model scenarios) in the Western U.S. from 1980–2010 from Boisramé and colleagues[45]. We assumed that carbon made up 50% of total fuel weight and that 100-h fuels comprised 50% of all dead fuels (in keeping with ratios of Fuel Model 10 [91]), yielding a yearly 100-h fuel load increase of 0.036 Mg ha^{-1} yr^{-1}.

Simulation structure

We ran simulations where we varied either mean fuel aridity or fuel loading, while holding the other at constant mean values. A single simulation replicate involved 1000 ignitions, each of which had a unique, randomly simulated ignition day and timeseries of fuel moisture values and windspeeds (i.e., weather scenario). Using this ignition-day and weather scenario, we then simulated fire spread independently for either 1) all levels of fuel loading, while holding mean fire season fuel aridity constant (VPD of 1.17 kPa), or 2) all levels of mean fuel aridity, while holding fuel loading constant (100-h fuel loading of 11.23 Mg ha^{-1}). For each of these simulated fire-spread events, we also modeled all four scenarios of fire suppression (Maximum, High, Moderate, and Progressive) in addition to the no-suppression scenario. We then replicated a single simulation 40 times, for a total of 5 million simulated fires across each range of mean fuel aridity or fuel loading (1000 ignitions ×25 levels of fuel aridity or fuel loading ×5 levels of suppression ×40 replicates).

Summarizing the cumulative impacts of fire suppression

To assess the effect of fire suppression on patterns of fire severity, for each fire we calculated the proportion that burned at high severity (CBI values ≥ 2.25; sensu Parks & Abatzoglou[53]) and the weighted mean fire severity. For each simulation we calculated the required change in mean fuel aridity or fuel load for fires with no suppression to yield the same fire severity as suppressed fires. We divided this value by estimated yearly rates of change in mean fuel aridity and fuel loading, to evaluate how many years of climate change or fuel accumulation it would take for unsuppressed fires to burn at the same mean fire severity. To investigate how fire suppression affected patterns of burned area, we calculated the total area burned for each fire. For each simulation, we also calculated the average multiplicative yearly rate of increase (△) in burned area across the 240-year ranges of fuel aridity and fuel loading. We calculated the diversity of fire severity for each fire using the method detailed by Steel and colleagues[43], with CBI as the single input fire trait—which is equivalent to the mean absolute deviation of CBI values. We investigated how equally burned area was spread across fires by calculating Lorenz curves of area burned under each suppression scenario.

Within a replicate (i.e., 1000 ignitions × 25 fuel aridity or fuel loading levels), for each suppression scenario we calculated the mean values for parameters of interest, at each level of fuel aridity or fuel loading. We then calculated overall means across the 40 simulation replications and used 95% confidence intervals to display variability. We conducted all simulation and analysis in R[92].

Data availability

The source data generated in this study have been deposited in a public database[93] [https://doi.org/10.5281/zenodo.10729478].

Code availability

The R code to reproduce all our results and figures is provided in a public database[93] [https://doi.org/10.5281/zenodo.10729478].

References

1. Balch, J. K. et al. Warming weakens the night-time barrier to global fire. *Nature* **602**, 442–448 (2022).
2. Ellis, T. M., Bowman, D. M. J. S., Jain, P., Flannigan, M. D. & Williamson, G. J. Global increase in wildfire risk due to climate-driven declines in fuel moisture. *Glob. Change Biol.* **28**, 1544–1559 (2022).
3. Bowman, D. M. J. S. et al. Vegetation fires in the Anthropocene. *Nat. Rev. Earth Environ.* **1**, 500–515 (2020).
4. Xu, R. et al. Wildfires, Global Climate Change, and Human Health. *N. Engl. J. Med.* **383**, 2173–2181 (2020).
5. Iglesias, V. et al. Fires that matter: reconceptualizing fire risk to include interactions between humans and the natural environment. *Environ. Res. Lett.* **17**, 045014 (2022).
6. Higuera, P. E., Abatzoglou, J. T., Littell, J. S. & Morgan, P. The Changing Strength and Nature of Fire-Climate Relationships in the Northern Rocky Mountains, U.S.A., 1902-2008. *PLOS One* **10**, e0127563 (2015).
7. Godfree, R. C. et al. Implications of the 2019–2020 megafires for the biogeography and conservation of Australian vegetation. *Nat. Commun.* **12**, 1023 (2021).
8. Moreira, F. et al. Wildfire management in Mediterranean-type regions: paradigm change needed. *Environ. Res. Lett.* **15**, 011001 (2020).
9. Shive, K. L. et al. Ancient trees and modern wildfires: Declining resilience to wildfire in the highly fire-adapted giant sequoia. *For. Ecol. Manag.* **511**, 120110 (2022).
10. North, M. P. et al. Reform forest fire management. *Science* **349**, 1280–1281 (2015).
11. Stephens, S. L. et al. Managing Forests and Fire in Changing Climates. *Science* **342**, 41–42 (2013).
12. US Forest Service. *Confronting the Wildfire Crisis: A Strategy for Protecting Communities and Improving Resilience in America's Forests* (US Department of Agriculture Forest Service Fire and

Aviation Management and Department of the Interior Office of Wildland Fire, 2022).
13. *Spreading like Wildfire: The Rising Threat of Extraordinary Landscape Fires*. UNEP - UN Environment Programme (UNEP2, 022).
14. Calkin, D. E. et al. Wildland-urban fire disasters aren't actually a wildfire problem. *Proc. Natl Acad. Sci.* **120**, e2315797120 (2023).
15. Jones, M. W. et al. Global and Regional Trends and Drivers of Fire Under Climate Change. *Rev. Geophys.* **60**, e2020RG000726 (2022).
16. Abatzoglou, J. T., Williams, A. P. & Barbero, R. Global Emergence of Anthropogenic Climate Change in Fire Weather Indices. *Geophys. Res. Lett.* **46**, 326–336 (2019).
17. Miller, J. D., Safford, H. D., Crimmins, M. & Thode, A. E. Quantitative Evidence for Increasing Forest Fire Severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. *Ecosystems* **12**, 16–32 (2009).
18. Roos, C. I. et al. Fire Suppression Impacts on Fuels and Fire Intensity in the Western U.S.: Insights from Archaeological Luminescence Dating in Northern New Mexico. *Fire* **3**, 32 (2020).
19. Balch, J. K. et al. Human-started wildfires expand the fire niche across the United States. *Proc. Natl Acad. Sci.* **114**, 2946–2951 (2017).
20. Fried, J. S. et al. Predicting the effect of climate change on wildfire behavior and initial attack success. *Clim. Change* **87**, 251–264 (2008).
21. Arienti, M. C., Cumming, S. G. & Boutin, S. Empirical models of forest fire initial attack success probabilities: the effects of fuels, anthropogenic linear features, fire weather, and management. *Can. J. Res.* **36**, 3155–3166 (2006).
22. Bowman, D. M. J. S., O'Brien, J. A. & Goldammer, J. G. Pyrogeography and the Global Quest for Sustainable Fire Management. *Annu. Rev. Environ. Resour.* **38**, 57–80 (2013).
23. Plucinski, M. P. Fighting Flames and Forging Firelines: Wildfire Suppression Effectiveness at the Fire Edge. *Curr. Forestry Rep.* **5**, 1–19 (2019).
24. Plucinski, M. P. Contain and Control: Wildfire Suppression Effectiveness at Incidents and Across Landscapes. *Curr. Forestry Rep.* **5**, 20–40 (2019).
25. Berkey, J. K., Miller, C. & Larson, A. J. *A history of wilderness fire management in the Northern Rockies*. Gen. Tech. Rep. RMRS-GTR-428. (U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Statio, 2021).
26. Dodge, M. Forest Fuel Accumulation—A Growing Problem. *Science* **177**, 139–142 (1972).
27. Parisien, M.-A. et al. Fire deficit increases wildfire risk for many communities in the Canadian boreal forest. *Nat. Commun.* **11**, 2121 (2020).
28. Arno, S. F. & Brown, J. K. Overcoming the paradox in managing wildland fire. *West. Wildlands* **17**, 40–46 (1991).
29. Ingalsbee, T. Whither the paradigm shift? Large wildland fires and the wildfire paradox offer opportunities for a new paradigm of ecological fire management. *Int. J. Wildl. Fire* **26**, 557–561 (2017).
30. Parsons, D. J. & DeBenedetti, S. H. Impact of fire suppression on a mixed-conifer forest. *For. Ecol. Manag.* **2**, 21–33 (1979).
31. Schoennagel, T., Veblen, T. T. & Romme, W. H. The Interaction of Fire, Fuels, and Climate across Rocky Mountain Forests. *BioScience* **54**, 661–676 (2004).
32. Steel, Z. L., Safford, H. D. & Viers, J. H. The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere* **6**, art8 (2015).
33. Calkin, D. E., Thompson, M. P. & Finney, M. A. Negative consequences of positive feedbacks in US wildfire management. *Ecosyst.* **2**, 9 (2015).
34. Katuwal, H., Calkin, D. E. & Hand, M. S. Production and efficiency of large wildland fire suppression effort: A stochastic frontier analysis. *J. Environ. Manag.* **166**, 227–236 (2016).
35. Silva, F. R. Y., O'Connor, C. D., Thompson, M. P., Martinez, J. R. M., & Calkin, D. E., Modelling suppression difficulty: Current and future applications. *Int. J. Wildl. Fire*. https://doi.org/10.1071/WF19042 (2020).
36. Andrews, P. Heinsch, F., Schelvan, L. *How to Generate and Interpret Fire Characteristics Charts for Surface and Crown Fire Behavior* (USDA Forest Service - General Technical Report RMRS-GTR, 2011).
37. Calkin, D. E., Cohen, J. D., Finney, M. A. & Thompson, M. P. How risk management can prevent future wildfire disasters in the wildland-urban interface. *Proc. Natl Acad. Sci.* **111**, 746–751 (2014).
38. Miller, C. & Aplet, G. H. Progress in Wilderness Fire Science: Embracing Complexity. *J. Forestry* **114**, 373–383 (2016).
39. Seielstad, C. Reconside ring wildland fire use: Perspectives from the Northern Rockies. In *Proceedings of the large wildland fires conference*. (eds. Keane, R.E., Jolly, M., Parsons, R., Riley, K.) 73, 207–212 (U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 2015).
40. Miller, C. The hidden consequences of fire suppression. *Park Sci.* **28**, 75–80 (2012).
41. Daniels, M. C. et al. Multiple social and environmental factors affect wildland fire response of full or less-than-full suppression. *J. Environ. Manag.* **351**, 119731 (2024).
42. St. Denis, L. A. et al. All-hazards dataset mined from the US National Incident Management System 1999–2020. *Sci. Data* **10**, 112 (2023).
43. Steel, Z. L., Collins, B. M., Sapsis, D. B. & Stephens, S. L. Quantifying pyrodiversity and its drivers. *Proc. R. Soc. B Biol. Sci.* **288**, 20203202 (2021).
44. Ficklin, D. L. & Novick, K. A. Historic and projected changes in vapor pressure deficit suggest a continental-scale drying of the United States atmosphere. *J. Geophys. Res. Atmos.* **122**, 2061–2079 (2017).
45. Boisramé, G. F. S., Brown, T. J. & Bachelet, D. M. Trends in western USA fire fuels using historical data and modeling. *Fire Ecol.* **18**, 8 (2022).
46. Key, C. H. & Benson, N. C. *Landscape Assessment: Sampling and Analysis Methods*. USDA Forest Service General Technical Report RMRS-GTR-164-CD, 55 (SDA Forest Service, 2006).
47. Prichard, S. J. et al. Adapting western North American forests to climate change and wildfires: 10 common questions. *Ecol. Appl.* **31**, e02433 (2021).
48. Reilly, M. J. et al. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). *Ecosphere* **8**, e01695 (2017).
49. Williams, J. N., Safford, H. D., Enstice, N., Steel, Z. L. & Paulson, A. K. High-severity burned area and proportion exceed historic conditions in Sierra Nevada, California, and adjacent ranges. *Ecosphere* **14**, e4397 (2023).
50. Collins, L. et al. The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. *Environ. Res. Lett.* **16**, 044029 (2021).
51. Fernández-García, V. & Alonso-González, E. Global Patterns and Dynamics of Burned Area and Burn Severity. *Remote Sens.* **15**, 3401 (2023).
52. Borrie, W., McCool, S. & Whitmore, J. Wildland Fire Effects on Visits and Visitors to the Bob Marshal Wilderness Complex. *Int. J. Wilderness* **12**, 32–38 (2006).
53. Parks, S. A. & Abatzoglou, J. T. Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests From 1985 to 2017. *Geophys. Res. Lett.* **47**, e2020GL089858 (2020).
54. Schoennagel, T. et al. Adapt to more wildfire in western North American forests as climate changes. *PNAS* **114**, 4582–4590 (2017).

55. Kais, S. M. & Islam, M. S. Community Capitals as Community Resilience to Climate Change: Conceptual Connections. *Int. J. Environ. Res. Public Health* **13**, 1211 (2016).
56. Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J. & Bradstock, R. A. Fire as an evolutionary pressure shaping plant traits. *Trends Plant Sci.* **16**, 406–411 (2011).
57. Tubbesing, C. L., York, R. A., Stephens, S. L. & Battles, J. J. Rethinking fire-adapted species in an altered fire regime. *Ecosphere* **11**, e03091 (2020).
58. Seidl, R. & Turner, M. G. Post-disturbance reorganization of forest ecosystems in a changing world. *Proc. Natl Acad. Sci.* **119**, e2202190119 (2022).
59. Hagmann, R. K. et al. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecol. Appl.* **31**, e02431 (2021).
60. Young, D. J. N. et al. Post-fire forest regeneration shows limited climate tracking and potential for drought-induced type conversion. *Ecology* **100**, e02571 (2019).
61. Larson, A. J. et al. Tamm Review: Ecological principles to guide post-fire forest landscape management in the Inland Pacific and Northern Rocky Mountain regions. *For. Ecol. Manag.* **504**, 119680 (2022).
62. Harvey, B. J., Donato, D. C. & Turner, M. G. High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Glob. Ecol. Biogeogr.* **25**, 655–669 (2016).
63. Coop, J. D. et al. Wildfire-Driven Forest Conversion in Western North American Landscapes. *BioScience* **70**, 659–673 (2020).
64. Davis, K. T. et al. Reduced fire severity offers near-term buffer to climate-driven declines in conifer resilience across the western United States. *Proc. Natl Acad. Sci.* **120**, e2208120120 (2023).
65. Haire, S., McGarigal, K., Miller, C. Wilderness shapes contemporary fire size distributions across landscapes of the western United States. *Ecosphere* **4**, 1–20 (2013).
66. van Wagtendonk, J. W. & Lutz, J. A. Fire Regime Attributes of Wildland Fires in Yosemite National Park, USA. *Fire Ecol.* **3**, 34–52 (2007).
67. Rivera-Huerta, H., Safford, H. D. & Miller, J. D. Patterns and Trends in Burned Area and Fire Severity from 1984 to 2010 in the Sierra de San Pedro Mártir, Baja California, Mexico. *Fire Ecol.* **12**, 52–72 (2016).
68. Rothermel, R. C. *A mathematical model for predicting fire spread in wildland fuels*. Res. Pap. INT-115. (U.S. Department of Agriculture, Intermountain Forest and Range Experiment Station, 1972).
69. Hirsch, K. G., Corey, P. N. & Martell, D. L. Using Expert Judgment to Model Initial Attack Fire Crew Effectiveness. *For. Sci.* **44**, 539–549 (1998).
70. Cullen, A. C., Axe, T. & Podschwit, H. High-severity wildfire potential – associating meteorology, climate, resource demand and wildfire activity with preparedness levels. *Int. J. Wildland Fire* **30**, 30–41 (2020).
71. Calkin, D. E., Gebert, K. M., Jones, J. G. & Neilson, R. P. Forest service large fire area burned and suppression expenditure trends, 1970-2002. *J. Forestry* **103**, 179–183 (2005).
72. Moritz, M. A. et al. Learning to coexist with wildfire. *Nature* **515**, 58–66 (2014).
73. Olsen, C. S., Sharp, E., Olsen, C. S. & Sharp, E. Building community–agency trust in fire-affected communities in Australia and the United States. *Int. J. Wildland Fire* **22**, 822–831 (2013).
74. Steelman, T. A. & McCaffrey, S. Best practices in risk and crisis communication: Implications for natural hazards management. *Nat. Hazards* **65**, 683–705 (2013).
75. Long, J. et al., Comparing smoke emissions and impacts under alternative forest management regimes. *Ecol. Soc.* **27**, 26–42 (2022).
76. Schultz, C. A. et al. Policy barriers and opportunities for prescribed fire application in the western United States. *Int. J. Wildland Fire* **28**, 874–884 (2019).
77. US Environmental Protection Agency (EPA). *Wildfire Smoke: A Guide for Public Health Officials* (US Environmental Protection Agency, 2021).
78. Thompson, M. P. et al. Potential operational delineations: new horizons for proactive, risk-informed strategic land and fire management. *Fire Ecol.* **18**, 17 (2022).
79. Hoffman, K. M. et al. Conservation of Earth's biodiversity is embedded in Indigenous fire stewardship. *Proc. Natl Acad. Sci.* **118**, e2105073118 (2021).
80. Lake, F. K. et al. Returning Fire to the Land: Celebrating Traditional Knowledge and Fire. *J. Forestry* **115**, 343–353 (2017).
81. Levins, R. The Strategy of Model Building in Population Biology. *Am. Scientist* **54**, 421–431 (1966).
82. Geary, W. L. et al. A guide to ecosystem models and their environmental applications. *Nat. Ecol. Evol.* **4**, 1459–1471 (2020).
83. Finney, M. A., McAllister, S. S., Grumstrup, T. P., Forthofer, J. M. *Wildland Fire Behaviour* (CSIRO Publishing, 2021).
84. Anderson, D. H., Catchpole, E. A., Mestre, N. J. D. & Parkes, T. Modelling the spread of grass fires. *ANZIAM J.* **23**, 451–466 (1982).
85. Ziegler, J. P., Hoffman, C. M. & Mell, W. firebehavioR: An R Package for Fire Behavior and Danger Analysis. *Fire* **2**, 41 (2019).
86. Scott, J., Reinhardt, E. *Assessing Crown Fire Potential by Linking Models of Surface and Crown Fire Behavior*. Research Paper RMRS-RP (USDA Forest Service, 2001).
87. Finney, M. A. *FARSITE: Fire A rea Simulator-model development and evaluation*. Res. Pap. RMRS-RP-4, Revis. 2004. (U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 1998)..
88. Catchpole, E. A., Mestre, N. D., Gill, A. Intensity of fire at its perimeter. *Aust. For. Res.* **12**, 47–54 (1982).
89. Ryan, K. & Noste, N. Evaluating Prescribed Fires. In *Proc. - Symposium and Workshop on Wilderness Fire* 230–238 (USDA Forest Service Intermountain Forest and Range Experiment Station, 1985).
90. Abatzoglou, J. T. Development of gridded surface meteorological data for ecological applications and modelling. *Int. J. Climatol.* **33**, 121–131 (2011).
91. Anderson, H. E. *Aids to determining fuel models for estimating fire behavior*. Gen. Tech. Rep. INT-122. (U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, 1982).
92. R Core Team. *R: A language and environment for statistical computing* (R Core Team, 2023).
93. Kreider, M. Scripts for manuscript "Fire suppression makes wildfires more severe and accentuates impacts of climate change and fuel accumulation." *Nat. Commun.* https://doi.org/10.5281/zenodo.10729478 (2024).

Acknowledgements

We thank Mark Finney and members of the University of Montana Systems Ecology Writing Seminar for suggestions that improved this work. This work was supported by a Graduate Research Fellowship from the National Science Foundation, award 1745048 (M.R.K.). Additional support came from the USDA Forest Service, Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute through agreement 19-JV-11221639-098 (M.R.K. and A.J.L.) and from the Department of the Interior North Central Climate Adaptation Science Center through Cooperative Agreement G18AC00325 from the United States Geological Survey (P.E.H.). The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA, USGS, or U.S. Government determination or policy.

Author contributions

M.R.K., P.E.H., S.A.P. and A.J.L. designed research; M.R.K. wrote the model and ran computer simulations; M.R.K. analyzed data; M.R.K wrote the paper; M.R.K., P.E.H., S.A.P., W.L.R., N.W. and A.J.L. conducted review and editing.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41467-024-46702-0.

Correspondence and requests for materials should be addressed to Mark R. Kreider.

Peer review information *Nature Communications* thanks Gabrielle Boisrame, Miguel Cruz, and the other, anonymous, reviewer for their contribution to the peer review of this work. A peer review file is available.

Reprints and permissions information is available at http://www.nature.com/reprints

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2024

Effects of Fine Sediment Inputs from a Logging Road on Stream Insect Communities

David P. Kreutzweiser*, Scott S. Capell, and Kevin P. Good

Canadian Forest Service, Natural Resources Canada, 1219 Queen St. East, Sault Ste. Marie, ON P6A 2E5; 705-541-5648; dkreutzw@nrcan.gc.ca

Introduction/Objectives

One of the challenges in addressing forest sustainability objectives is scientifically determining the ecological implications of anthropogenic disturbances to the forest environment. Logging activity, and particularly the road construction associated with it, can result in degradation of aquatic habitats through fine sediment inputs to streams and siltation of stream beds. The biological consequences of sedimentation in streams can include perturbations to benthic insect communities resulting in declines in abundance and (or) changes in community structure. However, most studies that have examined the effects of fine sediments on stream insect communities have relied on small-scale manipulative approaches in artificial stream channels or flumes, on comparative studies between reference and sediment-impacted sites after the disturbance, or on comparisons along a gradient of sedimentation. These provide useful information on the potential for effects of sedimentation on stream insects, but may not be representative of real-world responses by benthic insects to fine sediment inputs because of limitations in scale and the lack of baseline or pre-disturbance community measures.

Effects of fine sediments on stream insects from logging activity have been reported from field monitoring studies, but the negative impacts on benthos may have been confounded by other catchment disturbances such as canopy modification or changes in nutrient flux. We conducted a stream manipulation study to examine effects of fine sediment inputs on stream insect communities, and focused on time trends over pre-disturbance and post-disturbance periods with comparisons to a nearby reference stream. This approach integrated the realism of a natural stream study with the experimental control of a manipulative study by including pre-sedimentation measurements to establish baseline trends, and by excluding other catchment disturbances. The objective was to determine the impacts on stream insect communities of fine sediment inputs at a magnitude that could occur from an active logging road.

Approach

A road crossing over a forest headwater stream was amended (gravel road surface upgraded, road-side ditches cleared) to induce fine sediment inputs to a stream reach. Sediment bed load in the study reach and at a nearby reference stream was quantified before and after the manipulation by extraction of fine sediments from core samples. Aquatic insect communities were sampled in spring and fall for 2 years before and 3 years after the sediment inputs, and compared to insect communities at the reference stream. Quantitative sampling was conducted with modified (increased size, 0.32 m^2) Suber-type samplers, n=10, over 120-m study reaches. Insect community structure was compared between the sediment site and the reference stream before and after the disturbance by multivariate ordination (nonmetric multidimensional scaling), multivariate analysis of similarity, and by time series analyses of univariate community metrics (repeated measures orthogonal polynomial coefficient analysis). Divergence in trends over time at the sediment and reference sites and (or) significant time X treatment interaction in the repeated measures analyses were considered evidence of treatment effects.

Buse, L.J. and A.H. Perera (comp.). 2003. Meeting emerging ecological, economic, and social challenges in the Great Lakes region: Popular summaries. Ont. Min. Nat. Resour, Ont. For. Res. Inst., Sault Ste. Marie, ON. For. Res. Inf. Pap. No. 155.

Results and Discussion

Fine sediment bed load at the manipulated site increased from a pre-disturbance average of about 800 g m^{-2} to over 5000 g m^{-2} that persisted for over 2 years. Fine sediment inputs were 97% inorganic and about 80% of the particles were in the coarse silt (40-63 μm) size range. This resulted in an average stream-bottom sediment coverage of 46.7%, compared to a fine sediment coverage of 14.5% in the reference stream by the end of the study period.

Despite these increases in fine sediment bed load at the manipulated site, only small changes in aquatic insect community structure could be detected. No obvious patterns to suggest sediment impacts and no significant differences in time trends between the sediment and reference sites were detected for total insect abundance or biomass. An examination of community structure by multivariate ordination (NMDS) demonstrated that over the 5-yr study period there were generally greater differences between sites than among years, but that these differences were as large or larger before the sediment inputs. This occurred despite the similarities between these paired sites in catchment size, stream widths, study reach lengths and orientation, forest composition, canopy structure and density, environmental influences (given the proximity of sites), and substrate characteristics. The distinct natural differences in community structure of these paired streams underscores the need for establishing baseline or pre-treatment conditions to which after-impact conditions can be compared in unreplicated, whole-stream experiments such as this one. A paired-stream comparison after the disturbance would have indicated distinct differences in aquatic insect community structure, suggesting a marked effect of sedimentation on benthic insects, but it is clear that distinct differences in community structure in these streams were present before the disturbance. The patterns in community structure over time illustrated by the ordination plots showed only subtle divergence in trends between sites after the disturbance.

Among the univariate metrics examining spring and fall communities at the sediment and reference sites (16 time series analyses in total), six gave evidence of a sediment impact on community structure. Of those, the clearest indications of an effect on community structure were small reductions in diversity and richness of spring communities (Figure 1). These were primarily the result of a decline in the proportion of spring shredders (insects feeding on leaf material) after the disturbance, accompanied by a significant increase in the percent Chironomidae (Figure 2). None of these community metrics gave evidence of a sediment impact on fall communities.

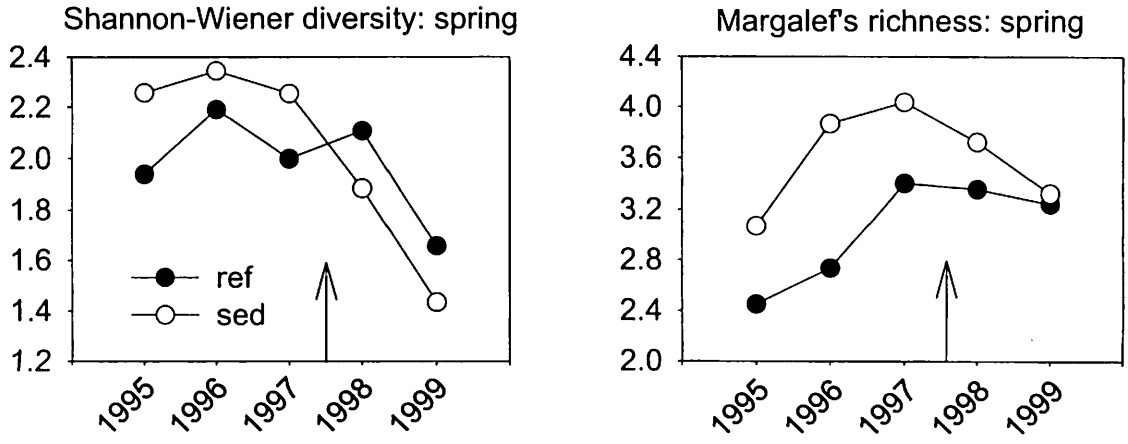


Figure 1. *Average insect diversity and richness indices based on spring samples. Arrows indicate sediment inputs.*

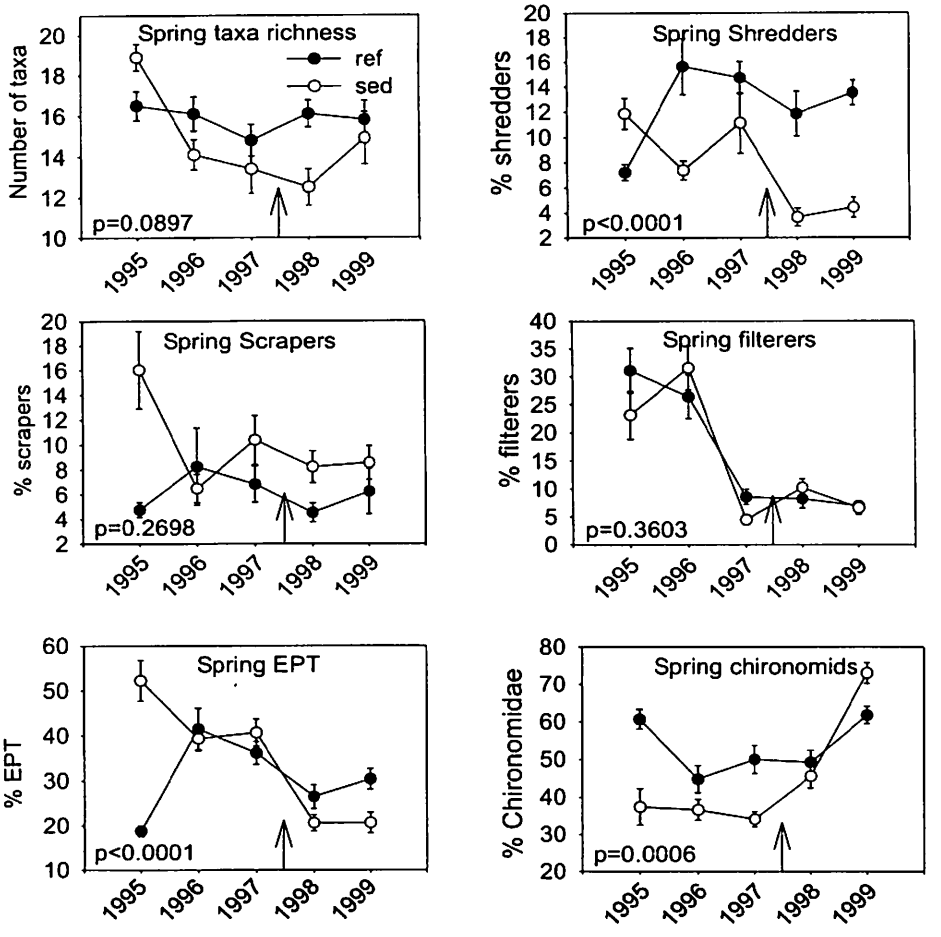


Figure 2. *Average insect community metrics in spring samples. Arrows indicate sediment inputs, p values are for time X treatment interaction terms.*

Conclusions

Despite large and sustained increases in fine sediment bed load (about 7-fold increase for 3 yr), only small changes in aquatic insect communities were detected. The insect community exhibited a high degree of resistance to fine sediment deposition of this magnitude. No effects on total insect abundance, biomass, or 10 of 16 community metric analyses were observed. A significant decline in the proportion of spring shredders (aquatic insects that feed on leaf material) may have resulted from reduced quality of food resources through siltation of benthic organic matter. An increase in the proportion of spring chironomids reflects their general tolerance of sediment-degraded habitats.

The large-scale experimental approach of this study integrated the realism of a whole-stream study with the experimental control of a manipulative study by including pre-sedimentation measurements and excluding other confounding catchment disturbances. In this regard, it may provide a more realistic measure of community-level effects on benthic insects of sedimentation at a magnitude that might be associated with logging activity, than most previous studies.



Notes

Effects of Post-Fire Salvage Logging on Cavity-Nesting Birds and Small Mammals in Southeastern Montana

WILLIAM J. KRONLAND[1] and MARCO RESTANI[2]

[1]Department of Biological Sciences, St. Cloud State University, St. Cloud, Minnesota 56301 USA
Current address: Center for Natural Lands Management, 215 West Ash Street, Fallbrook, California 92028 USA
[2]Department of Biological Sciences, St. Cloud State University, St. Cloud, Minnesota 56301 USA; corresponding author (email: restani@stcloudstate.edu)

Kronland, William J., and Marco Restani. 2011. Effects of post-fire salvage logging on cavity-nesting birds and small mammals in southeastern Montana. Canadian Field-Naturalist 125(4): 316-326.

We investigated how post-fire salvage logging of Ponderosa Pine (*Pinus ponderosa*) affected populations of cavity-nesting birds and small mammals in southeastern Montana in 2004 and 2005. We examined two salvage and two control plots with three point-count stations and one small mammal trap site randomly distributed across each plot. We used point counts and distance sampling methods to estimate density of cavity-nesting birds on each treatment. We also searched each plot for nests and used program MARK to construct a set of candidate models to investigate variations in nest survival related to treatment, year, and time. We used live traps arranged in webs centered on trapping sites and distance sampling methods to estimate small mammal density. Habitat characteristics were also quantified on each plot. Density of all cavity-nesting birds combined and of Hairy Woodpeckers (*Picoides villosus*) in particular were higher on the control than the salvage treatment. Density of large trees and abundance of active cavities were higher on the control treatment. Nest cavities on the salvage treatment were most often located in non-logged watersheds. Nest survival estimates were uniformly high, with only marginal variations attributed to treatment and year. Density of Deer Mice (*Peromyscus maniculatus*) was higher on the salvage than the control treatment, reflecting the amount of downed woody debris created during harvest.

Key Words: cavity-nesting birds, downed woody debris, forest management, nest survival, salvage logging, wildfire, Hairy Woodpecker, *Picoides villosus,* Deer Mouse, *Peromyscus maniculatus,* Custer National Forest, Montana.

The current fire regime within the Ponderosa Pine (*Pinus ponderosa*) forest type in western North America is thought to differ significantly from historical patterns and processes as a result of fire suppression, logging, and livestock grazing (Agee 1993; Arno and Allison-Bunnell 2002). The accumulation of woody fuels from decades of fire suppression is driving a shift from an historical regime of slow-burning ground fires to one that has a greater proportion of severe crown fires (Covington and Moore 1994; Allen et al. 2002). As a result, U.S. state and federal agencies are implementing the Healthy Forest Initiative and the Healthy Forest Restoration Act of 2003 to reduce fuels and the associated risk of severe wildfires and to address demand for commercial timber (Franklin et al. 2003). Federal policy promotes post-fire logging by exempting sales <100 ha from environmental review and allows operations to occur on lands otherwise unavailable for harvest (Federal Register 2003*). Ecologists are questioning the merit of salvage logging because of documented negative effects on soil, vegetation, and wildlife (McIver and Starr 2001; Beschta et al. 2004; Lindenmayer and Noss 2006; Hutto 2006). In addition, salvage logging may actually promote conditions suitable for severe wildfire and hinder forest regeneration (Donato et al. 2006; Greene et al. 2006).

Although burned forests are rare habitats at the landscape scale, spatial heterogeneity created by the patchy distribution of fire severities supports high biodiversity (Turner et al. 2003; Schmiegelow et al. 2006; Hutto 2006). Salvage logging homogenizes this forest structure and alters the post-fire wildlife community. Typically, large trees (>23 cm diameter at breast height [DBH]) favored by foraging and breeding cavity-nesting birds (Covert-Bratland et al. 2006; Pope et al. 2009) are harvested during salvage logging. Consequently, the abundance of cavity-nesting birds declines (Hutto 1995; McIver and Starr 2001; Kotliar et al. 2002) as they are replaced by ground- and shrub-nesting species (Morissette et al. 2002; Cahall and Hayes 2009; Castro et al. 2010). Size and distribution of burned tree stands that remain after salvage logging also shape composition of the cavity-nesting bird assemblage. For example, Black-backed Woodpeckers (*Picoides arcticus*) and American Three-toed Woodpeckers (*P. dorsalis*) require relatively large stands of burned trees, whereas Lewis's Woodpeckers (*Melanerpes lewis*) often occupy smaller stands typical of logged areas (Saab and Vierling 2001; Morissette et al. 2002; Hutto and Gallo 2006). In addition to spatial scale, temporal scale (measured as time since fire) affects the abundance of insect prey of primary and secondary cavity nesters and thus the composition of the post-fire bird assemblage (Saab et al. 2004; Smucker et al. 2005; Covert-Bratland et al. 2006; Hutto 2006).

Little is known about the effects of post-fire salvage logging on fauna other than cavity-nesting birds (McIver and Starr 2001; but see Converse et al. 2006). Salvage logging may increase the amount of downed woody debris (Donato et al. 2006), which provides

small mammals with additional habitat for reproduction, foraging, and predator avoidance (Harmon et al. 1986). The accumulation of downed woody debris following wildfire correlates with the rate of recolonization and an increase in the diversity of small mammals (Carey and Johnson 1995; Fisher and Wilkinson 2005; Converse et al. 2006). In contrast, removal of downed woody debris following salvage of trees damaged by a tornado was correlated with a decrease in the abundance of small mammals (Loeb 1999).

A stand-replacement fire of moderate to high intensity that was ignited by lightning occurred over 26 527 hectares of Ponderosa Pine in southeastern Montana in 2002. The U.S. Forest Service implemented a management plan in summer 2003 to reduce the risk of fire by salvage logging all standing dead trees >25 cm DBH on 485 ha. Literature reviews (McIver and Starr 2001; Kotliar et al. 2002) urged more research into the effects of post-fire salvage logging, so we took the opportunity to compare the density of cavity-nesting birds and the density of small mammals on salvage-logged and control plots. We also estimated breeding success of cavity-nesting birds, because most studies investigating the effects of logging have not measured this important parameter (Sallabanks et al. 2000; Kotliar et al. 2002; but see Saab et al. 2011).

Nest abundance and foraging activity of cavity-nesting birds after fire has been shown to be positively correlated with the size and density of standing snags (Haggard and Gaines 2001; Nappi et al. 2003). Therefore, we predicted that salvage logging would lead to a significant decrease in the number of active nest sites and a significant decrease in the overall abundance of cavity-nesting species. We expected that the volume of downed woody debris would be greater on logged areas (Donato et al. 2006), and we predicted that the density of small mammals would be greater on salvage plots.

Methods

Study area

The study area is located in a Ponderosa Pine forest approximately 40 km southeast of Ekalaka, Montana, U.S.A., in the Long Pines unit of the Custer National Forest (45°38'N, 104°11'W). The study site (1320 ha) is part of a larger forested area (28 368 ha) intermixed with pine savannah, native grassland (*Achnatherum* spp., *Bouteloua* spp., *Carex* spp., and *Pseudoroegneria* spp.), and woody draws. The area consists of hills and rocky buttes (elevation 1000–1200 m) surrounded by lower elevation sagebrush shrubland (*Artemisia* spp.), native grassland, and cultivated hayfields. Mean annual temperature in 2004 and 2005 (January through September) was 7°C and 10°C, respectively, with mean precipitation of 20 cm and 42 cm, respectively (National Oceanic and Atmospheric Administration 2005*). All surface water was ephemeral except for cattle tanks and a few small reservoirs. The area was managed for multiple use, including recreation, grazing, and timber harvest.

We were limited in our study design by management activities and fire behavior. The U.S. Forest Service selected salvage sites based on the presence of pre-existing roads and merchantable timber rather than by randomization, a problem common to wildlife forest management studies (Marzluff et al. 2000; Sallabanks et al. 2000). Distribution and size of patches of burned forest also limited the number and interspersion of independent replicates we were able to consider. Other studies that examined effects of salvage logging faced similar design limitations (Saab and Dudley 1998; Hutto and Gallo 2006). Consistency in the results of multiple independent examinations of salvage logging could overcome lack of power associated with individual efforts. We therefore saw value in conducting this study despite the limitations in randomization, sample size, and interspersion.

We examined the response of the vertebrate community to a reduction in fuels on two salvage-logged and two control plots in 2004 and 2005 (two and three years post-fire; Figure 1). We used Geographic Information Systems (GIS) timber data to select control sites with burn severity and commercial timber value similar to pre-logged salvage sites, distributing two control and two salvage plots (45 to 50 ha), each representing continuous patches of salvaged and non-salvaged forested habitat, to improve experimental design (Hurlbert 1984; Underwood 1997). The salvage areas were mechanically logged in summer 2003. All trees >25 cm DBH with an intact bole and <50% live green crown cover were removed. Trembling Aspen (*Populus tremuloides*) and Green Ash (*Fraxinus pennsylvanica*) were not harvested, and a no-cut buffer of 15.2 m was placed on either side of ephemeral streams to maintain watershed quality.

We used the Minnesota Department of Natural Resources Sample Generator Extension v. 1.1 for ArcView 3.0 to randomly place three point-count stations and one small mammal trap site per plot, positioning point-count stations ≥250 m apart in order to reduce the likelihood of double counting individual cavity-nesting birds (Hutto et al. 1986) (Figure 1). Small mammal trap sites were placed ≥500 m apart, also to maintain sample independence, and all points were positioned ≥50 m from treatment boundaries to avoid collecting data beyond treatment boundaries.

Bird sampling

We conducted 10-minute surveys of cavity-nesting birds from each point-count station from mid-April to 1 July. Point counts were conducted from sunrise to 0900 following standard protocols (Hutto et al. 1986), and an estimated distance of detection was assigned at 10-m intervals from the observer to each bird (Buckland et al. 2001). We excluded from analyses all fly-overs or birds detected >100 m from the observer.

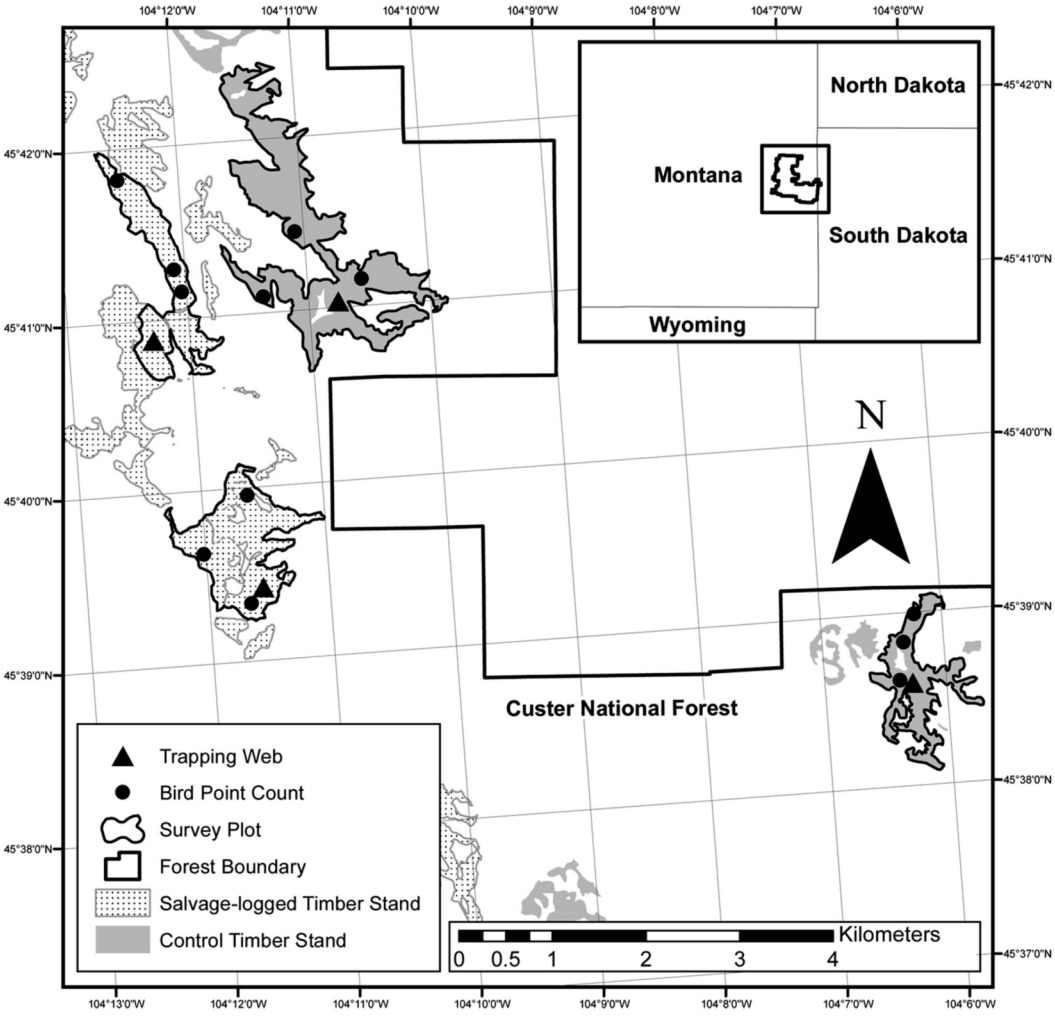


FIGURE 1. Plots and survey points sampled on salvage-logged and control treatments, Custer National Forest, Montana, 2004 and 2005.

Nest searches were conducted from mid-April through 1 July 2004 and 2005. We visited each plot every one to two days and located nests by observing adult behavior and systematically searching for cavities. Target species included Northern Flicker (*Colaptes auratus*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), Hairy Woodpecker (*P. villosus*), Eastern Bluebird (*Sialia sialis*), Mountain Bluebird (*S. currucoides*), and European Starling (*Sturnus vulgaris*). We recorded the location of active nests with a Garmin E-trex Global Positioning System (GPS) receiver and flagged a bearing tree no closer than 30 m away.

We visited each cavity every three days for up to 30 minutes, or until the status of the nest (active or inactive) could be determined by observing adults or nestlings inside the cavity (Martin and Geupel 1993; Kronland 2007). We estimated nest stage according to courtship displays, duration of adult visits to the nest (courtship and egg laying vs. incubation), food deliveries, and nestling vocalizations. We monitored active cavities from the time of location to the completion of the nesting effort. We determined that a nest had failed if predation or usurpation was observed, or if the nest stage was known and inactivity occurred before the estimated fledge date (Martin and Geupel 1993; Kronland 2007). We considered a nest successful if fledglings were observed <20 m from the cavity, or if the fledge date was known and the cavity did not show signs of predation (e.g., enlarged cavity entrance or feathers at base of tree).

Small mammal sampling

We used trapping webs (one for each area) and distance sampling methods to estimate density based

on likelihood of detection rather than area trapped (Anderson et al. 1983). Each web consisted of 12 traplines radiating from a central point at 30° intervals (Jett and Nichols 1987). Trap stations consisted of two Sherman style live traps (8 cm × 8 cm × 25 cm) placed every 20 m along a trapline (l = 130 m) using 100-m tapes, starting 10 m from the center, for 168 traps per web. We covered exposed traps with aluminum flashing, rocks, or bark to provide shade, and we baited all traps with peanut butter. We trapped each web over four consecutive nights in August 2004 and 2005 in random order. Traps were checked daily beginning at sunrise and baited after each check. We applied a uniquely numbered ear tag to each individual (No. 1005-1 Monel, National Band and Tag Company, Newport, Kentucky, USA) and examined capture histories to determine if new animals were being detected at the innermost ring on the final night of trapping. We also examined data *post hoc* to ensure that movement of individuals across trap stations within trapping webs did not occur (Buckland et al. 2001).

We identified the species and sex of each captured animal. We measured tail, body, ear, and hind foot to the nearest mm with a stainless steel 30-cm ruler, and we weighed individuals to the nearest 1 g with a 100-g spring scale. Numerous Deer Mice (*Peromyscus maniculatus*) were captured in 2004 (n = 761) and 2005 (n = 869). We aged Deer Mice as juvenile or adult based on mass after examining the distribution of 20 to 30 individuals aged by pelage in the field (Pearson et al. 2003). We recorded ear tag number and trap location (trapline and ring) within the web before releasing animals at the trap site.

Habitat sampling

We measured habitat characteristics, such as size and density of burned trees, because of their known influence on the distribution and abundance of cavity-nesting birds (Hutto 1995; Murphy and Lehnhausen 1998; Nappi et al. 2003; Smucker et al. 2005). We recorded habitat features on plots of 11.3 m radius at the random point-count locations used to sample cavity-nesting birds in 2005 (Figure 1). Three subplots were arranged 120° from each other and 30 m from a central subplot centered on point-count locations, for a total of four subplots (Martin et al. 1997). Bearing of the first subplot from each point-count location was chosen semi-randomly in the field by multiplying the time in seconds by 6.

We measured DBH of all trees >7.5 cm DBH on each subplot, and we also recorded species and status (alive or dead). We categorized each subplot (1 = least decayed, 7 = most decayed) according to crown condition, bark retention (%), and the severity of the burn (%) (Nappi et al. 2003). In 2005, we also arranged four subplots around each nest tree found on the two replicates per treatment, and we conducted the same habitat measurements to describe these nest sites (salvage: n = 22; control: n = 27). For each nest tree, we recorded species, DBH, crown condition, bark retention (%), and the severity of the burn (%). Nest trees were often used by multiple pairs in a single season, and we considered measurements taken at these sites as independent samples when representing different species. We measured each nest site and nest tree only once if it was reused by the same species (Hutto and Gallo 2006).

Small mammal abundance has been positively correlated with the amount of downed woody debris (Carey and Johnson 1995). We therefore measured downed woody debris on subplots centered on each random point count used to survey cavity-nesting birds (Figure 1). We recorded downed woody debris lying at an angle of less than 45° with the ground that intersected a plane 1.8 m high and extended 11.3 m from the subplot center in a random direction (Brown and Roussopoulos 1974). Mean kg of downed woody debris per ha per point was calculated following methods described in Brown and Roussopoulos (1974).

Statistical analyses

We considered mean number of detections per point across years as an index of individual species abundance between treatments. We used distance sampling methods to estimate density (individuals per ha) of all cavity-nesting birds per treatment because we lacked sufficient observations to fit detection curves to species-specific data. Concern about independence of errors associated with sampling points within replicates over multiple occasions led us to pool data across visits and within replicates. We binned observations into five distance categories (0-20 m, 21-40 m, 41-60 m, 61-80 m, 81-100 m,) and used program DISTANCE 6.0 to fit global detection curves to salvage-logged and control treatment datasets (Buckland et al. 2001; Thomas et al. 2005*). We considered the full combination of uniform, half-normal, and hazard rate key functions with cosine, simple-polynomial, and Hermite-polynomial expansion terms, and we removed models with poor fit according to shape of the detection curve (shape criterion) and χ^2 goodness-of-fit tests (Buckland et al. 2001).

We used Program MARK (White and Burnham 1999*) and methods described by Dinsmore et al. (2002) to estimate nest survival (S). We first constructed a set of candidate models that included the full combination of underlying treatment-, year-, and time-varying effects on S. We then ranked models according to difference in Akaike's Information Criterion for small samples (ΔAIC_c), removed models that contained virtually no Akaike weight ($w_i < 0.01$) and failed to estimate parameters, and calculated a weighted-average survival estimate ($\hat{\bar{S}}$) across the remaining models (Burnham and Anderson 2002). We ended nest observation while some nests were still active, so we used only nests with complete histories (i.e., fledged or failed) to estimate reproductive success (n = 39). Nest survival estimates represent the period of mid-April through 1 July and were calculated for all cavity-

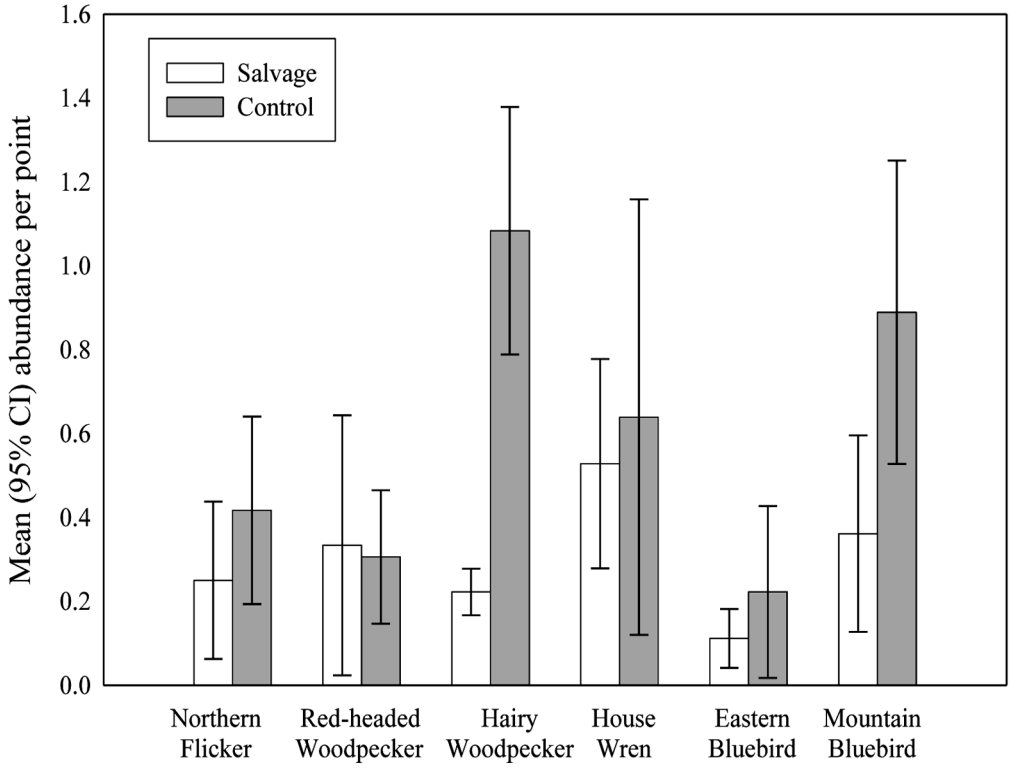


FIGURE 2. Mean (95% CI) abundance of selected cavity-nesting species per point count (pooled across years) on salvage-logged and control treatments, Custer National Forest, Montana, 2004 and 2005.

nesting species combined because sample sizes for individual species were small. We accounted for variation in size of nest-search plots by dividing the number of nests located by plot size to estimate density of active cavity nests (number of nests ha^{-1}).

We used program DISTANCE 6.0 to estimate small mammal density (individuals per ha) from initial captures by fitting detection curves to the full combination of uniform and cosine key functions combined with cosine, simple-polynomial, and Hermite-polynomial expansion terms (Buckland et al. 2001; Thomas et al. 2005*). We did not consider the hazard-rate or negative-exponential key functions because these models have been shown to overestimate density (D) and perform poorly with trapping-web data (Parmenter et al. 2003). We removed models with poor fit according to shape of the detection curve (shape criterion) and χ^2 goodness-of-fit test (Buckland et al. 2001), ranked remaining models based on difference in Akaike's Information Criterion (ΔAIC), assigned Akaike weights, and calculated weighted-average estimates of density ($\hat{D}$) across models (Burnham and Anderson 2002). Variance and 95% confidence intervals were calculated using formulas described in Buckland et al. (2001) and Burnham and Anderson (2002). Data were pooled across sampling occasions at each trapping web, and reported estimates represent the mean density of small mammals across sites within each treatment.

We used nested MANOVA to compare habitat characteristics between treatments at point-count locations (salvage: $n = 6$; control: $n = 6$) and nest sites (salvage: $n = 22$; control: $n = 27$). Variables included mean density of large trees, mean density of small trees, mean crown condition, the mean percentage of bark remaining on the tree bole, and the mean percentage of the tree that had been burned (severity). We also used nested MANOVA to examine difference in mean DBH, the crown condition, the bark remaining (%), and the severity of the burn (%) of individual nest trees on each treatment.

Results

Birds

We recorded the highest mean number of detections per point across years for Hairy Woodpecker ($\bar{x} = 0.65$, SE = 0.21), Mountain Bluebird ($\bar{x} = 0.63$, SE = 0.18), and House Wren (*Troglodytes aedon*) ($\bar{x} = 0.58$, SE = 0.2), followed by Northern Flicker ($\bar{x} = 0.33$, SE = 0.1), Red-headed Woodpecker ($\bar{x} = 0.32$, SE = 0.12), and Eastern Bluebird ($\bar{x} = 0.17$, SE = 0.08).

TABLE 1. Akaike's Information Criterion (AIC_c) ranking, Akaike weight (w_i), number of parameters estimated (K), and log likelihood (−2log(L)) of candidate models examining treatment (g), year (y), and constant (.) effects on nest survival.

Model	AIC_c	ΔAIC_c	w_i	K	−2log(L)
S(g)	137.8717	0	0.4114	2	133.8546
S(.)	138.2474	0.3757	0.3409	1	136.2417
S(y)	140.1623	2.2906	0.1309	2	136.1452
S(g*y)	140.3893	2.5176	0.1168	4	132.3322

White-breasted Nuthatch (*Sitta carolinensis*), American Kestrel (*Falco sparverius*), and Red-breasted Nuthatch (*S. canadensis*) were rarely detected during point counts (mean detections per point <0.1). No cavity-nesting species was found exclusively on either treatment, but mean abundance per point was greater on the control than the salvage treatment for Hairy Woodpecker (i.e., non-overlapping 95% CI, Figure 2).

The uniform key function with cosine expansion term was the only model that fit cavity-nesting bird data according to shape of detection curves and χ^2 goodness-of-fit tests (control: $\chi^2 = 5.7$, df = 3, $P = 0.13$; salvage: $\chi^2 = 0.1$, df = 1, $P = 0.75$). Estimated density of cavity-nesting birds was greater in 2005 ($\hat{D} = 3.83$; 95% CI – 3.5 to 4.11) than 2004 ($\hat{D} = 2.05$; 95% CI – 1.61 to 2.49) on the control treatment, and did not differ between years on the salvage treatment (2004: $\hat{D} = 1.39$; 95% CI – 0.98 to 1.59; 2005: $\hat{D} = 2.33$; 95% CI – 1.5 to 2.72). Density of cavity-nesting birds across both years was greater on the control ($\hat{D} = 2.94$; 95% CI – 2.7 to 3.15) than the salvage ($\hat{D} = 1.86$; 95% CI – 1.24 to 2.17) treatment.

We located 36 nest cavities on the control treatment (2004: $n = 17$; 2005: $n = 19$), representing 48 nest attempts (1.3 attempts per cavity), and 29 nest cavities on the salvage treatment (2004: $n = 15$; 2005: $n = 14$), representing 43 nest attempts (1.5 attempts per cavity). Red-headed Woodpeckers accounted for 34% of located cavities, and were the only species that had higher nest density on the salvage than the control treatment (0.20 nests/ha versus 0.12 nests/ha, respectively, $n = 31$). Other cavity nesters included Hairy Woodpecker (salvage: 0.07 nest/ha; control: 0.14 nests/ha; $n = 20$), Mountain Bluebird (salvage: 0.05 nests/ha; control: 0.11 nest/ha; $n = 15$), Northern Flicker (salvage: 0.06 nests/ha; control: 0.07 nests/ha; $n = 12$), Eastern Bluebird (salvage: 0.03 nests/ha; control: 0.05 nests/ha; $n = 8$), and European Starling (salvage: 0.02 nests/ha; control: 0.03 nests/ha; $n = 5$). Hairy Woodpeckers were known, through direct observation, to have constructed 32% ($n = 21$) of the located nest cavities. Excavator was uncertain for 52% ($n = 34$) of cavities, Red-headed Woodpeckers produced 11% ($n = 7$) of cavities, and 5% ($n = 3$) of cavities were created naturally.

We compared eight candidate models of nest survival, and four models received some support (Table 1). Weighted-average estimates of S between treatments and across years were high (salvage: $\ddot{\hat{S}} = 0.96$, SE = 0.01 (2004), $\hat{S} = 0.97$, SE = 0.01 (2005); control: = 0.98, SE = 0.01 (2004), $\hat{S} = 0.98$, SE = 0.01 (2005)) and strongly overlapped, indicating that differences in nest survival between treatments were negligible. Eight of 19 nest attempts with known histories failed on the salvage treatment, compared to 9 of 20 attempts on the control treatment. Red-headed Woodpeckers were responsible for 11 nest failures (65%) by depredating or usurping nests. House Wrens were observed filling 2 Mountain Bluebird cavities with twigs, and the cause of 5 nest failures remained unknown.

Small mammals

We captured 1630 Deer Mice and 64 Meadow Voles (*Microtus pennsylvanicus*) in 2004 and 2005. Other species that accounted for <1% of captures included Hispid Pocket Mouse (*Chaetodipus hispidus*), Thirteen-lined Ground Squirrel (*Spermophilus tridecemlineatus*), Olive-backed Pocket Mouse (*Perognathus fasciatus*), Western Harvest Mouse (*Reithrodontomys megalotis*), Bushy-tailed Woodrat (*Neotoma cinerea*), White-footed Mouse (*P. leucopus*), and Eastern Cottontail (*Sylvilagus floridanus*).

We estimated density of Deer Mice only, because other species did not comprise a large enough sample to use distance-based models. We derived yearly estimates of density because excessive lumping of detections between 70 m and 110 m in the pooled dataset prevented us from fitting a detection curve. Models consisting of the uniform and half-normal key functions with cosine adjustment had strong support across treatments and years (Table 2). Density of Deer Mice was greater on salvage-logged (2004: $\hat{D} = 24.2$, 95% CI – 18.9 to 30.9; 2005: $\hat{D} = 21.5$, 95% CI – 15.4 to 30.0) than control areas (2004: $\hat{D} = 6.5$, 95% CI – 3.3 to 12.6; 2005: $\hat{D} = 5.8$, 95% CI – 3.5 to 9.5). We categorized Deer Mice weighing ≤17 g as juveniles, based on mass of a subset of individuals that were aged by pelage. The mean ratio of juveniles to adults captured per trapping web was 1:1.3 on salvage-logged and 1:0.8 on control sites.

Habitat

Large trees (>23 cm DBH) were less abundant on salvage-logged ($\bar{x} = 6.64$ trees ha^{-1}, SE = 2.62) than control sites ($\bar{x} = 53.1$ trees ha^{-1}, SE = 8.64), as determined by habitat measurements at point-count locations (Table 3). Microsites surrounding nest trees on

the control treatment also had greater mean density of trees >23 cm DBH (salvage: $\bar{x}$ = 26.45 trees ha^{-1}, SE = 4.97; control: $\bar{x}$ = 62.27 trees ha^{-1}, SE = 3.64) and more bark remaining on the tree bole (salvage: $\bar{x}$ = 5.17, SE = 0.29; control: $\bar{x}$ = 1.95, SE = 0.08) than salvage-logged sites (Table 3).

Nest trees on the salvage had more deteriorated crowns (salvage: $\bar{x}$ = 5.00, SE = 2.37; control: $\bar{x}$ = 2.85, SE = 1.85) and less bark remained on the tree bole (salvage: $\bar{x}$ = 3.86, SE = 2.34; control: $\bar{x}$ = 2.63, SE = 1.62) than nest trees on the control plots (Table 3). Nest attempts on the salvage were most often (61%; n = 15) located in non-logged stands of green Ponderosa Pine, Trembling Aspen, or Green Ash. Only 7% (n = 2) of nest attempts in control areas occurred in those trees.

Mean volume of downed woody debris was greater on the salvage ($\bar{x}$ = 1964 kg/ha, 95% CI – 822 to 3160) than the control treatments ($\bar{x}$ = 460 kg/ha, 95% CI – 189 to 731). Mean number of downed woody debris pieces on the salvage treatment was 5.7 per replicate with a mean volume of 89 cm^3. Mean number of pieces of downed woody debris on the control treatment was 1.9 per replicate with a mean volume of 122 cm^3.

Discussion

Our results were consistent with the growing body of evidence demonstrating that post-fire salvage logging has significant negative effects on cavity-nesting birds, at least two to three years following a wildfire (Hutto 1995; Saab and Dudley 1998; Smucker et al. 2005; Hutto and Gallo 2006). Density of cavity-nesting birds was lower on the salvage than the control treatment. Moreover, few potential nest sites existed on the salvage treatment and occupied cavities were most often located in riparian buffer strips or in stands of green trees and hardwoods not subject to harvest. In contrast, abundance of Deer Mice was greater on salvage-logged than on control plots, and was closely associated with the high amount of downed woody debris on the salvage treatments.

Dense stands of trees >23 cm DBH were also more common on the control than the salvage treatment. The stands provided potential foraging opportunities for primary cavity nesters, such as Hairy Woodpeckers, probably because large trees contain high densities of beetle larvae (Cerambycidae and Buprestidae) (Mannan et al. 1980; Nappi et al. 2003; Hanson and North 2008). Cavity nesters, particularly Hairy Woodpeckers, were infrequently detected during point counts in areas dominated by small trees. At least 18% of the excavations produced by Hairy Woodpeckers were used by other cavity nesters, and the paucity of Hairy Woodpeckers in salvage-logged areas probably had a negative effect on secondary cavity nesters. For example, both Mountain Bluebirds and House Wrens nested less often in the salvage-logged than the control areas. Post-fire logging therefore had both direct and indirect negative effects on the cavity-nesting assemblage.

TABLE 2. Akaike's Information Criterion (AIC_c) ranking, Akaike weight (w_i), number of parameters estimated (K), log likelihood (−2log(L)), and results of χ^2 goodness-of-fit test for candidate models used to estimate population density of Deer Mice on salvage-logged and control treatments, 2004 and 2005.

Treatment	Year	Model	AIC	ΔAIC	w_i	K	−2log(L)	χ^2	df	P
Salvage	2005	Half-normal + cosine	2155.73	0	0.70	4	−1073.87	2.12	2	0.35
		Uniform + cosine	2157.43	1.69	0.30	4	−1074.71	3.83	2	0.15
Salvage	2004	Half-normal + cosine	2281.54	0	0.67	2	−1138.77	7.75	4	0.10
		Uniform + cosine	2282.97	1.44	0.33	3	−1138.49	7.9	3	0.07
Control	2005	Half-normal + cosine	1180.28	0	0.54	3	−587.14	3.96	3	0.27
		Uniform + cosine	1180.56	0.29	0.46	3	−587.28	4.3	3	0.23
Control	2004	Uniform + cosine	354.95	0	0.24	2	−175.48	1.33	2	0.52
		Uniform + Hermite polynomial	355.2	0.25	0.21	2	−175.6	1.65	2	0.44
		Uniform + simple polynomial	355.2	0.25	0.21	2	−175.6	1.65	2	0.44
		Half-normal + cosine	356.22	1.27	0.13	3	−175.11	0.58	1	0.45
		Half-normal + Hermite polynomial	256.41	1.46	0.11	3	−175.21	0.77	1	0.38
		Half-normal + simple polynomial	356.56	1.61	0.11	3	−175.28	0.92	1	0.34

The distribution and abundance of breeding habitat that remained after salvage logging differed between treatments and affected nest site use. Stands of high tree density on salvage treatments existed only in non-harvested areas. Non-logged areas represented approximately 15% of the total area on salvage treatments, yet they contained 71% of nest cavities. In contrast, most nest cavities on the control were in habitats that would have been logged (e.g., stands of large dead Ponderosa Pine). Trembling Aspen and Green Ash accounted for only 6% of nest attempts on the control while representing 40% of attempts on the salvage. If Trembling Aspen and Green Ash had been preferred breeding habitat, the number of nest attempts in these habitats would probably have been similar between treatments. Regardless of treatment, cavity nesters were found most often in areas with high densities of large trees, habitat features considered important legacies in burned forests (Franklin et al. 2000; Hutto 2006).

Post-fire salvage logging did not reduce reproductive success of cavity-nesting birds on our study area in southeastern Montana, despite negative effects on bird abundance. To our knowledge, only three other studies have reported reproductive information while investigating effects of post-fire logging on cavity-nesting birds. One study found no effect and two studies found reduced reproductive success, but only for Hairy and Lewis's woodpeckers (reviewed by McIver and Starr 2001; Saab et al. 2011). The small number of existing studies on post-fire effects reflects the general pattern reported by Sallabanks et al. (2000), where only 13% of studies investigating effects of silviculture on birds collected demographic data. Clearly, data on reproductive success and survival remain a research priority (Kotliar et al. 2002).

Density of Deer Mice was greater on salvage than control plots. This reflected the four-fold difference in volume of downed woody debris across treatments. Mechanical removal of trees during logging led to an incidental and rapid accumulation of downed branches, debris used by small mammals for breeding, foraging, and predator avoidance (Harmon et al. 1986; Ucitel et al. 2003). Dead trees on the control remained standing two to three years post-fire and had not yet replaced downed woody debris consumed during the fire. Debris on the control would be expected to continue to accumulate as trees deteriorated (Tinker and Knight 2001; Russell et al. 2006), whereas the amount of debris on the salvage treatment had probably reached its maximum because most standing dead trees had been harvested.

Although Deer Mice responded favorably to the accumulation of downed woody debris on the salvage treatment, density of small mammals may not reflect habitat quality if dominant individuals exclude subordinates from the best habitats (Van Horne 1983; Rodenhouse et al. 1997). Adult Deer Mice defend territories against non-reproducing juveniles (Long and Mont-

TABLE 3. Results of Multivariate Analysis of Variance (MANOVA) tests comparing habitat characteristics at point-count locations in salvage-logged and control plots and at nest sites on salvage-logged and control plots, and comparing nest-tree characteristics on salvage-logged and control treatments, Custer National Forest, Montana, 2004 and 2005.

	Point counts salvage: $n = 6$; control: $n = 6$			Nest sites salvage: $n = 22$; control: $n = 27$			Nest trees salvage: $n = 22$; control: $n = 27$		
Habitat characteristic	F	df	P	F	df	P	F	df	P
Trees 10–23 cm DBH ha^{-1}	0.003	1,8	0.958	1.576	1,45	0.216	NA	NA	NA
Trees >23 cm DBH ha^{-1}	22.519	1,8	0.001	38.761	1,45	<0.001	NA	NA	NA
$\bar{x}$ tree DBH (cm)	NA	NA	NA	NA	NA	NA	3.267	1,45	0.077
Crown condition [a]	0.096	1,8	0.764	3.111	1,45	0.085	12.434	1,45	0.001
Bark retention [b]	0.183	1,8	0.68	163.139	1,45	<0.001	5.28	1,45	0.026
Burn severity [c]	0.019	1,8	0.894	0.748	1,45	0.392	2.987	1,45	0.091

[a] Relative amount of twigs, branches, and limbs on tree crown (1 = intact crown, 7 = broken top).
[b] Percentage of bark remaining on tree bole (1 = 100%, 7 = no bark).
[c] Percentage of tree burned (1 = unburned, 7 = completely burned).

gomerie 2006), so a large juvenile to adult ratio would indicate low-quality habitat. However, adults were more abundant than juveniles on the salvage treatment where densities of Deer Mice were highest. This supports the conclusion that density reflects high-quality habitat. Information regarding individual reproductive status (not recorded in this study) might have provided further insight into habitat quality between treatments for Deer Mouse.

Despite temporarily benefiting Deer Mice populations, the rapid accumulation of downed woody debris may have increased the short-term risk of wildfire because woody ground debris is a primary determinant of fire behavior (Donato et al. 2006). One of the goals of salvage logging is to reduce the probability of large wildfires, and failure to achieve fire management objectives is particularly important in southeastern Montana because of the historically high frequency of wildfires (Brown and Hull Sieg 1996). The risk of future fire could be reduced by creating heterogeneous landscapes of logged and non-logged areas, where woody debris would accumulate and deteriorate at different rates, thus creating fuel breaks. Retaining some intact stands of large trees (>23 cm DBH) could also mitigate the negative effects of salvage logging on cavity nesters.

Current federal and state guidelines recommend retaining 6 to 10 dead trees per hectare (Hutto 2006). However, salvage prescriptions that retain a specific number of trees per hectare or uniformly remove a specific size class of tree (e.g., >25 cm DBH) accelerate post-fire succession and create homogeneous landscapes unsuitable for many cavity-nesting birds (Hutto 1995; Kotliar et al. 2002; Hutto 2006; Schmiegelow et al. 2006). Conserving intact stands of large trees would create heterogeneous landscapes that resemble natural post-fire conditions and harbor many of the legacies deemed important in such landscapes (Franklin et al. 2000). Although further investigation is needed to determine the size and distribution of burned tree stands that should be retained, conditions resulting from salvage logging in this study provided lower quality habitat than unlogged areas.

Acknowledgements

We thank T. Whitford for initiating and supporting the study. B. Haase contributed field assistance in 2005, and the Sioux Ranger District provided housing during field seasons. S. Carson and A. Messer provided small mammal traps and helped with species identification. Trapping and marking of small mammals was approved by the Institutional Animal Care and Use Committee at St. Cloud State University, in cooperation with Montana Fish, Wildlife and Parks. J. Arriagada and L. Onyiah commented on the draft manuscript, and J. Marzluff provided advice on experimental design and data analysis. We thank D. Nagorsen and an anonymous reviewer for helpful comments on the final version. Funding was provided by the U.S. Forest Service, Custer National Forest (Agreement No. 04-PA-11010803-008) and St. Cloud State University.

Documents Cited (marked * in text)

Federal Register. 2003. Notices. 68: 44598-44608.

National Oceanic and Atmospheric Administration. 2005. Climatological data publications. http://www7.ncdc.noaa.gov/IPS/cd/cd.html. (Last accessed March 28, 2006).

Thomas, L., J. L. Laake, S. Stringberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, J. R. B. Bishop, and **T. A. Marques.** 2005. Distance 6.0. Research Unit for Wildlife Population Assessment, University of St. Andrews, U.K. Downloaded August 2010.

White, G. C., and **K. P. Burnham.** 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement: 120-138. Downloaded September 2008.

Literature Cited

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Covelo, California.

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Haffman, and **J. T. Klingle.** 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Application 12: 1418-1433.

Anderson, D. R., K. P. Burnham, G. C. White, and **D. L. Otis.** 1983. Density estimation of small-mammal populations using a trapping web and distance sampling methods. Ecology 64: 674-680.

Arno, S. F., and **S. Allison-Bunnell.** 2002. Flames in our forest. Island Press, Washington, D.C.

Beschta, R. L, J. J. Rhodes, J. B. Kauffman, R. E. Gresswell, G. W. Minshall, J. R. Karr, D. A. Perry, F. R. Hauer, and **C. A. Frissell.** 2004. Post fire management on forested public lands of the western United States. Conservation Biology 18: 957-967.

Brown, J. K., and **P. J. Roussopoulos.** 1974. Eliminating biases in the planar intersect method for sampling small fuel volumes. Forest Science 20: 350-356.

Brown, P. M., and **C. Hull Sieg.** 1996. Fire history in interior ponderosa pine communities of the Black Hills, South Dakota, USA. International Journal of Wildland Fire 6: 97-105.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and **L. Thomas.** 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York.

Burnham, K. P., and **D. R. Anderson.** 2002. Model selection and multimodel inference: a practical information-theoretical approach. Second edition. Springer Science and Business Media, Inc., New York.

Cahall, R. E., and **J. P. Hayes.** 2009. Influences of postfire salvage logging on forest birds in the eastern Cascades, Oregon, USA. Forest Ecology and Management 257: 1119-1128.

Carey, A. B., and **M. L. Johnson.** 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological Applications 5: 336-352.

Castro, J., G. Moreno-Rueda, and **J. A. Hodar.** 2010. Experimental test of postfire management in pine forests: impact of salvage logging versus partial cutting and non-

intervention on bird-species assemblages. Conservation Biology 24: 810-819.

Converse, S. J., G. C. White, and **W. M. Block.** 2006. Small mammal responses to thinning and wildlife in ponderosa pine-dominated forests of the southwestern United States. Journal of Wildlife Management 70: 1711-1722.

Covert-Bratland, K. A., W. M. Block, and **T. C. Theimer.** 2006. Hairy woodpecker winter ecology in ponderosa pine forests representing different ages since wildlife. Journal of Wildlife Management 70: 1379-1392.

Covington, W. W., and **M. M. Moore.** 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. Journal of Forestry 92: 39-47.

Dinsmore, S. J., G. C. White, and **F. L. Knopf.** 2002. Advanced techniques for modeling avian nest survival. Ecology 83: 3476-3488.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and **B. E. Law.** 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science 311: 352.

Fisher, J. T., and **L. Wilkinson.** 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review 35: 51-81.

Franklin, J. F., D. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnuson, D. A. Perry, R. Waide, and **D. Foster.** 2000. Threads of continuity. Conservation Biology in Practice 1: 8-16.

Franklin, T. M., C. A. Burke, and **R. S. Fritsky.** 2003. Restoring the Kodiak National Wildlife Refuge: turning tragedy into conservation achievement. Wildlife Society Bulletin 31: 560-564.

Greene, D. F., S. Gauthier, J. Noël, M. Rousseau, and **Y. Bergeron.** 2006. A field experiment to determine the effect of postfire salvage on seedbeds and tree regeneration. Frontiers in Ecology and the Environment 4: 69-74.

Haggard, M., and **W. L. Gaines.** 2001. Effects of stand-replacement fire and salvage logging on a cavity-nesting bird community in eastern Cascades, Washington. Northwest Science 75: 387-396.

Hanson, C. T., and **M. P. North.** 2008. Postfire woodpecker foraging in salvage-logged and unlogged forests of the Sierra Nevada. Condor 110: 777-782.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedel, G. W. Liendaemper, K. Cromack Jr., and **K. W. Cummins.** 1986. Ecology of coarse woody debris in temperate ecosystems. Advanced Ecological Research 15: 133-302.

Hurlbert, S. H. 1984. Psuedoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. Conservation Biology 9: 1041-1058.

Hutto, R. L. 2006. Toward meaningful snag-management guidelines for post fire salvage logging in North American conifer forests. Conservation Biology 20: 984-993.

Hutto, R. L., and **S. M. Gallo.** 2006. The effects of postfire salvage logging on cavity-nesting birds. Condor 108: 817-831.

Hutto, R. L., S. M. Pletschet, and **P. Hendricks.** 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103: 593-602.

Jett, D. A., and **J. D. Nichols.** 1987. A field comparison of nested grid and trapping web density estimators. Journal of Mammalogy 68: 888-892.

Kotliar, N. B., S. J. Hejl, R. L. Hutto, V. A. Saab, C. P. Melcher, and **M. E. McFadzen.** 2002. Effects of fire and postfire salvage logging on avian communities in conifer-dominated forests of the western United States. Studies in Avian Biology 25: 49-64.

Kronland, W. J. 2007. Nest usurpation by red-headed woodpeckers in southeastern Montana. Wilson Journal of Ornithology 119: 486-489.

Lindenmayer, D. B., and **R. F. Noss.** 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology 20: 949-958.

Loeb, S. C. 1999. Responses of small mammals to coarse woody debris in a Southeastern pine forest. Journal of Mammalogy 80: 460-471.

Long, T. A. F., and **R. Montgomerie.** 2006. Ejaculate investment in a promiscuous rodent, *Peromyscus maniculatus*: effects of population density and social role. Evolutionary Ecology Research 8: 345-356.

Mannan, R. W., E. C. Meslow, and **H. M. Wight.** 1980. Use of snags by birds in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44: 787-797.

Martin, T. E., and **G. R. Geupel.** 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64: 507-519.

Martin, T. E., C. R. Pain, C. J. Conway, W. M. Hochachka, P. Allen, and **W. Jenkins.** 1997. BBIRD field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, USA.

Marzluff, J. M., M. G. Raphael, and **R. Sallabanks.** 2000. Understanding the effects of forest management on avian species. Wildlife Society Bulletin 28: 1132-1143.

McIver, J. D., and **L. Starr.** 2001. A literature review on the environmental effects of post fire logging. Western Journal of Applied Forestry 16: 159-168.

Morissette, J. L., T. P. Cobb, R. M. Brigham, and **P. C. James.** 2002. The response of boreal forest songbird communities to fire and postfire harvesting. Canadian Journal of Forest Research 32: 2169-2183.

Murphy, E. G., and **W. H. Lehnhausen.** 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. Journal of Wildlife Management 62: 1359-1372.

Nappi, A., P. Drapeau, J-F. Girouz, and **J-P. L. Savard.** 2003. Snag use by foraging black-backed woodpeckers (*Picoides arcticus*) in a recently burned eastern boreal forest. Auk 120: 505-511.

Parmenter, R. R., T. Y. Yates, D. R. Anderson, K. P. Burnham, J. L. Dunnum, A. B. Franklin, M. T. Friggens, B. C. Lubow, M. Miller, G. S. Olson, C. A. Parmenter, J. Pollard, E. Rexstad, T. M. Shenk, T. R. Stanley, and **G. C. White.** 2003. Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. Ecological Monographs 73: 1-26.

Pearson, D. D., Y. K. Ortega, and **L. F. Ruggiero.** 2003. Trap-induced mass declines in small mammals: mass as a population index. Journal of Wildlife Management 67: 684-691.

Pope, T. L., W. M. Block, and **P. Beier.** 2009. Prescribed fire effects on wintering, bark-foraging birds in northern Arizona. Journal of Wildlife Management 73: 695-700.

Rodenhouse, N. L., T. W. Sherry, and **R. T. Holmes.** 1997. Site-dependent regulation of population size: a new synthesis. Ecology 78: 2025-2042.

Russell, R. E., V. A. Saab, J. A. Dudley, and **J. J. Rotella.** 2006. Snag longevity in relation to wildfire and postfire salvage logging. Forest Ecology and Management 232: 179-187.

Saab, V. A., and **J. G. Dudley.** 1998. Responses of cavity-nesting birds to stand-replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. U.S. Forest Service, Rocky Mountain Research Station, RMRS-RS-11.

Saab, V. A., and **K. T. Vierling.** 2001. Reproductive success of Lewis's woodpecker in burned pine and cottonwood riparian forests. Condor 103: 491-501.

Saab, V. A., J. Dudley, and **W. L. Thompson.** 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor 106: 20-36.

Saab, V. A., R. E. Russell, J. Rotella, and **J. G. Dudley.** 2011. Modeling nest survival of cavity-nesting birds in relation to postfire salvage logging. Journal of Wildlife Management 75: 794-804.

Sallabanks, R., E. B. Arnett, and **J. M. Marzluff.** 2000. An evaluation of research on the effects of timber harvest on bird populations. Wildlife Society Bulletin 28: 1144-1155.

Schmiegelow, F. K. A., D.P. Stepnisky, C.A. Stambaugh, and **M. Koivula.** 2006. Reconciling salvage logging of boreal forests with a natural-disturbance management model. Conservation Biology 20: 971-983.

Smucker, K. M., R. L. Hutto, and **B. M. Steele.** 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications 15: 1535-1549.

Tinker, D. B., and **D. H. Knight.** 2001. Temporal and spatial dynamics of coarse woody debris in harvested and unharvested lodgepole pine forests. Ecological Modeling 141: 125-149.

Turner, M. G., W. H. Romme, and **D. B. Tinker.** 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and the Environment 1: 351-358.

Ucitel, D., D. P. Christian, and **J. M. Granham.** 2003. Vole use of coarse woody debris and implications for habitat and fuel management. Journal of Wildlife Management 67: 65-72.

Underwood, A. J. 1997. Experiments in Ecology. Cambridge University Press, New York.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893-901.

Received 4 September 2011
Accepted 23 December 2011

Check for updates

Received: 16 October 2023 | Accepted: 26 August 2024

DOI: 10.1002/pan3.10733

PEOPLE AND NATURE | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Informing proactive wildfire management that benefits vulnerable communities and ecological values

L. Mae Lacey[1] | Justin P. Suraci[1] | Caitlin E. Littlefield[1] | Blake S. Busse[2] | Brett G. Dickson[1]

[1]Conservation Science Partners, Inc., Truckee, California, USA

[2]The Pew Charitable Trusts, Washington, District of Colombia, USA

Correspondence
L. Mae Lacey
Email: mae@csp-inc.org

Funding information
Pew Charitable Trusts

Handling Editor: Ricardo Correia

Abstract

1. In response to mounting wildfire risks, land managers across the country will need to dramatically increase proactive wildfire management (e.g. fuel and forest health treatments). While human communities vary widely in their vulnerability to the impacts of fire, these discrepancies have rarely informed prioritizations for wildfire mitigation treatments. The ecological values and ecosystem services provided by forests have also typically been secondary considerations.
2. To identify locations across the conterminous US where proactive wildfire management is likely to be effective at reducing wildfire severity and to yield co-benefits for vulnerable communities and ecological values, we developed a set of spatial models that estimated wildfire mitigation potential (based on wildfire hazard and biophysical forest conditions) and either included or excluded information on vulnerable human communities, ecological values and ecosystem services. We then compared areas with high wildfire mitigation potential alone to refined 'focal areas' that overlaid social and ecological considerations to quantify the potential benefits of targeted wildfire mitigation treatments.
3. Inclusion of social and ecological considerations substantially increased representation of vulnerable communities and ecological values in focal areas relative to the model that considered wildfire alone. For instance, restoration in these refined focal areas would cover 28% greater imperilled species richness, 45% greater water importance and 26% more families falling below the poverty line.
4. By examining overlap between our refined focal areas and U.S. Forest Service top ranked firesheds (a prominent existing wildfire prioritization scheme), we show that our analysis can help to target wildfire mitigation efforts within firesheds to areas with particularly high social vulnerability and/or ecological value, providing an important compliment to a prioritization scheme based largely on risk to structures.
5. Our results highlight the importance of considering ecological and social factors when implementing wildfire mitigation treatments and provide actionable guidance for integrating these considerations into existing prioritizations.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.
© 2024 The Author(s). *People and Nature* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

KEYWORDS
ecosystem services, fire ecology, fuel treatments, landscape planning, restoration, social vulnerability, spatial prioritization, wildfire

1 | BACKGROUND

Forest fire activity has been on the rise due to fire suppression, changing climatic conditions, exclusion of indigenous burning, human-caused ignitions and tree mortality caused by the compounding stressors of climate change, pests and disease (Balch et al., 2017; Hessburg et al., 2021; Parks & Abatzoglou, 2020). Simultaneously, conversion of forested areas to development has expanded the wildland-urban interface (WUI), enhancing the threat of fire to human infrastructure, lives and livelihoods (Balch et al., 2017; Mietkiewicz et al., 2020; Radeloff et al., 2018).

Increased wildfire activity has the potential to impact not only human communities, but also critical ecological values and ecosystem services. While fire is indeed a natural component of a healthy landscape, an increasing number of wildfires are growing to atypical sizes with larger areas burning at high severity (Parks & Abatzoglou, 2020). These 'megafires' can alter or impede post-fire recruitment and ecosystem recovery, even in systems well-adapted to natural fire regimes (Brown & Johnstone, 2012; Davis et al., 2018). A reduction in fire severity could better enable ecosystem recovery, especially as warmer and drier conditions complicate tree regeneration (Davis et al., 2023).

Fuel treatments, including prescribed fire and mechanical thinning, can reduce fire severity with the potential to support biodiversity, habitat quality and vegetation diversity (Hessburg et al., 2021; Jones et al., 2022; Stephens et al., 2024). They have also been shown to decrease the overall cost of future wildfire response, reduce the likelihood of structure loss or risk to firefighters, and maintain beneficial ecosystem services (Bayham et al., 2022). As a result, fuel treatments have been the dominant method of mitigating wildfire risk. For instance, the Biden Administration has committed $1.5 billion to reducing wildfire risk, including safeguarding communities, via proactive wildfire management such as fuel treatments on both federal and non-federal lands (The White House, 2022a, 2022b; U.S. Department of the Interior, 2022). Likewise, the U.S. Forest Service (USFS) 'Confronting the Wildfire Crisis' strategy commits to an 'all-lands' approach to treating up to 8.1-million ha (20-million acres) of national forest (NF) lands and 12.1-million ha (30-million acres) of other federal, state, tribal and private lands over the next 10 years with the goal of protecting human communities and improving forest health and resilience (U.S. Department of Agriculture, 2022; USFS, 2023).

Our goal with this analysis was to identify places where the proactive application of fuel and forest health treatments (hereafter 'restoration', but see Stephens et al., 2020) is likely to be effective in reducing wildfire risk while also directing restoration efforts towards socially vulnerable communities and areas of particularly high ecological value. Typically, restoration is directed towards areas biophysically prone to wildfire and where risk to structures is relatively high (i.e. the WUI); however, research has shown that this approach does not always distribute resources to the communities with the greatest need. In some instances, these resources have even disproportionately gone to more affluent communities at a direct cost to more vulnerable communities (Evans et al., 2007; Morton, 2003; Poudyal et al., 2012; Program for Watershed and Community Health, 2003).

Indeed, communities considered 'socially vulnerable' are less likely to receive or engage in restoration efforts, even when they are at a high wildfire risk (Gaither et al., 2011; Ojerio, 2008; Ojerio et al., 2011; Poudyal et al., 2012). Social vulnerability describes "the ability of individuals and communities to plan for, respond to, and recover from natural disasters" (Ojerio et al., 2011, p.29). The concept centres on a lack of (or limited) access to political power, representation, physical and intellectual resources, social capital, physical health or ability, and infrastructure and is often measured as an integration of contributing factors (Cutter et al., 2003; Cutter & Finch, 2000). For example, in the context of wildfire, prevalence of respiratory conditions including chronic obstructive pulmonary disease (COPD) and asthma are highly relevant due to potential smoke exposure. Likewise, income level reflects the ability to pay for restoration efforts (e.g. brush removal) or to recover from loss of property or livelihood. Discrepancies in social vulnerability necessitate the development of more equitable risk mitigation measures.

The ecological value of forest ecosystems and the services they provide to human communities are also frequently left out of restoration prioritizations. For example, the capacity of forests to support habitat and connectivity (Thompson et al., 2021) as well as provide clean drinking water and carbon storage (Thom & Seidl, 2016; Vukomanovic & Steelman, 2019) can be threatened by wildfire and should be considered in restoration prioritizations (Chamberlain & Jones, 2023). Moving forward, it will be necessary to focus restoration efforts on locations with the greatest restoration efficacy and broader social and ecological co-benefits (Gaither et al., 2011; Poudyal et al., 2012; Wigtil et al., 2016).

To date, restoration prioritizations, such as the USFS Fireshed Registry (Ager et al., 2021), have largely centred on risk to infrastructure, particularly in the WUI. Our research was thus motivated by the need for an intentional shift towards more equitable restoration priorities. Specifically, our research objective was to identify places where restoration is likely to be effective in both reducing subsequent fire severity and in safeguarding socially vulnerable communities as well as important ecological values and services. We developed a tool that highlights the potential co-benefits of restoration for vulnerable communities and ecosystems and that can be used to further refine existing prioritizations (e.g. firesheds)

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

following an 'all-lands' approach across the conterminous U.S. (CONUS). We then compared a spatial prioritization that included only 'wildfire mitigation potential' (i.e. the potential for restoration to effectively mitigate future wildfire behaviour) with a model that integrated wildfire mitigation potential with social and ecological considerations. This allowed us to quantify the potential benefits of targeted restoration efforts for vulnerable communities and ecosystems. Rather than attempting to highlight exact locations where fire management activities should occur, our intent was to identify landscapes that can serve as starting points for consideration when the USFS or other land management agencies are determining which areas to target for restoration. Once landscapes have been identified, collaboration with local communities, tribes, and stakeholders will be necessary to guide the design and implementation of these projects on the ground.

2 | METHODS

To achieve our research objective, we developed two composite indices (Burgass et al., 2017; Greco et al., 2019; Wiréhn et al., 2015; see Appendix S1) describing (i) the potential to reduce future wildfire severity (hereafter, the 'wildfire mitigation potential index' or WMPI) and (ii) social vulnerability of communities and ecological values and services that are potentially at risk from wildfire (hereafter, the 'social-eco index' or SEI). The WMPI was derived from existing spatial indicators describing forest condition and wildfire hazard potential. To derive the SEI, we developed and combined three sub-indices, each describing a distinct category of factors potentially at risk from wildfire (social vulnerability, ecological value, ecosystem services; Figure 1) and each composed of a unique set of social or ecological indicators. We then overlaid the WMPI and SEI to identify areas for restoration that achieve multiple objectives (Figure 1). Spatial data used to derive each of these indicators are described below.

The method of combining indicators to derive a particular index (or sub-index) varied between models, drawing on the most appropriate approach for a particular index type. Most of the indices described below were derived as the weighted linear sum of the underlying indicator values such that

$$y_i = \sum_{j=1}^{J} x_{ij} w_j \quad (1)$$

where y_i is the value of the index at location i, x_{ij} is the (standardized) value of indicator j at location i, and w_j is the weight applied to indicator j. We utilized a recently developed method for deriving indicator weights, w_j, such that each indicator had a predefined influence on the resulting index value, y_i while accounting for correlations among indicators (Becker et al., 2017; Paruolo et al., 2013; Suraci, Farwell, et al., 2023; see also Appendix). Analyses were conducted in R (v4.2.1), ArcGIS Pro (v3.0.0) and Google Earth Engine (GEE; Gorelick et al., 2017) via the Earth Engine Python application programming interface. Final model layers (indices and sub-indices) were resampled to 90-m resolution in GEE.

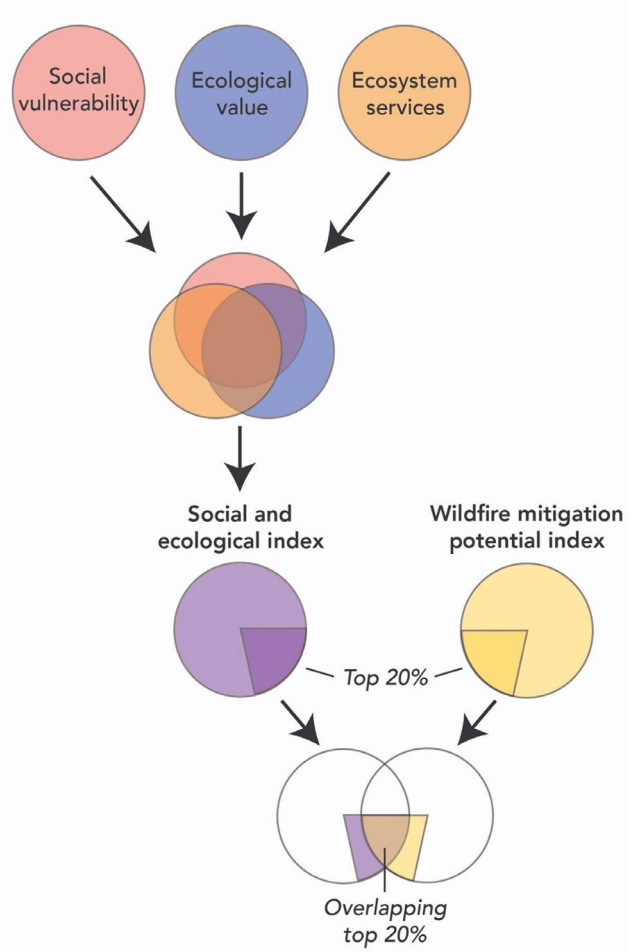


FIGURE 1 Workflow for identifying areas where restoration has the potential to both reduce subsequent fire severity and to safeguard vulnerable communities and important ecological values and services. Spatial sub-indices defining social vulnerability, ecological value and ecosystem services were combined into a 'social and ecological index'. Pixels of this index and a separately derived 'wildfire mitigation potential index' were thresholded to identify areas falling in the top 20% for each index within each U.S. Forest Service administrative region (USFS regions shown in Figure 2). Locations where the top 20% of both indices overlapped were identified as targets, or 'focal areas', for restoration.

2.1 | Wildfire mitigation potential index

The WMPI integrates forest conditions and wildfire hazard potential to suggest where restoration may be most effective from a biophysical perspective and may therefore moderate future wildfire behaviour. Specifically, we included the following datasets in this index (see also Appendix S1):

25783814, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

- *Wildfire hazard potential* (*WHP*) quantifies the relative potential that a wildfire will occur at a given location and that the fire will be difficult to control through standard suppression techniques (Dillon et al., 2015; Scott et al., 2020).
- *Percent low-severity fire* (*PLS*) estimates the historical proportion of low-severity fire relative to mixed- and high-severity fires prior to European settlement (LANDFIRE, 2020).
- *Vegetation departure* (*VDep*) depicts the degree to which present-day vegetation is different from historical conditions prior to European settlement (LANDFIRE, 2020).

We included WHP to ensure that our model focused on areas most likely to experience difficult-to-control wildfire. We included VDep to capture locations where human actions have drawn forests far from the conditions historically maintained by natural dynamics. For example, widespread fire suppression has led to substantial changes in forest composition, structure and fuel accumulation in many contexts (Hagmann et al., 2021). Lastly, we included PLS because high VDep cannot independently discern where restoration may be most beneficial. High VDep may occur in locations such as tree plantations in moist climates (e.g. the southeastern U.S.) where vegetation departures are substantial but where restoration is not known to reduce fire severity. Accordingly, areas that historically experienced high degrees of low-severity fire (high PLS) are elevated in our index. These locations tend to experience arid conditions conducive to frequent burning and have historically not had high accumulations of fuel, but fire suppression has interrupted that dynamic (e.g. ponderosa pine or oak woodlands in the western U.S.). Ample evidence points to the efficacy of restoration in moderating fire behaviour in such contexts (e.g. Jones et al., 2022), whereas there is limited evidence that restoration is effective in forest types that historically experienced less low-severity fire and more mixed or high-severity fire (Halofsky et al., 2018; Schoennagel et al., 2004).

We derived the WMPI as the weighted linear sum (see above) of WHP, VDep and PLS, with each layer rescaled to 0–100. We used the optimization procedure described in Appendix S1 to identify the set of weights that lead to relative influence of 2:1:1 for WHP, VDep and PLS, respectively, on the final index values (i.e. WHP was twice as influential as VDep and PLS in determining the index result for a given pixel). We chose this set of relative influence values to ensure that our index highlighted areas with relatively high probability of actually experiencing a wildfire.

2.2 | Social and ecological index

The SEI was derived by combining three separate sub-indices, each describing a set of characteristics or values that may be threatened *if an uncharacteristic wildfire were to occur* and was designed to be agnostic to the actual likelihood of wildfire in a given location. It is important to note that these sub-indices do not necessarily quantify the expected loss of a given value *to* wildfire (e.g. amount of forest carbon or degree of connectivity potentially lost to fire), but rather are meant to highlight locations where these values are high and where restoration may jointly protect these values and yield substantial co-benefits as a result.

2.2.1 | Social vulnerability sub-index

The social vulnerability sub-index identifies places where communities may be particularly impacted by, or least able to recover from, wildfire due to factors such as income, prevalence of health issues, or other demographic characteristics. We focused on census tracts as the spatial unit of analysis given data availability and the common usage of census tract-level data in deriving similar indices (e.g. Davies et al., 2018). We reviewed indicators across 14 existing indices of social vulnerability and selected indicators most salient to wildfire (see Appendix S1). The final set of indicators encompassed nine themes (Table 1). All indicators, with the exception of median household income, were provided as a percentage of the census tract population or an otherwise regionally adjusted value to reduce potential bias associated with regional variation.

These 22 indicators were combined in a principal components analysis (PCA) using the 'factoextra' package in R to reduce the dimensionality of the indicator set and account for correlation among them. Any missing indicator values at individual census tracts (3% of the total dataset) were imputed using a regularized iterative PCA algorithm in the R package 'missMDA' (see Appendix S1). PCA scores for all census tracts with imputed values were then predicted from the original PCA run only on complete records.

We used the inverse of the first principal component (PC1) as our metric of social vulnerability (i.e. social vulnerability $= -1 \times$ PC1). Our intent with the PCA was not to explain as much variance as possible (PC1 explained 27.6% of variance across all indicators), but rather to reduce the dimensionality of a large set of indicators. In our view, the inverse of PC1 serves this purpose well in that all social indicators vary with our social vulnerability metric in an intuitive direction. For instance poverty, unemployment and minority status all increase with our vulnerability index while income level, broadband access and voter turnout all decrease (see Figure S1.1). Incorporating PC2 into the index would indeed have explained more of the overall variation in the set of social indicators, but the PC2 axis did not map clearly onto social vulnerability (see Appendix S1). We acknowledge the limitations associated with PCA, namely its assumption that linearity can be established between variables. However, given our primary goals of reducing data dimensionality and deriving a continuous metric of social vulnerability, PCA remained the most readily interpretable approach in this context and is consistent with similar analyses (e.g. Wigtil et al., 2016). We calculated social vulnerability values for each census tract, and tracts were then rasterized at a 90-m resolution for subsequent analysis.

25783814, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 The 22 indicators of social vulnerability in the context of wildfire used to represent the social vulnerability sub-index, organized by theme.

Theme	Dataset
Education level	% of the total population (25+ years old) without a high school diploma[a]
Employment status	% of the civilian labour force (16+ years old) currently unemployed[a]
Health status and access to care	Prevalence (%) of COPD[b]
	Prevalence (%) of asthma[b]
	% of the total population with a disability[b]
	% of the total population without health insurance[b]
	Number of ICU beds available per 100k people[c]
Living situation	% of housing units that are mobile homes[a]
	% of crowded housing (i.e. housing units with more than one occupant per room)[a]
	% of households with children under 18 that are headed by a single parent[a]
	% of the total population living within institutionalized group quarters[a]
	% of the total population living in nursing and skilled nursing facilities[d]
Income	% of families whose income is below the poverty line[a]
	Median household income[a]
Cost of living	Median gross rent as a percentage of income[a]
Demographics	% of the total population (5+ years old) that speaks limited English[a]
	% of the total population with minority status[a]
Community engagement	Voter turnout in the 2020 presidential election (as a percentage of the total population over 18)[e]
Quality of life	% of households with a broadband subscription[a]
	% of households with phone service[a]
	% of households without complete plumbing[a]
	% of housing units without a vehicle[a]

[a]Manson et al. (2022).
[b]Centers for Disease Control and Prevention (2021).
[c]Schulte et al. (2020).
[d]Department of Homeland Security (2022).
[e]Atlas of U.S. Presidential Elections (2022).

2.2.2 | Ecological value sub-index

The ecological value sub-index estimates the potential for a location to contribute to important ecological processes such as supporting biodiversity, connectivity and climate adaptation. The set of indicators included the following (see also Appendix S1):

- *Climate accessibility* estimates the degree to which the local climate conditions currently experienced by a species will be accessible in the future (by the year 2055; higher climate accessibility = greater ability of species to adapt to climate change via movement). This metric is effectively the inverse of climate velocity (Hamann et al., 2015).
- *Imperilled species richness* estimates the number of species of conservation concern likely to occur in a given area (NatureServe, 2020).
- *Vertebrate species richness* estimates the number of terrestrial, non-volant species likely to occur in a given area (Conservation Science Partners, 2021).
- *Ecological intactness* estimates the degree to which a given location remains in a natural state (i.e. little to no influence from contemporary human land use changes; Parrish et al., 2003; Suraci, Farwell, et al., 2023).
- *Ecological connectivity* estimates the ability of a given location to support the natural movement of organisms through processes such as dispersal, migration and gene flow and to provide linkages between areas of high quality habitat (Dickson et al., 2017; Suraci, Littlefield, et al., 2023).
- *Vegetation diversity* describes the diversity of plant communities, defined here as groups of 'plant community types (associations) that tend to co-occur within landscapes with similar ecological processes, substrates, and/or environmental gradients' (Comer et al., 2003).

The above indicators were standardized (*z*-score transformation), resampled to a common resolution (90-m) and combined using the weighted linear sum method described above. We applied the set of weights such that each indicator had equal influence in the resulting sub-index (see Appendix S1).

2.2.3 | Ecosystem services sub-index

The ecosystem services sub-index captured two key ecosystem services that forests provide – (1) the provisioning of clean drinking water and (2) carbon storage. This sub-index identifies areas where wildfire may negatively impact the capacity of forests to provide these services. While recognizing that forests provide many ecosystem services beyond those discussed here (e.g. recreational value), we focused on water supply and carbon sequestration because they are (i) readily quantifiable at the national scale and (ii) largely non-redundant with the values in the ecological value sub-index. As noted above, these indicators are not intended to capture the actual loss of carbon or drinking water to fire, but rather to focus attention on locations where these values are relatively high (see also Appendix S1):

- *Total forest carbon* estimates current (circa 2018) carbon storage as tons of carbon per pixel across forests in CONUS (USFS Forest Inventory & Analysis, 2022; Wilson et al., 2018).

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

- *Relative importance to surface drinking water* quantifies a watershed's ability to provide clean drinking water to human communities (National Forests to Faucets v2.0—Mack et al., 2022).

The ecosystem services sub-index was derived by standardizing (*z*-score transformation) the indicator layers, resampling them to 90 m and calculating a weighted linear sum using the set of weights that yielded equal influence of the two indicators.

2.2.4 | Deriving the social-eco index

Finally, we combined each of the three sub-indices (social vulnerability, ecological value and ecosystem services) into the SEI using the same weighted linear sum approach described above. We acknowledge that our approach of applying the social vulnerability metric across entire census tracts will result in some uninhabited areas being considered socially vulnerable. However, there is a trade-off between generalizing social vulnerability to uninhabited areas and focusing instead on mapped developed areas, which risks inadvertently overlooking some of the most socially vulnerable rural and isolated communities. Given this, we maintained our census tract-wide social vulnerability values when combining these three sub-indices. We recognize this would lead to some areas (specifically those with higher ecological values and ecosystem services) being elevated in the SEI, despite a relatively limited number of people affected. However, the communities that could be affected in or near those areas are among the most underserved in risk reduction investments (Morgan et al., 2024; Ojerio et al., 2011), and thus we deem this trade-off warranted.

We standardized the three sub-indices (*z*-score transformation) and derived weights such that each sub-index had equal influence on the resulting index values. While our goal here was to ensure equal influence of each sub-index, there is inherent subjectivity in selecting any particular weighting scheme for combining metrics into a composite index. Accordingly, we emphasize the exploratory nature of this analysis and the potential for similar analyses to produce varying results depending on researcher or practitioner priorities and variable weights assigned, which we find to be a valuable opportunity for future research.

2.3 | Combining the wildfire mitigation potential and social-eco indices

To identify target landscapes for management considerations across CONUS, we smoothed each index by taking the mean within a 405 ha (1000 acre) moving window. This smoothing process retained the original data resolution but removed spatial artefacts or anomalies (e.g. single high-value pixels surrounded by those of lower value), thus identifying contiguous areas of similarly high value for a given index. We chose 405 ha to ensure that our smoothing would be done at a scale substantially smaller than what typically constitutes a project planning area (on the order of 10,000 ha; Ager et al., 2021). To avoid targeting areas where active management is administratively constrained, we masked out of the smoothed rasters designated Wilderness and Wild and Scenic Rivers (both categories of GAP 1 protected area within which natural disturbances are allowed to occur; USGS, 2020).

For each smoothed index (WMPI and SEI), we then identified areas with pixel values in the top 20% of index values within each USFS region (Figure 1). Finally, we identified contiguous groups of pixels falling within the top 20% of both the WMPI and SEI within a given USFS region and drew polygons around these areas (Figure 2). These polygons containing the overlapping top 20% of WMPI and SEI values (hereafter, 'focal areas') were considered as potential targets for restoration given the co-benefits they represent. We chose the 20% cut-off as a conservative decision rule meant to focus attention on the lands with greatest potential for co-benefits. To remove potential artefacts and polygons too small to be of relevance to management, we filtered the focal areas to only those greater than 405 ha.

2.4 | Identifying coincidence and complementarity between focal areas and alternative management targets

To assess the complementarity between prioritizations focused solely on biophysical wildfire risk or structural impacts and our alternative that *also* integrates social and ecological considerations, we then compared our focal areas to (1) areas within the top 20% of the WMPI (identified based on biophysical wildfire risk) and (2) the USFS' top 10 firesheds within each USFS region (identified based on wildfire ignitions on NF land, restoration feasibility, and risk to structures; Ager et al., 2021). Given that our indices followed an 'all-lands' approach and were scaled relative to values within each USFS region, we selected the 'all-lands' top 10 firesheds ranked relative to all firesheds within each region for use in our comparisons.

The CONUS-wide mean value for each indicator that contributed to the three sub-indices of the SEI (e.g. prevalence of COPD, ecological connectivity) was extracted within the following domains: (1) areas within the top 20% of the WMPI, (2) all focal areas (i.e. where the top 20% of both the WMPI and SEI overlap), (3) USFS top 10 firesheds in each region, and (4) all areas in which focal areas and the USFS top 10 firesheds overlap. These values were then used to compute the percent change in each indicator value when (1) refining targets from the top 20% of the WMPI down to focal areas alone and (2) refining targets from all USFS top 10 firesheds per region down to only locations in which those firesheds overlap with our focal areas.

3 | RESULTS

The top 20% of values within the WMPI for each USFS region encompassed 106.2 million ha. Retaining areas within the top 20% of

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

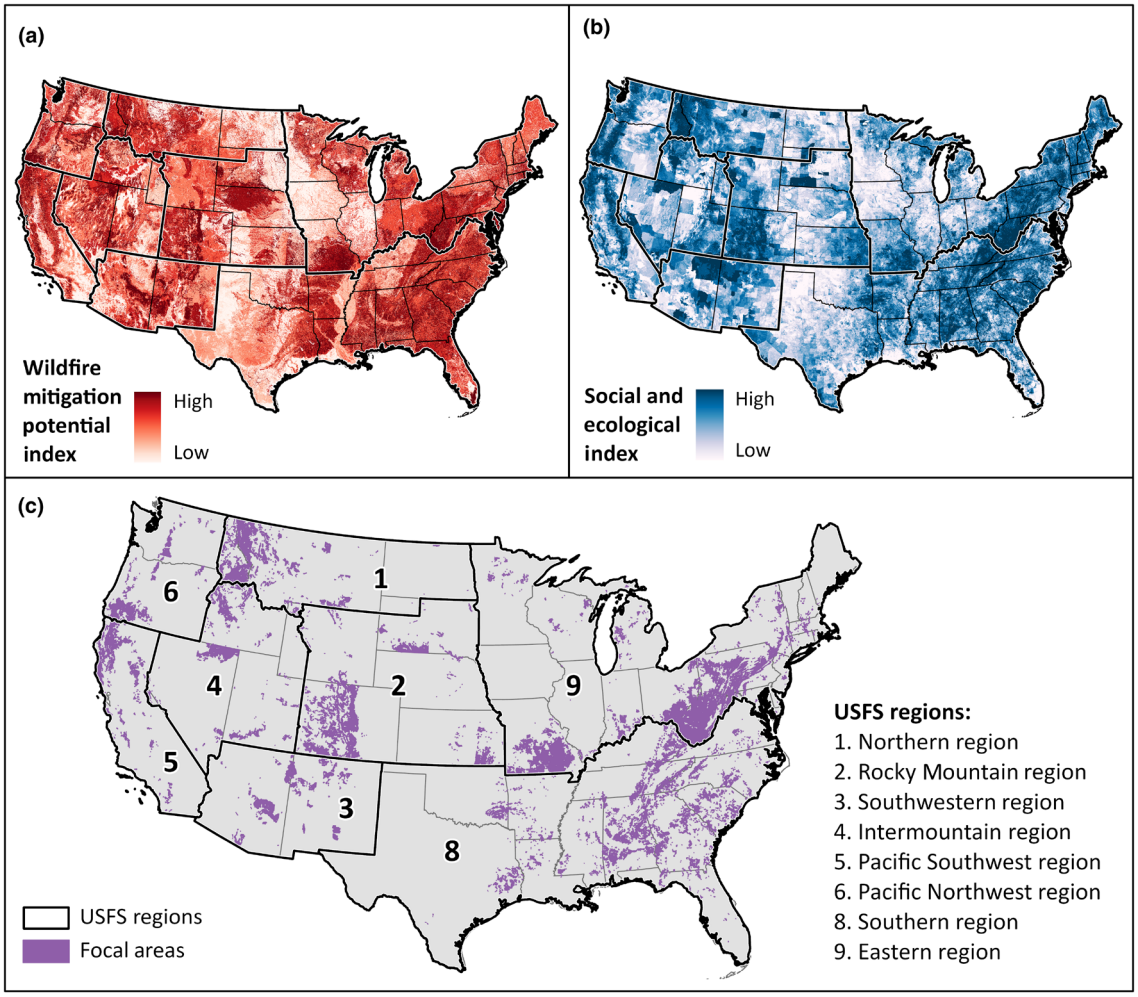


FIGURE 2 CONUS-wide distribution of (a) the WMPI, (b) the SEI, and (c) focal areas (areas of overlap between the top 20% of WMPI values and top 20% of SEI values). Both indices were scaled relative to values within each USFS region (regions indicated by bold black lines and listed according to region ID).

both the WMPI and SEI (i.e. focal areas) reduced this land area by more than half, to 41.9 million ha. These focal areas are locations where restoration is likely to be effective in both reducing the severity of future wildfires and safeguarding vulnerable communities and important ecological values and were generally concentrated along the Appalachian Mountains, Ozarks, Rocky Mountains and the Pacific Coastal Ranges (Figure 2). The Eastern Region contained the largest amount of land within focal areas (14.2-million ha; 8.3% of total region area), and the smallest amount was found in the Pacific Northwest Region (2.0-million ha; 4.7% of total region area; Table 2).

The addition of the SEI in identifying focal areas substantially increased representation of ecological values, ecosystem services and social vulnerability. Relative to conducting restoration within areas defined only by high values (top 20% per region) of the WMPI, prioritizing focal areas would target restoration to locations with, on average, 28% greater imperilled species richness and 45% greater drinking water importance and would increase the representation of families falling below the poverty line and populations with COPD by 26% and 14%, respectively (Figure 3a).

There is a high degree of complementarity between our focal areas and the top 10 firesheds within each USFS region, with 33.6% (2.9-million ha) of the top 10 firesheds overlapping focal areas (Figure 4). If the USFS were to target restoration on the 2.9-million ha in which firesheds and focal areas coincide, they would capture more climate resilient and intact landscapes that provide greater connectivity for wildlife and that also support greater overall species richness than firesheds do on average (Figure 3b). Likewise, these areas of overlap present opportunities to preserve 14% more clean drinking water and 39% greater forest carbon as well as reach nearly 50% more families below the poverty line and 42% more individuals with COPD. The region around Boise, Idaho, provides a localized example of the complementarity between areas prioritized by USFS firesheds and the focal areas developed here, refining the overall footprint of firesheds to focus on locations that are particularly high for both wildfire mitigation potential and social and ecological considerations (Figure 5, see Section 4 for more details). Additional case studies for Denver, Colorado and Charleston, West Virginia are presented in Appendix S2.

25783814, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 2 Total area of identified focal areas (in millions of hectares) within each USFS region across CONUS. Focal area is also expressed as a percentage of total region area.

Region name[a]	Region area	Focal area
Northern	64.7	4.3 (6.6%)
Rocky Mountain	105.3	6.1 (5.8%)
Southwestern	61.0	2.5 (4.1%)
Intermountain	72.6	2.9 (4.0%)
Pacific Southwest	42.3	2.5 (5.9%)
Pacific Northwest	42.5	2.0 (4.7%)
Southern	220.7	7.4 (3.4%)
Eastern	171.5	14.2 (8.3%)

[a]Regions correspond to those shown in Figure 2c.

4 | DISCUSSION

The mounting threat of uncharacteristic wildfire and its inequitable impacts necessitate swift and strategic action from land managers as they identify restoration priorities. Here we have integrated critical social and ecological considerations and developed an index that is complementary to existing prioritizations based on potential structural loss, a combination that is essential to better understand where and when communities and resources are likely to be impacted by wildfire. Our results suggest that focusing on biophysical components of wildfire risk alone may not account for some of the important ecological values and services and vulnerable human communities that would be compromised if a wildfire were to occur. By integrating our focal areas with existing prioritizations, managers

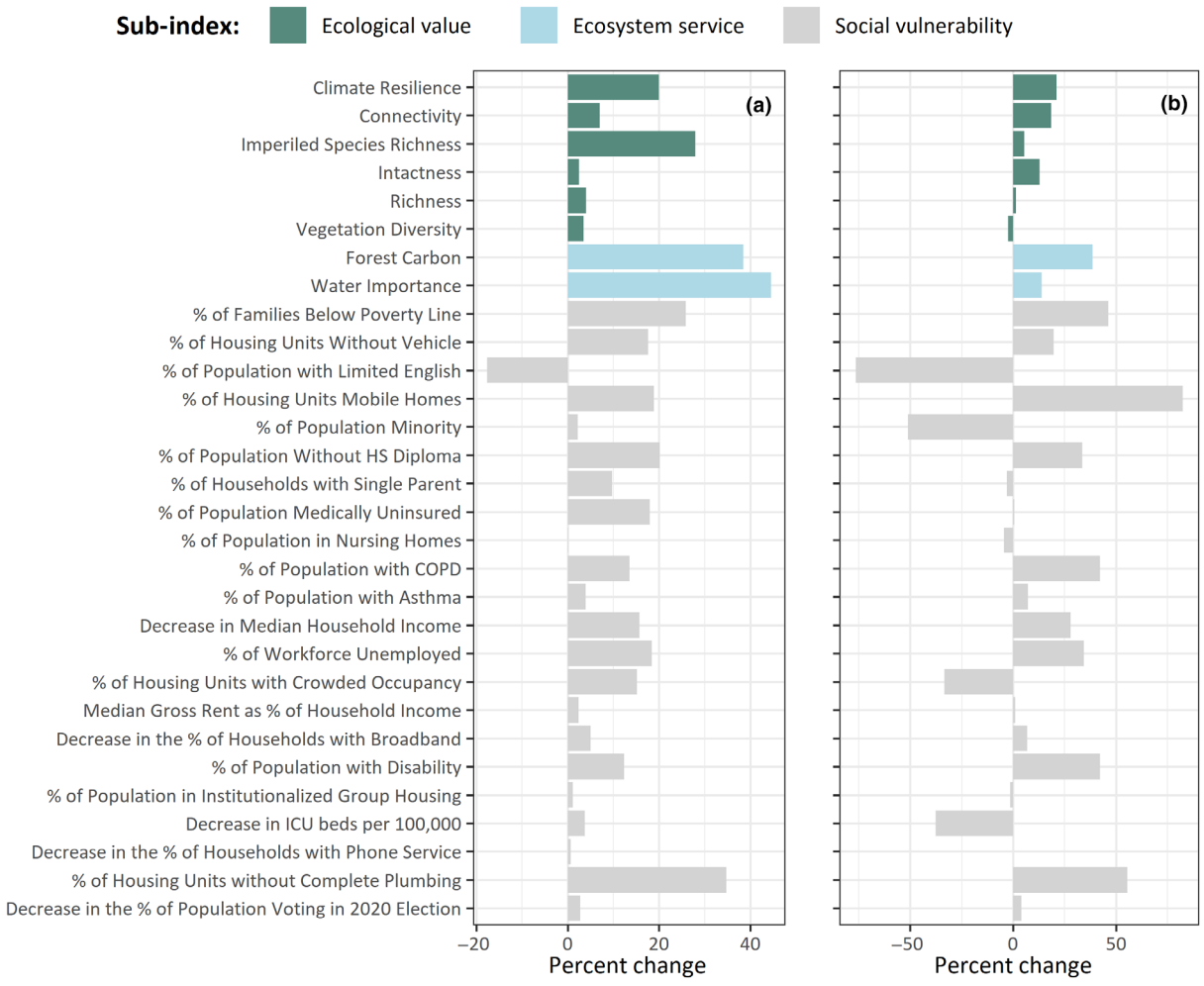


FIGURE 3 The percent change in all ecological value (green), ecosystem service (blue) and social vulnerability (grey) indicators that contributed to the SEI within target areas when (a) refining the target areas from the top 20% of the WMPI down to focal areas alone (i.e. where the top 20% of both the WMPI and SEI overlap) and (b) refining the target areas from USFS top ten firesheds per region to only areas of overlap between those firesheds and focal areas. Five indicators were quantified such that a decrease in their value indicates greater representation of social vulnerability: Median household income (USD), % of households with broadband, % of households with phone service, % of population participating in voting and the number of ICU beds per 100,000 people. These indicators have been represented as the percent change in the *decrease* of their values. See Appendix S2 for tables of values.

25783314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

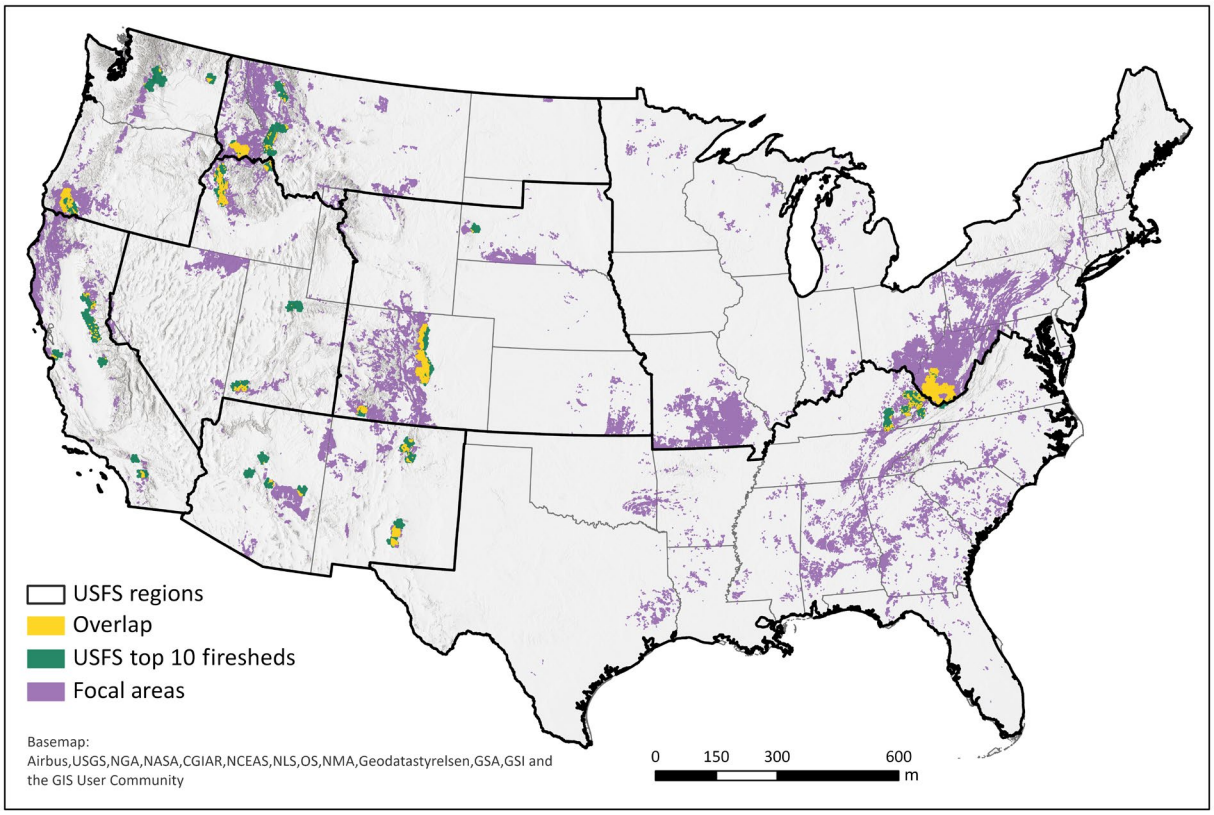


FIGURE 4 USFS top 10 firesheds (green) for each USFS region overlaid with all focal areas (purple), which were identified as the locations in which the top 20% of the WMPI coincided with the top 20% of the SEI. Areas of overlap between firesheds and focal areas are indicated in yellow.

can strategically focus their efforts in areas with the greatest co-benefits across all of these factors.

The region around Boise, Idaho, demonstrates some of the distinct opportunities to capture greater overall social and ecological values through a strategic refinement of USFS management targets. Wildfires in this region have the potential to threaten human communities as well as nearby highly intact, connected and climate resilient landscapes, including Boise NF. Boise NF also contains some of the most important watersheds in all of Idaho for the provisioning of clean drinking water, making it essential to many of the human and ecological communities found here. The areas of overlap between the top ranked firesheds and our focal areas in this region (a total of 236,900 ha) capture some of the highest values within both indices and could help focus restoration that would maximize combined benefits to human communities and ecological systems (Figure 5). This strategic management will be necessary given the wide range of costs associated with fuel treatments and land managers' limitations in restoration funding (Hunter & Taylor, 2022).

In a time of increasingly frequent, large and destructive wildfires and mounting ecological crises, understanding which locations are at the nexus of these diverse priorities will be essential to efficiently deploy a finite amount of funding and resources for restoration. This is particularly salient given that wildfire is a nationwide issue, with the greatest number of wildfires occurring in the southeastern U.S. and the largest in terms of burn area occurring in the west (Mitchell et al., 2014; Schoennagel et al., 2017; U.S. Environmental Protection Agency, 2022). This issue also extends beyond the U.S. (e.g. Australia's bushfires (Deb et al., 2020), Canada's Northwest Territory fires and record-breaking 2023 season (Kochtubajda et al., 2019; Kolden et al., 2024), and a dramatic increase in wildfire across the Amazon in Brazil (Kolden et al., 2024)), thus this analysis can inform a more integrated approach to prioritizing wildfire restoration efforts worldwide as governments work to fight a global increase in extreme wildfire (United Nations Environment Programme, 2022). The all-lands approach employed here paired with the balanced consideration of social, ecological, and wildfire-based metrics will ensure a more even distribution of priority landscapes identified across the whole of CONUS, rather than emphasizing any single region and could serve as a transferable model for similar analyses elsewhere.

Although previous research has integrated a variety of social, ecological and/or wildfire-relevant biophysical metrics in identifying priority areas for restoration (e.g. Ager et al., 2015; Baskent et al., 2020; Davies et al., 2018; D'Evelyn et al., 2022; Peeler et al., 2023; Wigtil et al., 2016), none integrated all three at once as we have done here. Giving these important ecological values and services and vulnerable communities ample consideration is necessary given their dependence on healthy, functioning forests. For example, forest conversion in fire-prone landscapes could alter biodiversity and habitat connectivity (Sitters & Di Stefano, 2020; Thompson et al., 2021) and affect vegetation diversity (Forrestel

25783814, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

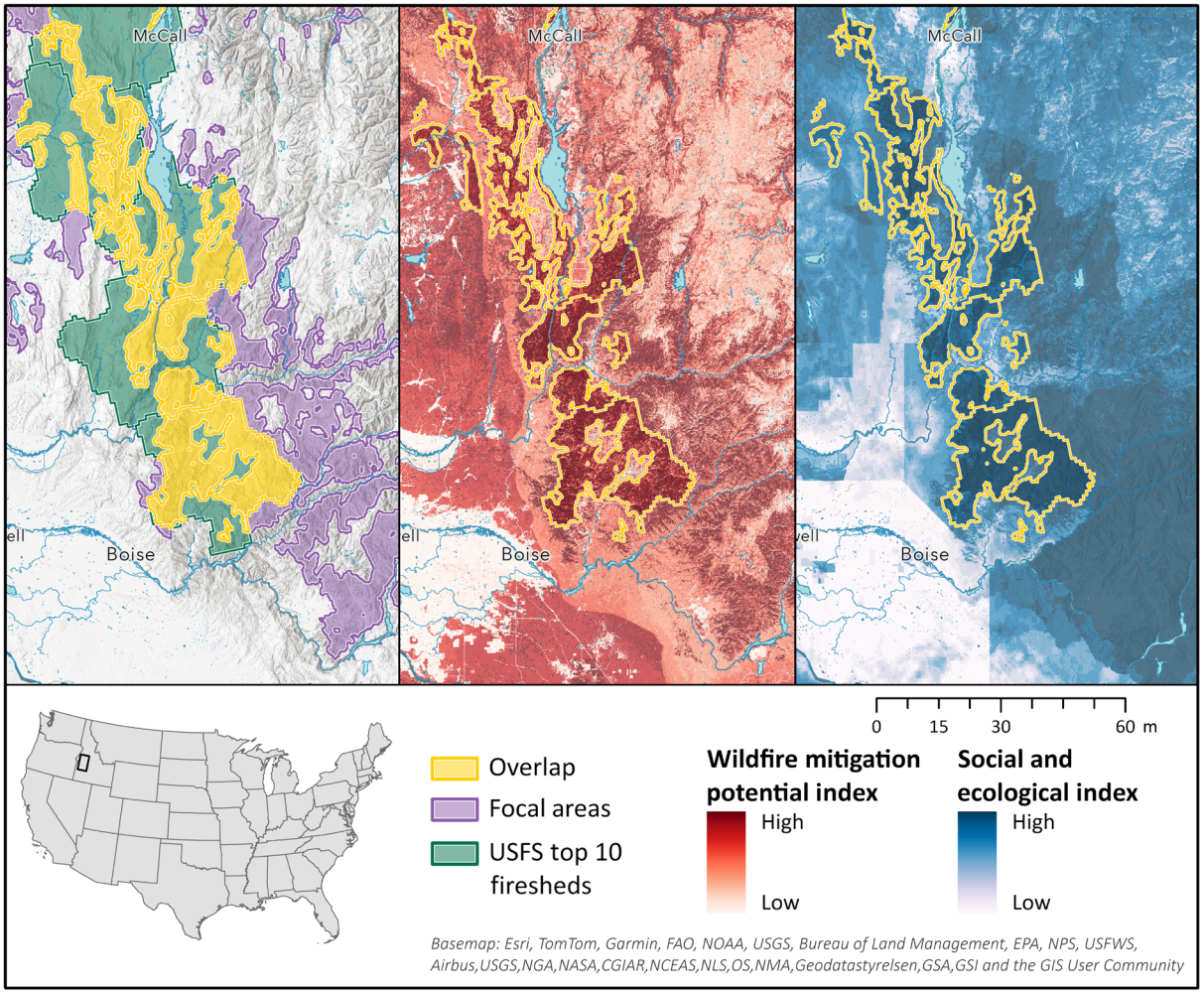


FIGURE 5 The overlapping area (236,900 ha) between a portion of the USFS top 10 firesheds and our focal areas (left) near Boise, Idaho, and the WMPI (centre) and SEI values (right) that are contained within those overlapping polygons.

et al., 2011; Keeley et al., 2003). By integrating social and ecological values and ecosystem services into our prioritization, we were able to increase the representation of families below the poverty line by 26%, imperilled species richness by 28%, climate resilient landscapes by 20%, and clean water provisioning by 45% when compared to areas identified by the WMPI alone. We also increased the representation of populations with COPD and asthma by 14% and 4%, respectively, which is critical given a positive association between exposure to wildfire smoke and aggravation of these respiratory conditions (Cascio, 2018; D'Evelyn et al., 2022).

The overall representation of social vulnerability, ecological values and ecosystem services increased, on average, by 10%, 11%, and 42%, respectively, compared to prioritizations based on wildfire mitigation potential alone. The focal areas identified here could therefore serve as a complement to similar analyses, including that of Peeler et al. (2023) examining hotspots of wildfire-caused carbon loss and risk to human communities across USFS firesheds, to ensure even greater gains for human and ecological communities alike. An examination of our results alongside those of Peeler et al. (2023), Wigtil et al. (2016), and other similar studies underscores how the spatial distribution of landscape priorities can shift based on researcher or practitioner priorities and that these priorities must be thoughtfully identified and results interpreted with caution.

We used the best available CONUS-scale datasets, drawing on USFS and other federally derived datasets where available (e.g. WHP, PLS, VDep, Census Bureau data) and employed established methods for combining these datasets into a set of composite indices (Suraci, Farwell, et al., 2023). However, all spatial datasets are subject to uncertainties, which are inherently propagated into our indices. These datasets serve as approximations that should be interpreted with caution at finer scales. We also note that the datasets used here had variable native resolutions (90-m to 2-km), or in the case of social vulnerability, were based on data summarized at the level of census tracts. We therefore anticipate that our results will be most relevant for landscape-level prioritizations, rather than localized decision-making. We have accounted for this consideration in part by smoothing and filtering our focal areas to 405 ha. Given this, we suggest that the focal areas identified here can best serve as starting points to direct attention to landscapes that may provide substantial co-benefits if managed to reduce wildfire risk.

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

More detailed, on-the-ground investigations of proposed focal areas, as well as collaboration with local communities, tribes and stakeholders, would be necessary in making any final determination about where to apply treatments. These collaborations, especially an integration of Indigenous Knowledge and Western science, could help scientists and practitioners garner valuable historical context for land management practices in a given area while gathering localized details that can inform fine-scale decision-making (Ray et al., 2012).

When incorporating these results into community level decisions, it will be essential to carefully consider the complex and varied relationships between different communities and the role of fire on the landscape, as well as the historical dynamics of power surrounding decision-making regarding dominant land management practices (Bourke et al., 2020; Christianson et al., 2022). Great care and respect should be given to understanding and elevating Indigenous fire stewardship practices that have historically been excluded from post-colonization land management practices (Bourke et al., 2020; Hoffman et al., 2022; Peeler et al., 2023), as well as the social and cultural dynamics within a community (e.g. livelihood, income level, upbringing) that may influence how individuals perceive or respond to wildfire risk (Hamilton et al., 2019; McFarlane et al., 2011). The interplay of these dynamics must be thoughtfully addressed in the process of identifying wildfire treatment areas, particularly through identifying and bridging 'collaboration gaps' to establish more coordinated, collaborative, supportive and incentivized wildfire restoration efforts moving forward through an interweaving of Indigenous Knowledge and Western science (Charnley et al., 2020; Eisenberg et al., 2024; Hamilton et al., 2021).

In practice, these efforts could include participatory mapping initiatives or multi-criteria analyses and planning activities that engage communities and reveal local priorities. Such efforts could also improve researchers' and land managers' understanding of finer-scale interactions between wildfire risk and community-defined social and ecological values (Gamboa et al., 2023; McBride et al., 2017). McBride et al. (2017) highlight how participatory mapping can facilitate more effective communication and integration of Indigenous Knowledge and Western science in forest management by compiling information in a Geographic Information Systems (GIS) interface and thus can provide a roadmap for similar applications. Another approach could centre on establishing collaborative organizations composed of members representing community groups, government agencies and non-profits at local, regional and/or national levels. These collaboratives can then coordinate and scale large-scale analyses and guidance to local-scale needs and existing social and political infrastructure within a community (Edgeley & Paveglio, 2024; Huayhuaca et al., 2023). For example, the USFS Collaborative Forest Landscape Restoration Program (CFLRP) was established in 2009 with the goal of encouraging collaborative, science-based forest ecosystem restoration on USFS lands by integrating local, national and private stakeholders and resources (Schultz et al., 2012). Through the CFLRP, communities can apply for funding and the opportunity to work collaboratively with USFS land managers to implement community-led landscape-scale restoration projects. This program has helped to bridge information gaps between community members and federal agency staff and has served as a valuable incubator and model for a collaborative, multi-scale approach to land management (Schultz et al., 2012; Urgenson et al., 2017). The proposed National Old Growth Amendment is another example of how a national direction for adaptive management can be used to develop local solutions through close collaboration with Tribes and other governmental and non-governmental stakeholders, particularly through the development of an *Adaptive Strategy for Old-Growth Forest Conservation* for each national forest to ensure locally appropriate management and monitoring (U.S. Forest Service, 2024).

Lastly, we acknowledge that while we identify the ecological values, ecosystem services and socially vulnerable communities that could be protected by or benefit from restoration, we cannot say that high-severity fire will diminish any of the indicators contributing to these sub-indices. Further analysis is necessary to deepen our understanding of how much of these indicators may in fact be lost in the absence of restoration if a wildfire were to occur (Peeler et al., 2023). Regardless, the ecological, social, and biophysical aspects of wildfire risk are highly interconnected. For example, wildfire can impact biodiversity, which could result in carbon loss that may affect ecosystem services that can determine human community health. As we increasingly recognize these dynamics, we must begin to reflect them in our restoration prioritizations.

5 | CONCLUSION

The focal areas we have identified can inform a strategic shift or refinement of current management prioritizations, including the USFS' top ranked firesheds approach. Based on an average treatment cost per hectare of just over $3700 ($1500/acre; Hunter & Taylor, 2022), the $1.5 billion pledged by the Biden Administration could support fewer than 405,000 ha (1 million acres) of restoration activities, requiring tough decisions about which areas to prioritize. To begin these decision-making conversations, we have provided the model results, sub-indices comprising the SEI, and a set of focal area polygons summarized to areas within and immediately adjacent to USFS lands in a web application for viewing at https://csp-inc.github.io/pew-usfs-app/. While the analysis described here followed an 'all-lands' approach across CONUS, the results provided in the web application are intended to specifically inform USFS management and thus were limited to the extent of NFs and their intersecting firesheds. Irrespective of analysis extent, we can ensure the USFS and other land managers secure the maximum possible co-benefits while working within budgetary constraints by focusing restoration on areas with the greatest identified wildfire mitigation potential while also considering social and ecological values within and around their existing fireshed framework. Safeguarding these values now will be essential to ensure their resilience in an uncertain future.

25783314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

AUTHOR CONTRIBUTIONS

Justin P. Suraci, Blake S. Busse and Brett G. Dickson conceived the ideas. Caitlin E. Littlefield, L. Mae Lacey, Justin P. Suraci, Blake S. Busse and Brett G. Dickson designed the methodology. Justin P. Suraci, L. Mae Lacey and Caitlin E. Littlefield collected and analysed the data; L. Mae Lacey led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank The Pew Charitable Trusts for supporting this project, and in particular, wish to acknowledge Jon Fisher and John Seebach for their contributions in conceiving of and refining this work. We are also grateful to the U.S. Forest Service for valuable guidance on our selection of indicator layers for each index and sub-index. We would also like to thank Travis Belote and one anonymous reviewer for their valuable feedback on this methodology.

CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data supporting this analysis are publicly available, and all analysis outputs are available at https://doi.org/10.6084/m9.figshare.c.7430305.v2.

ORCID

L. Mae Lacey https://orcid.org/0000-0002-7355-1124
Justin P. Suraci https://orcid.org/0000-0001-5952-2186
Caitlin E. Littlefield https://orcid.org/0000-0003-3771-7956
Brett G. Dickson https://orcid.org/0000-0003-4160-839X

REFERENCES

Ager, A. A., Day, M. A., Ringo, C., Evers, C. R., Alcasena, F. J., Houtman, R. M., Scanlon, M., Scanlon, M., & Ellersick, T. (2021). *Development and application of the fireshed registry* (RMRS-GTR-425). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. https://doi.org/10.2737/RMRS-GTR-425

Ager, A. A., Kline, J. D., & Fischer, A. P. (2015). Coupling the biophysical and social dimensions of wildfire risk to improve wildfire mitigation planning: Coupling the biophysical and social dimensions of wildfire risk. *Risk Analysis*, *35*(8), 1393–1406. https://doi.org/10.1111/risa.12373

Atlas of U.S. Presidential Elections. (2022). *Voter registration & turnout data by county*. [dataset]. https://uselectionatlas.org/

Balch, J. K., Bradley, B. A., Abatzoglou, J. T., Nagy, R. C., Fusco, E. J., & Mahood, A. L. (2017). Human-started wildfires expand the fire niche across the United States. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(11), 2946–2951. https://doi.org/10.1073/pnas.1617394114

Baskent, E. Z., Borges, J. G., Kašpar, J., & Tahri, M. (2020). A design for addressing multiple ecosystem services in forest management planning. *Forests*, *11*(10), 1108. https://doi.org/10.3390/f11101108

Bayham, J., Yoder, J. K., Champ, P. A., & Calkin, D. E. (2022). The economics of wildfire in the United States. *Annual Review of Resource Economics*, *14*(1), 379–401. https://doi.org/10.1146/annurev-resource-111920-014804

Becker, W., Saisana, M., Paruolo, P., & Vandecasteele, I. (2017). Weights and importance in composite indicators: Closing the gap. *Ecological Indicators*, *80*, 12–22. https://doi.org/10.1016/j.ecolind.2017.03.056

Bourke, M., Atkinson, A., & Neale, T. (2020). Putting country back together: A conversation about collaboration and Aboriginal fire management. *Postcolonial Studies*, *23*(4), 546–551. https://doi.org/10.1080/13688790.2020.1751909

Brown, C. D., & Johnstone, J. F. (2012). Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *Forest Ecology and Management*, *266*, 34–41. https://doi.org/10.1016/j.foreco.2011.11.006

Burgass, M. J., Halpern, B. S., Nicholson, E., & Milner-Gulland, E. J. (2017). Navigating uncertainty in environmental composite indicators. *Ecological Indicators*, *75*, 268–278. https://doi.org/10.1016/j.ecolind.2016.12.034

Cascio, W. E. (2018). Wildland fire smoke and human health. *Science of the Total Environment*, *624*, 586–595. https://doi.org/10.1016/j.scitotenv.2017.12.086

Centers for Disease Control and Prevention. (2021). *PLACES: Local data for better health, census tract data 2021 release* [dataset]. https://chronicdata.cdc.gov/500-Cities-Places/PLACES-Local-Data-for-Better-Health-Census-Tract-D/cwsq-ngmh

Chamberlain, J. L., & Jones, K. W. (2023). Sociocultural mapping of ecosystem service values can inform where to mitigate wildfire risk: A case study from Colorado. *Journal of Environmental Planning and Management*, *67*, 1–19. https://doi.org/10.1080/09640568.2022.2161876

Charnley, S., Kelly, E. C., & Fischer, A. P. (2020). Fostering collective action to reduce wildfire risk across property boundaries in the American West. *Environmental Research Letters*, *15*(2), 025007. https://doi.org/10.1088/1748-9326/ab639a

Christianson, A. C., Sutherland, C. R., Moola, F., Gonzalez Bautista, N., Young, D., & MacDonald, H. (2022). Centering indigenous voices: The role of fire in the boreal forest of North America. *Current Forestry Reports*, *8*(3), 257–276. https://doi.org/10.1007/s40725-022-00168-9

Comer, P. J., Faber-Langendoen, D., Evans, R., Gawler, S. C., Josse, C., Kittel, G., Menard, S., Pyne, M., Reid, M., Schulz, K., Snow, K., & Teague, J. (2003). *Ecological systems of the United States: A working classification of U.S. terrestrial systems*. NatureServe.

Conservation Science Partners. (2021). *Ecological value of national forests at the administrative unit level* [Technical Report]. Conservation Science Partners.

Cutter, S. L., Boruff, B. J., & Shirley, W. L. (2003). Social vulnerability to environmental hazards. *Social Science Quarterly*, *84*(2), 242–261. https://doi.org/10.1111/1540-6237.8402002

Cutter, S. L., & Finch, C. (2000). Temporal and spatial changes in social vulnerability to natural hazards. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(7), 2301–2306.

Davies, I. P., Haugo, R. D., Robertson, J. C., & Levin, P. S. (2018). The unequal vulnerability of communities of color to wildfire. *PLoS One*, *13*(11), e0205825. https://doi.org/10.1371/journal.pone.0205825

Davis, K. T., Higuera, P. E., & Sala, A. (2018). Anticipating fire-mediated impacts of climate change using a demographic framework. *Functional Ecology*, *32*, 1729–1745. https://doi.org/10.1111/1365-2435.13132

Davis, K. T., Robles, M. D., Kemp, K. B., Higuera, P. E., Chapman, T., Metlen, K. L., Peeler, J. L., Rodman, K. C., Woolley, T., Addington, R. N., Buma, B. J., Cansler, C. A., Case, M. J., Collins, B. M., Coop, J. D., Dobrowski, S. Z., Gill, N. S., Haffey, C., Harris, L. B., … Campbell, J. L. (2023). Reduced fire severity offers near-term buffer to climate-driven declines in conifer resilience across the western United States. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(11), e2208120120. https://doi.org/10.1073/pnas.2208120120

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Deb, P., Moradkhani, H., Abbaszadeh, P., Kiem, A. S., Engström, J., Keellings, D., & Sharma, A. (2020). Causes of the widespread 2019–2020 Australian bushfire season. *Earth's Future*, *8*(11), e2020EF001671. https://doi.org/10.1029/2020EF001671

Department of Homeland Security. (2022). *Homeland infrastructure foundation-level data (HIFLD): Nursing homes* [dataset]. https://hifld-geoplatform.opendata.arcgis.com/datasets/geoplatform::nursing-homes/about

D'Evelyn, S. M., Jung, J., Alvarado, E., Baumgartner, J., Caligiuri, P., Hagmann, R. K., Henderson, S. B., Hessburg, P. F., Hopkins, S., Kasner, E. J., Krawchuk, M. A., Krenz, J. E., Lydersen, J. M., Marlier, M. E., Masuda, Y. J., Metlen, K., Mittelstaedt, G., Prichard, S. J., Schollaert, C. L., … Spector, J. T. (2022). Wildfire, smoke exposure, human health, and environmental justice need to be integrated into forest restoration and management. *Current Environmental Health Reports*, *9*(3), 366–385. https://doi.org/10.1007/s40572-022-00355-7

Dickson, B. G., Albano, C. M., McRae, B. H., Anderson, J. J., Theobald, D. M., Zachmann, L. J., Sisk, T. D., & Dombeck, M. P. (2017). Informing strategic efforts to expand and connect protected areas using a model of ecological flow, with application to the western United States: Mapping ecological flow to inform planning. *Conservation Letters*, *10*(5), 564–571. https://doi.org/10.1111/conl.12322

Dillon, G. K., Menakis, J., & Fay, F. (2015). *Wildland fire potential: A tool for assessing wildfire risk and fuels management needs* (USDA Forest Service Proceedings RMRS-P-73; Proceedings of the Large Wildland Fires Conference; May 19–23, 2014; Missoula, MT). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. https://www.fs.usda.gov/rm/pubs/rmrs_p073/rmrs_p073_060_076.pdf

Edgeley, C. M., & Paveglio, T. B. (2024). Bridging scales for landscape-level wildfire adaptation: A case study of the Kittitas fire adapted communities coalition. *Journal of Environmental Management*, *351*, 119818. https://doi.org/10.1016/j.jenvman.2023.119818

Eisenberg, C., Prichard, S., Nelson, M. P., & Hessburg, P. (2024). *Braiding indigenous and western knowledge for climate-adapted forests: An ecocultural state of science report*. The Wise Path Forward. https://depts.washington.edu/flame/mature_forests/

Evans, A., DeBonis, M., Krasilovsky, E., & Melton, M. (2007). *Measuring community capacity for protection from wildfire*. Forest Stewards Guild. https://www.foreststewardsguild.org/wp-content/uploads/2019/06/community_capacity_wildfire.pdf

Forrestel, A. B., Moritz, M. A., & Stephens, S. L. (2011). Landscape-scale vegetation change following fire in Point Reyes, California, USA. *Fire Ecology*, *7*(2), 114–128. https://doi.org/10.4996/fireecology.0702114

Gaither, C. J., Poudyal, N. C., Goodrick, S., Bowker, J. M., Malone, S., & Gan, J. (2011). Wildland fire risk and social vulnerability in the southeastern United States: An exploratory spatial data analysis approach. *Forest Policy and Economics*, *13*(1), 24–36. https://doi.org/10.1016/j.forpol.2010.07.009

Gamboa, G., Otero, I., Bueno, C., Arilla, E., Ballart, H., Camprubí, L., Canaleta, G., Tolosa, G., & Castellnou, M. (2023). Participatory multi-criteria evaluation of landscape values to inform wildfire management. *Journal of Environmental Management*, *327*, 116762. https://doi.org/10.1016/j.jenvman.2022.116762

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google earth engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, *202*, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Greco, S., Ishizaka, A., Tasiou, M., & Torrisi, G. (2019). On the methodological framework of composite indices: A review of the issues of weighting, aggregation, and robustness. *Social Indicators Research*, *141*(1), 61–94. https://doi.org/10.1007/s11205-017-1832-9

Hagmann, R. K., Hessburg, P. F., Prichard, S. J., Povak, N. A., Brown, P. M., Fulé, P. Z., Keane, R. E., Knapp, E. E., Lydersen, J. M., Metlen, K. L., Reilly, M. J., Sánchez Meador, A. J., Stephens, S. L., Stevens, J. T., Taylor, A. H., Yocom, L. L., Battaglia, M. A., Churchill, D. J., Daniels, L. D., … Waltz, A. E. M. (2021). Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecological Applications*, *31*(8), e02431. https://doi.org/10.1002/eap.2431

Halofsky, J. S., Donato, D. C., Franklin, J. F., Halofsky, J. E., Peterson, D. L., & Harvey, B. J. (2018). The nature of the beast: Examining climate adaptation options in forests with stand-replacing fire regimes. *Ecosphere*, *9*(3), 1–18. https://doi.org/10.1002/ecs2.2140

Hamann, A., Roberts, D. R., Barber, Q. E., Carroll, C., & Nielsen, S. E. (2015). Velocity of climate change algorithms for guiding conservation and management. *Global Change Biology*, *21*(2), 997–1004. https://doi.org/10.1111/gcb.12736

Hamilton, M., Fischer, A. P., & Jasny, L. (2021). Bridging collaboration gaps in fragmented environmental governance systems. *Environmental Science & Policy*, *124*, 461–470. https://doi.org/10.1016/j.envsci.2021.07.014

Hamilton, M., Salerno, J., & Fischer, A. P. (2019). Cognition of complexity and trade-offs in a wildfire-prone social-ecological system. *Environmental Research Letters*, *14*(12), 125017. https://doi.org/10.1088/1748-9326/ab59c1

Hessburg, P. F., Prichard, S. J., Hagmann, R. K., Povak, N. A., & Lake, F. K. (2021). Wildfire and climate change adaptation of western North American forests: A case for intentional management. *Ecological Applications*, *31*(8), e02432. https://doi.org/10.1002/eap.2432

Hoffman, K. M., Christianson, A. C., Dickson-Hoyle, S., Copes-Gerbitz, K., Nikolakis, W., Diabo, D. A., McLeod, R., Michell, H. J., Mamun, A. A., Zahara, A., Mauro, N., Gilchrist, J., Ross, R. M., & Daniels, L. D. (2022). The right to burn: Barriers and opportunities for Indigenous-led fire stewardship in Canada. *Facets*, *7*, 464–481. https://doi.org/10.1139/facets-2021-0062

Huayhuaca, C., Cheng, A., Beeton, T., Sanderson, J., Barton, A., Kimple, A., Colavito, M., Zebrowski, J., & Dunn, J. (2023). *Preparing landscapes and communities to receive and recover from wildfire through collaborative readiness: A concept paper*. Southwest Ecological Restoration Institutes.

Hunter, M. E., & Taylor, M. H. (2022). The economic value of fuel treatments: A review of the recent literature for fuel treatment planning. *Forests*, *13*(12), 2042. https://doi.org/10.3390/f13122042

Jones, G. M., Keyser, A. R., Westerling, A. L., Baldwin, W. J., Keane, J. J., Sawyer, S. C., Clare, J. D., Gutiérrez, R., & Peery, M. Z. (2022). Forest restoration limits megafires and supports species conservation under climate change. *Frontiers in Ecology and the Environment*, *20*(4), 210–216. https://doi.org/10.1002/fee.2450

Keeley, J. E., Lubin, D., & Fotheringham, C. J. (2003). Fire and grazing impacts on plant diversity and alience plant invasions in the southern Sierra Nevada. *Ecological Applications*, *13*(5), 1355–1374. https://doi.org/10.1890/02-5002

Kochtubajda, B., Stewart, R. E., Flannigan, M. D., Bonsal, B. R., Cuell, C., & Mooney, C. J. (2019). An assessment of surface and atmospheric conditions associated with the extreme 2014 wildfire season in Canada's Northwest Territories. *Atmosphere-Ocean*, *57*(1), 73–90. https://doi.org/10.1080/07055900.2019.1576023

Kolden, C. A., Abatzoglou, J. T., Jones, M. W., & Jain, P. (2024). Wildfires in 2023. *Nature Reviews Earth and Environment*, *5*(4), 238–240. https://doi.org/10.1038/s43017-024-00544-y

LANDFIRE. (2020). *LANDFIRE Remap 2016 Biophysical Settings (BPS) CONUS. v2.0.0. Earth Resources Observation and Science Center (EROS), U.S. Geological Survey* [dataset]. https://landfire.gov/fireregime.php

Mack, E., Lilja, R., Claggett, S., Sun, G., & Caldwell, P. (2022). *Forests to faucets 2.0: Connecting forests, water, and communities* (WO-GTR-99;

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

p. WO-GTR-99). U.S. Department of Agriculture, Forest Service. https://doi.org/10.2737/WO-GTR-99

Manson, S., Schroeder, J., Van Riper, D., Kugler, T., & Ruggles, S. (2022). *IPUMS national historical geographic information system: Version 17.0 [2020 American community survey: 5-year data]*. IPUMS. https://doi.org/10.18128/D050.V17.0

McBride, B. B., Sanchez-Trigueros, F., Carver, S. J., Watson, A. E., Stumpff, L. M., Matt, R., & Borrie, W. T. (2017). Participatory geographic information systems as an organizational platform for the integration of traditional and scientific knowledge in contemporary fire and fuels management. *Journal of Forestry*, *115*(1), 43–50. https://doi.org/10.5849/jof.14-147

McFarlane, B. L., McGee, T. K., & Faulkner, H. (2011). Complexity of homeowner wildfire risk mitigation: An integration of hazard theories. *International Journal of Wildland Fire*, *20*(8), 921. https://doi.org/10.1071/WF10096

Mietkiewicz, N., Balch, J. K., Schoennagel, T., Leyk, S., St. Denis, L. A., & Bradley, B. A. (2020). In the line of fire: Consequences of human-ignited wildfires to homes in the U.S. (1992–2015). *Firehouse*, *3*(3), 50. https://doi.org/10.3390/fire3030050

Mitchell, R. J., Liu, Y., O'Brien, J. J., Elliott, K. J., Starr, G., Miniat, C. F., & Hiers, J. K. (2014). Future climate and fire interactions in the southeastern region of the United States. *Forest Ecology and Management*, *327*, 316–326. https://doi.org/10.1016/j.foreco.2013.12.003

Morgan, G. R., Kemp, E. M., Habets, M., Daniels-Baessler, K., Waddington, G., Adamo, S., Hultquist, C., & Cutter, S. L. (2024). Defining disadvantaged places: Social burdens of wildfire exposure in the eastern United States, 2000–2020. *Firehouse*, *7*(4), 124. https://doi.org/10.3390/fire7040124

Morton, J. (2003). *An evaluation of fuel reduction projects in the eastern Cibola National Forest* [southwest region working paper]. National Community Forestry Center. https://foreststewardsguild.org/wp-content/uploads/2019/06/mapping_fuel_reduction.pdf

NatureServe. (2020). *Map of biodiversity importance*. NatureServe. https://www.natureserve.org/map-biodiversity-importance

Ojerio, R. S. (2008). *Equity in wildfire risk management: Does socioeconomic status predict involvement in federal programs to mitigate wildfire*. The Graduate School of the University of Oregon. https://scholarsbank.uoregon.edu/xmlui/bitstream/handle/1794/7529/Ojerio_final_project_2008.pdf?sequence=4&isAllowed=y

Ojerio, R. S., Moseley, C., Lynn, K., & Bania, N. (2011). Limited involvement of socially vulnerable populations in federal programs to mitigate wildfire risk in Arizona. *Natural Hazards Review*, *12*(1), 28–36. https://doi.org/10.1061/(ASCE)NH.1527-6996.0000027

Parks, S. A., & Abatzoglou, J. T. (2020). Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985 to 2017. *Geophysical Research Letters*, *47*(22), e2020GL089858. https://doi.org/10.1029/2020GL089858

Parrish, J. D., Braun, D. P., & Unnasch, R. S. (2003). Are we conserving what we say we are? Measuring ecological integrity within protected areas. *Bioscience*, *53*(9), 851. https://doi.org/10.1641/0006-3568(2003)053[0851:AWCWWS]2.0.CO;2

Paruolo, P., Saisana, M., & Saltelli, A. (2013). Ratings and rankings: Voodoo or science? *Journal of the Royal Statistical Society: Series A (Statistics in Society)*, *176*(3), 609–634. https://doi.org/10.1111/j.1467-985X.2012.01059.x

Peeler, J. L., McCauley, L., Metlen, K. L., Woolley, T., Davis, K. T., Robles, M. D., Haugo, R. D., Riley, K. L., Higuera, P. E., Fargione, J. E., Addington, R. N., Bassett, S., Blankenship, K., Case, M. J., Chapman, T. B., Smith, E., Swaty, R., & Welch, N. (2023). Identifying opportunity hot spots for reducing the risk of wildfire-caused carbon loss in western US conifer forests. *Environmental Research Letters*, *18*(9), 094040. https://doi.org/10.1088/1748-9326/acf05a

Poudyal, N. C., Johnson-Gaither, C., Goodrick, S., Bowker, J. M., & Gan, J. (2012). Locating spatial variation in the association between wildland fire risk and social vulnerability across six southern states. *Environmental Management*, *49*(3), 623–635. https://doi.org/10.1007/s00267-011-9796-z

Program for Watershed and Community Health. (2003). *Community capacity and wildfire protection: Indicators of rural, low capacity communities*. https://scholarsbank.uoregon.edu/xmlui/bitstream/handle/1794/2320/PWCH_poverty_indicators_9-23-03.pdf?sequence=1

Radeloff, V. C., Helmers, D. P., Kramer, H. A., Mockrin, M. H., Alexandre, P. M., Bar-Massada, A., Butsic, V., Hawbaker, T. J., Martinuzzi, S., Syphard, A. D., & Stewart, S. I. (2018). Rapid growth of the US wildland-urban interface raises wildfire risk. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(13), 3314–3319. https://doi.org/10.1073/pnas.1718850115

Ray, L. A., Kolden, C. A., & Chapin Iii, F. S. (2012). A case for developing place-based fire management strategies from traditional ecological knowledge. *Ecology and Society*, *17*(3), art37. https://doi.org/10.5751/ES-05070-170337

Schoennagel, T., Balch, J. K., Brenkert-Smith, H., Dennison, P. E., Harvey, B. J., Krawchuk, M. A., Mietkiewicz, N., Morgan, P., Moritz, M. A., Rasker, R., Turner, M. G., & Whitlock, C. (2017). Adapt to more wildfire in western North American forests as climate changes. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(18), 4582–4590. https://doi.org/10.1073/pnas.1617464114

Schoennagel, T., Veblen, T. T., & Romme, W. H. (2004). The interaction of fire, fuels, and climate across Rocky Mountain forests. *Bioscience*, *54*(7), 661. https://doi.org/10.1641/0006-3568(2004)054[0661:TIOFFA]2.0.CO;2

Schulte, F., Lucas, E., Rau, J., Szabo, L., & Hancock, J. (2020). *Millions of older Americans live in counties with no ICU beds As pandemic intensifies*. Kaiser Health News. https://kffhealthnews.org/news/as-coronavirus-spreads-widely-millions-of-older-americans-live-in-counties-with-no-icu-beds/

Schultz, C. A., Jedd, T., & Beam, R. D. (2012). The collaborative forest landscape restoration program: A history and overview of the first projects. *Journal of Forestry*, *110*(7), 381–391. https://doi.org/10.5849/jof.11-082

Scott, J. H., Gilbertson-Day, J. W., Moran, C., Dillon, G. K., Short, K. C., & Vogler, K. C. (2020). *Wildfire risk to communities: Spatial datasets of landscape-wide wildfire risk components for the United States* [dataset]. Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2020-0016

Sitters, H., & Di Stefano, J. (2020). Integrating functional connectivity and fire management for better conservation outcomes. *Conservation Biology*, *34*(3), 550–560. https://doi.org/10.1111/cobi.13446

Stephens, S. L., Battaglia, M. A., Churchill, D. J., Collins, B. M., Coppoletta, M., Hoffman, C. M., Lydersen, J. M., North, M. P., Parsons, R. A., Ritter, S. M., & Stevens, J. T. (2020). Forest restoration and fuels reduction: Convergent or divergent? *Bioscience*, *71*, biaa134. https://doi.org/10.1093/biosci/biaa134

Stephens, S. L., Foster, D. E., Battles, J. J., Bernal, A. A., Collins, B. M., Hedges, R., Moghaddas, J. J., Roughton, A. T., & York, R. A. (2024). Forest restoration and fuels reduction work: Different pathways for achieving success in the Sierra Nevada. *Ecological Applications*, *34*(2), e2932. https://doi.org/10.1002/eap.2932

Suraci, J. P., Farwell, L. S., Littlefield, C. E., Freeman, P. T., Zachmann, L. J., Landau, V. A., Anderson, J. J., & Dickson, B. G. (2023). Achieving conservation targets by jointly addressing climate change and biodiversity loss. *Ecosphere*, *14*(4), e4490. https://doi.org/10.1002/ecs2.4490

Suraci, J. P., Littlefield, C. E., Nicholson, C. C., Hunter, M. C., Sorensen, A., & Dickson, B. G. (2023). Mapping connectivity and conservation opportunity on agricultural lands across the conterminous United States. *Biological Conservation*, *278*, 109896. https://doi.org/10.1016/j.biocon.2022.109896

The White House. (2022a). Executive order 14072 of April 22, 2022: Strengthening the nation's forests, communities, and local

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

economies. *Federal Register*, *87*(81), 24851–24855. https://www.govinfo.gov/content/pkg/FR-2022-04-27/pdf/2022-09138.pdf

The White House. (2022b). *FACT SHEET: President biden signs executive order to strengthen America's forests, boost wildfire resilience, and combat global deforestation*. https://www.whitehouse.gov/briefing-room/statements-releases/2022/04/22/fact-sheet-president-biden-signs-executive-order-to-strengthen-americas-forests-boost-wildfire-resilience-and-combat-global-deforestation/

Thom, D., & Seidl, R. (2016). Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews*, *91*(3), 760–781. https://doi.org/10.1111/brv.12193

Thompson, C., Smith, H., Green, R., Wasser, S., & Purcell, K. (2021). Fisher use of postfire landscapes: Implications for habitat connectivity and restoration. *Western North American Naturalist*, *81*(2), 225–242. https://doi.org/10.3398/064.081.0207

U.S. Department of Agriculture. (2022). *Secretary vilsack announces new 10 year strategy to confront the wildfire crisis*. https://www.usda.gov/media/press-releases/2022/01/18/secretary-vilsack-announces-new-10-year-strategy-confront-wildfire

U.S. Department of the Interior. (2022). *Interior department releases five-year monitoring, maintenance and treatment plan to address wildfire risk*. https://www.doi.gov/pressreleases/interior-department-releases-five-year-monitoring-maintenance-and-treatment-plan

U.S. Environmental Protection Agency. (2022). *Climate change indicators: wildfires*. https://www.epa.gov/climate-indicators/climate-change-indicators-wildfires

U.S. Forest Service. (2024). *Amendments to land management plans to address old-growth forests across the national forest system: Draft environmental impact statement*.

United Nations Environment Programme. (2022). *Spreading like wildfire—The rising threat of extraordinary landscape fires*. A UNEP Rapid Response Assessment.

Urgenson, L. S., Ryan, C. M., Halpern, C. B., Bakker, J. D., Belote, R. T., Franklin, J. F., Haugo, R. D., Nelson, C. R., & Waltz, A. E. M. (2017). Visions of restoration in fire-adapted Forest landscapes: Lessons from the collaborative forest landscape restoration program. *Environmental Management*, *59*(2), 338–353. https://doi.org/10.1007/s00267-016-0791-2

USFS. (2023). *Confronting the wildfire crisis*. U.S. Department of Agriculture.

USFS Forest Inventory & Analysis. (2022). *CONUS total forest carbon 2018* [dataset]. https://usfs.maps.arcgis.com/home/item.html?id=bd3c2c1ba3844ebabd8df6d1c4932387

USGS. (2020). *U.S Geological Survey (USGS) Gap Analysis Project (GAP). Protected Areas Database of the United States (PAD-US) 2.1: U.S. Geological Survey data release*. [dataset].

Vukomanovic, J., & Steelman, T. (2019). A systematic review of relationships between mountain wildfire and ecosystem services. *Landscape Ecology*, *34*(5), 1179–1194. https://doi.org/10.1007/s10980-019-00832-9

Wigtil, G., Hammer, R. B., Kline, J. D., Mockrin, M. H., Stewart, S. I., Roper, D., & Radeloff, V. C. (2016). Places where wildfire potential and social vulnerability coincide in the coterminous United States. *International Journal of Wildland Fire*, *25*(8), 896. https://doi.org/10.1071/WF15109

Wilson, B. T., Knight, J. F., & McRoberts, R. E. (2018). Harmonic regression of Landsat time series for modeling attributes from national forest inventory data. *ISPRS Journal of Photogrammetry and Remote Sensing*, *137*, 29–46. https://doi.org/10.1016/j.isprsjprs.2018.01.006

Wiréhn, L., Danielsson, Å., & Neset, T.-S. S. (2015). Assessment of composite index methods for agricultural vulnerability to climate change. *Journal of Environmental Management*, *156*, 70–80. https://doi.org/10.1016/j.jenvman.2015.03.020

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supplementary methods.

Table S1.1. The fourteen indices of social vulnerability considered here and the indicators selected from each for inclusion in this analysis.

Figure S1.1. PCA biplot for the social vulnerability dataset, highlighting the mapping of demographic and health datasets along Principal Component (PC) 1 and PC2.

Figure S1.2. CONUS-wide distribution of the three sub-indices contributing to the SEI: (a) social vulnerability, (b) ecological values, and (c) ecosystem services.

Appendix S2. Supplementary results.

Table S2.1. Mean values (±SD) for all indicators within high value polygons summarized across CONUS as well as the percent change in those indicator values when refining areas within the top 20% of the WMPI by focusing solely on focal areas.

Table S2.2. Mean values (±SD) for all indicators within the top ten USFS firesheds by region summarized across CONUS, as well as the percent change in those indicator values when focusing solely on areas of overlap between these top firesheds and our focal areas.

Figure S2.1. The overlapping area between the USFS top 10 firesheds and our focal areas (left) around Denver, Colorado and the WMPI (center) and SEI (right) values that are contained within those overlapping polygons.

Figure S2.2. The overlapping area between the USFS top 10 firesheds and our focal areas (left) around Charleston, West Virginia and the WMPI (center) and SEI (right) values that are contained within those overlapping polygons.

How to cite this article: Lacey, L. M., Suraci, J. P., Littlefield, C. E., Busse, B. S., & Dickson, B. G. (2025). Informing proactive wildfire management that benefits vulnerable communities and ecological values. *People and Nature*, *7*, 52–66. https://doi.org/10.1002/pan3.10733

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10733, Wiley Online Library on [16/02/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Land use strategies to mitigate climate change in carbon dense temperate forests

Beverly E. Law[a,1], Tara W. Hudiburg[b], Logan T. Berner[c], Jeffrey J. Kent[b], Polly C. Buotte[a], and Mark E. Harmon[a]

[a]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97333; [b]Department of Forest, Rangeland, and Fire Sciences, University of Idaho, Moscow, ID 83844; and [c]EcoSpatial Services L.L.C., Flagstaff, AZ 86004

Edited by William H. Schlesinger, Duke University, Durham, NC, and approved January 22, 2018 (received for review November 16, 2017)

Strategies to mitigate carbon dioxide emissions through forestry activities have been proposed, but ecosystem process-based integration of climate change, enhanced CO_2, disturbance from fire, and management actions at regional scales are extremely limited. Here, we examine the relative merits of afforestation, reforestation, management changes, and harvest residue bioenergy use in the Pacific Northwest. This region represents some of the highest carbon density forests in the world, which can store carbon in trees for 800 y or more. Oregon's net ecosystem carbon balance (NECB) was equivalent to 72% of total emissions in 2011–2015. By 2100, simulations show increased net carbon uptake with little change in wildfires. Reforestation, afforestation, lengthened harvest cycles on private lands, and restricting harvest on public lands increase NECB 56% by 2100, with the latter two actions contributing the most. Resultant cobenefits included water availability and biodiversity, primarily from increased forest area, age, and species diversity. Converting 127,000 ha of irrigated grass crops to native forests could decrease irrigation demand by 233 billion $m^3 \cdot y^{-1}$. Utilizing harvest residues for bioenergy production instead of leaving them in forests to decompose increased emissions in the short-term (50 y), reducing mitigation effectiveness. Increasing forest carbon on public lands reduced emissions compared with storage in wood products because the residence time is more than twice that of wood products. Hence, temperate forests with high carbon densities and lower vulnerability to mortality have substantial potential for reducing forest sector emissions. Our analysis framework provides a template for assessments in other temperate regions.

forests | carbon balance | greenhouse gas emissions | climate mitigation

Strategies to mitigate carbon dioxide emissions through forestry activities have been proposed, but regional assessments to determine feasibility, timeliness, and effectiveness are limited and rarely account for the interactive effects of future climate, atmospheric CO_2 enrichment, nitrogen deposition, disturbance from wildfires, and management actions on forest processes. We examine the net effect of all of these factors and a suite of mitigation strategies at fine resolution (4-km grid). Proven strategies immediately available to mitigate carbon emissions from forest activities include the following: (*i*) reforestation (growing forests where they recently existed), (*ii*) afforestation (growing forests where they did not recently exist), (*iii*) increasing carbon density of existing forests, and (*iv*) reducing emissions from deforestation and degradation (1). Other proposed strategies include wood bioenergy production (2–4), bioenergy combined with carbon capture and storage (BECCS), and increasing wood product use in buildings. However, examples of commercial-scale BECCS are still scarce, and sustainability of wood sources remains controversial because of forgone ecosystem carbon storage and low environmental cobenefits (5, 6). Carbon stored in buildings generally outlives its usefulness or is replaced within decades (7) rather than the centuries possible in forests, and the factors influencing product substitution have yet to be fully explored (8). Our analysis of mitigation strategies focuses on the first four strategies, as well as bioenergy production, utilizing harvest residues only and without carbon capture and storage.

The appropriateness and effectiveness of mitigation strategies within regions vary depending on the current forest sink, competition with land-use and watershed protection, and environmental conditions affecting forest sustainability and resilience. Few process-based regional studies have quantified strategies that could actually be implemented, are low-risk, and do not depend on developing technologies. Our previous studies focused on regional modeling of the effects of forest thinning on net ecosystem carbon balance (NECB) and net emissions, as well as improving modeled drought sensitivity (9, 10), while this study focuses mainly on strategies to enhance forest carbon.

Our study region is Oregon in the Pacific Northwest, where coastal and montane forests have high biomass and carbon sequestration potential. They represent coastal forests from northern California to southeast Alaska, where trees live 800 y or more and biomass can exceed that of tropical forests (11) (Fig. S1). The semiarid ecoregions consist of woodlands that experience frequent fires (12). Land-use history is a major determinant of forest carbon balance. Harvest was the dominant cause of tree mortality (2003–2012) and accounted for fivefold as much mortality as that from fire and beetles combined (13). Forest land ownership is predominantly public (64%), and 76% of the biomass harvested is on private lands.

Significance

Regional quantification of feasibility and effectiveness of forest strategies to mitigate climate change should integrate observations and mechanistic ecosystem process models with future climate, CO_2, disturbances from fire, and management. Here, we demonstrate this approach in a high biomass region, and found that reforestation, afforestation, lengthened harvest cycles on private lands, and restricting harvest on public lands increased net ecosystem carbon balance by 56% by 2100, with the latter two actions contributing the most. Forest sector emissions tracked with our life cycle assessment model decreased by 17%, partially meeting emissions reduction goals. Harvest residue bioenergy use did not reduce short-term emissions. Cobenefits include increased water availability and biodiversity of forest species. Our improved analysis framework can be used in other temperate regions.

Author contributions: B.E.L. and T.W.H. designed research; B.E.L., T.W.H., and P.C.B. performed research; M.E.H. contributed new reagents/analytic tools; B.E.L., L.T.B., J.J.K., and P.C.B. analyzed data; B.E.L., T.W.H., L.T.B., and M.E.H. wrote the paper; and M.E.H. contributed the substitution model.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

Data deposition: The CLM4.5 model data are available at Oregon State University (terraweb.forestry.oregonstate.edu/FMEC). Data from the >200 intensive plots on forest carbon are available at Oak Ridge National Laboratory (https://daac.ornl.gov/NACP/guides/NACP_TERRA-PNW.html), and FIA data are available at the USDA Forest Service (https://www.fia.fs.fed.us/tools-data/).

[1]To whom correspondence should be addressed. Email: bev.law@oregonstate.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1720064115/-/DCSupplemental.

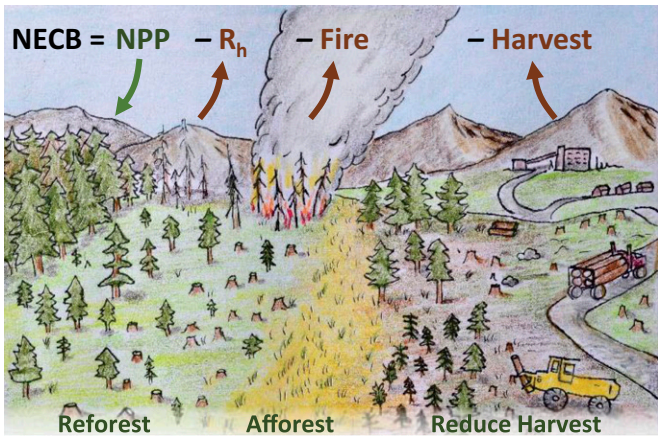


Fig. 1. Approach to assessing effects of mitigation strategies on forest carbon and forest sector emissions. NECB is productivity (NPP) minus Rh and losses from fire and harvest (red arrows). Harvest emissions include those associated with wood products and bioenergy.

Many US states, including Oregon (14), plan to reduce their greenhouse gas (GHG) emissions in accordance with the Paris Agreement. We evaluated strategies to address this question: How much carbon can the region's forests realistically remove from the atmosphere in the future, and which forest carbon strategies can reduce regional emissions by 2025, 2050, and 2100? We propose an integrated approach that combines observations with models and a life cycle assessment (LCA) to evaluate current and future effects of mitigation actions on forest carbon and forest sector emissions in temperate regions (Fig. 1). We estimated the recent carbon budget of Oregon's forests, and simulated the potential to increase the forest sink and decrease forest sector emissions under current and future climate conditions. We provide recommendations for regional assessments of mitigation strategies.

Results

Carbon stocks and fluxes are summarized for the observation cycles of 2001–2005, 2006–2010, and 2011–2015 (Table 1 and Tables S1 and S2). In 2011–2015, state-level forest carbon stocks totaled 3,036 Tg C (3 billion metric tons), with the coastal and montane ecoregions accounting for 57% of the live tree carbon (Tables S1 and S2). Net ecosystem production [NEP; net primary production (NPP) minus heterotrophic respiration (Rh)] averaged 28 teragrams carbon per year (Tg C y^{-1}) over all three periods. Fire emissions were unusually high at 8.69 million metric tons carbon dioxide equivalent ($tCO_2e\ y^{-1}$, i.e., 2.37 Tg C y^{-1}) in 2001–2005 due to the historic Biscuit Fire, but decreased to 3.56 million $tCO_2e\ y^{-1}$ (0.97 Tg C y^{-1}) in 2011–2015 (Table S4). Note that 1 million tCO_2e equals 3.667 Tg C.

Our LCA showed that in 2001–2005, Oregon's net wood product emissions were 32.61 million tCO_2e (Table S3), and 3.7-fold wildfire emissions in the period that included the record fire year (15) (Fig. 2). In 2011–2015, net wood product emissions were 34.45 million tCO_2e and almost 10-fold fire emissions, mostly due to lower fire emissions. The net wood product emissions are higher than fire emissions despite carbon benefits of storage in wood products and substitution for more fossil fuel-intensive products. Hence, combining fire and net wood product emissions, the forest sector emissions averaged 40 million $tCO_2e\ y^{-1}$ and accounted for about 39% of total emissions across all sectors (Fig. 2 and Table S4). NECB was calculated from NEP minus losses from fire emissions and harvest (Fig. 1). State NECB was equivalent to 60% and 70% of total emissions for 2001–2005 and 2011–2015, respectively (Fig. 2, Table 1, and Table S4). Fire emissions were only between 4% and 8% of total emissions from all sources (2011–2015 and 2001–2004, respectively). Oregon's forests play a larger role in meeting its GHG targets than US forests have in meeting the nation's targets (16, 17).

Historical disturbance regimes were simulated using stand age and disturbance history from remote sensing products. Comparisons of Community Land Model (CLM4.5) output with Forest Inventory and Analysis (FIA) aboveground tree biomass (>6,000 plots) were within 1 SD of the ecoregion means (Fig. S2). CLM4.5 estimates of cumulative burn area and emissions from 1990 to 2014 were 14% and 25% less than observed, respectively. The discrepancy was mostly due to the model missing an anomalously large fire in 2002 (Fig. S3*A*). When excluded, modeled versus observed fire emissions were in good agreement ($r^2 = 0.62$; Fig. S3*B*). A sensitivity test of a 14% underestimate of burn area did not affect our final results because predicted emissions would increase almost equally for business as usual (BAU) management and our scenarios, resulting in no proportional change in NECB. However, the ratio of harvest to fire emissions would be lower.

Projections show that under future climate, atmospheric carbon dioxide, and BAU management, an increase in net carbon uptake due to CO_2 fertilization and climate in the mesic ecoregions far outweighs losses from fire and drought in the semiarid ecoregions. There was not an increasing trend in fire. Carbon stocks increased by 2% and 7% and NEP increased by 12% and 40% by 2050 and 2100, respectively.

We evaluated emission reduction strategies in the forest sector: protecting existing forest carbon, lengthening harvest cycles, reforestation, afforestation, and bioenergy production with product substitution. The largest potential increase in forest carbon is in the mesic Coast Range and West Cascade ecoregions. These forests are buffered by the ocean, have high soil water-holding capacity, low risk of wildfire [fire intervals average 260–400 y (18)], long carbon residence time, and potential for high carbon density. They can attain biomass up to 520 Mg C ha^{-1} (12). Although Oregon has several protected areas, they account for only 9–15% of the total forest area, so we expect it may be feasible to add carbon-protected lands with cobenefits of water protection and biodiversity.

Reforestation of recently forested areas include those areas impacted by fire and beetles. Our simulations to 2100 assume regrowth of the same species and incorporate future fire responses to climate and cyclical beetle outbreaks [70–80 y (13)]. Reforestation has the potential to increase stocks by 315 Tg C by 2100, reducing forest sector net emissions by 5% by 2100 relative to BAU management (Fig. 3). The East and West Cascades ecoregions had the highest reforestation potential, accounting for 90% of the increase (Table S5).

Afforestation of old fields within forest boundaries and nonfood/nonforage grass crops, hereafter referred to as "grass crops," had to meet minimum conditions for tree growth, and crop grid cells had to be partially forested (*SI Methods* and Table S6). These crops are not grazed or used for animal feed. Competing land uses may decrease the actual amount of area that can be afforested. We calculated the amount of irrigated grass crops (127,000 ha) that could be converted to forest, assuming success of carbon offset programs (19). By 2100, afforestation increased stocks by

Table 1. Forest carbon budget components used to compute NECB

Flux, Tg C·y^{-1}	2001–2005		2006–2010		2011–2015		2001–2015
NPP	73.64	7.59	73.57	7.58	73.57	7.58	73.60
Rh	45.67	5.11	45.38	5.07	45.19	5.05	45.41
NEP	27.97	9.15	28.19	9.12	28.39	9.11	28.18
Harvest removals	8.58	0.60	7.77	0.54	8.61	0.6	8.32
Fire emissions	2.37	0.27	1.79	0.2	0.97	0.11	1.71
NECB	17.02	9.17	18.63	9.14	18.81	9.13	18.15

Average annual values for each period, including uncertainty (95% confidence interval) in Tg C y^{-1} (multiply by 3.667 to get million tCO_2e).

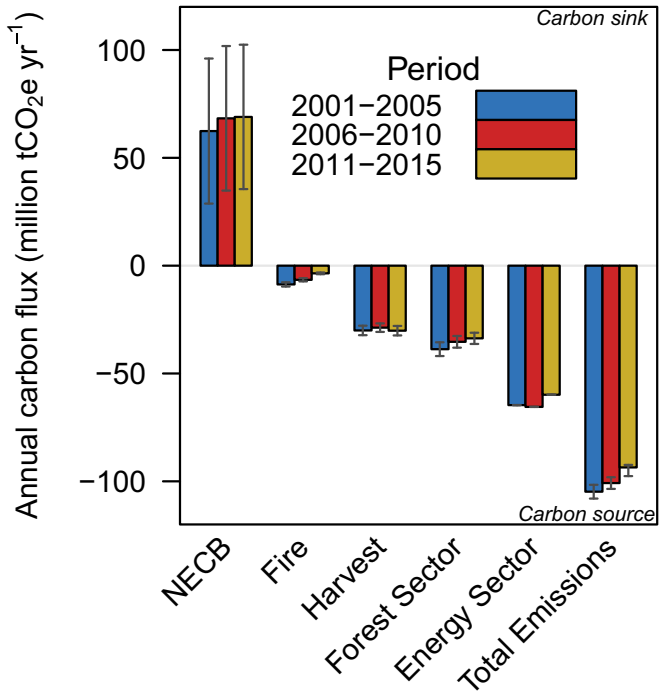


Fig. 2. Oregon's forest carbon sink and emissions from forest and energy sectors. Harvest emissions are computed by LCA. Fire and harvest emissions sum to forest sector emissions. Energy sector emissions are from the Oregon Global Warming Commission (14), minus forest-related emissions. Error bars are 95% confidence intervals (Monte Carlo analysis).

94 Tg C and cumulative NECB by 14 Tg C, and afforestation reduced forest sector GHG emissions by 1.3–1.4% in 2025, 2050, and 2100 (Fig. 3).

We quantified cobenefits of afforestation of irrigated grass crops on water availability based on data from hydrology and agricultural simulations of future grass crop area and related irrigation demand (20). Afforestation of 127,000 ha of grass cropland with Douglas fir could decrease irrigation demand by 222 and 233 billion $m^3 \cdot y^{-1}$ by 2050 and 2100, respectively. An independent estimate from measured precipitation and evapotranspiration (ET) at our mature Douglas fir and grass crop flux sites in the Willamette Valley shows the ET/precipitation fraction averaged 33% and 52%, respectively, and water balance (precipitation minus ET) averaged 910 $mm \cdot y^{-1}$ and 516 $mm \cdot y^{-1}$. Under current climate conditions, the observations suggest an increase in annual water availability of 260 billion $m^3 \cdot y^{-1}$ if 127,000 ha of the irrigated grass crops were converted to forest.

Harvest cycles in the mesic and montane forests have declined from over 120 y to 45 y despite the fact that these trees can live 500–1,000 y and net primary productivity peaks at 80–125 y (21). If harvest cycles were lengthened to 80 y on private lands and harvested area was reduced 50% on public lands, state-level stocks would increase by 17% to a total of ~3,600 Tg C and NECB would increase 2–3 Tg C y^{-1} by 2100. The lengthened harvest cycles reduced harvest by 2 Tg C y^{-1}, which contributed to higher NECB. Leakage (more harvest elsewhere) is difficult to quantify and could counter these carbon gains. However, because harvest on federal lands was reduced significantly since 1992 (NW Forest Plan), leakage has probably already occurred.

The four strategies together increased NECB by 64%, 82%, and 56% by 2025, 2050, and 2100, respectively. This reduced forest sector net emissions by 11%, 10%, and 17% over the same periods (Fig. 3). By 2050, potential increases in NECB were largest in the Coast Range (Table S5), East Cascades, and Klamath Mountains, accounting for 19%, 25%, and 42% of the total increase, whereas by 2100, they were most evident in the West Cascades, East Cascades, and Klamath Mountains.

We examined the potential for using existing harvest residue for electricity generation, where burning the harvest residue for energy emits carbon immediately (3) versus the BAU practice of leaving residues in forests to slowly decompose. Assuming half of forest residues from harvest practices could be used to replace natural gas or coal in distributed facilities across the state, they would provide an average supply of 0.75–1 Tg C y^{-1} to the year 2100 in the reduced harvest and BAU scenarios, respectively. Compared with BAU harvest practices, where residues are left to decompose, proposed bioenergy production would increase cumulative net emissions by up to 45 Tg C by 2100. Even at 50% use, residue collection and transport are not likely to be economically viable, given the distances (>200 km) to Oregon's facilities.

Discussion

Earth system models have the potential to bring terrestrial observations related to climate, vulnerability, impacts, adaptation,

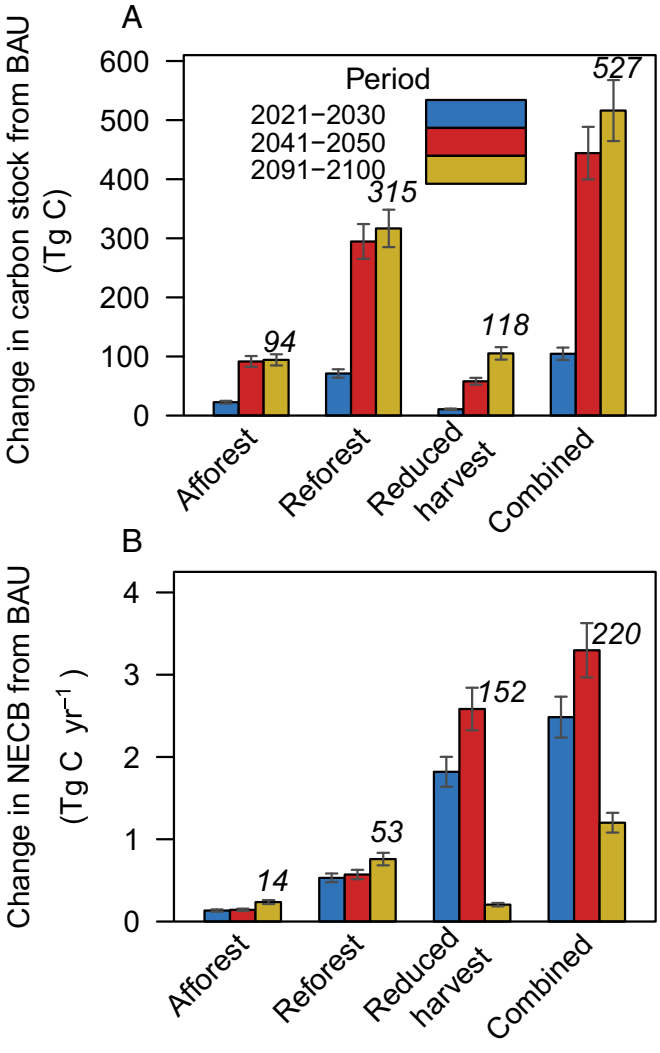


Fig. 3. Future change in carbon stocks and NECB with mitigation strategies relative to BAU management. The decadal average change in forest carbon stocks (*A*) and NECB relative to BAU (*B*) are shown. Italicized numbers over bars indicate mean forest carbon stocks in 2091–2100 (*A*) and cumulative change in NECB for 2015–2100 (*B*). Error bars are ±10%.

and mitigation into a common framework, melding biophysical with social components (22). We developed a framework to examine a suite of mitigation actions to increase forest carbon sequestration and reduce forest sector emissions under current and future environmental conditions.

Harvest-related emissions had a large impact on recent forest NECB, reducing it by an average of 34% from 2001 to 2015. By comparison, fire emissions were relatively small and reduced NECB by 12% in the Biscuit Fire year, but only reduced NECB 5–9% from 2006 to 2015. Thus, altered forest management has the potential to enhance the forest carbon balance and reduce emissions.

Future NEP increased because enhancement from atmospheric carbon dioxide outweighed the losses from fire. Lengthened harvest cycles on private lands to 80 y and restricting harvest to 50% of current rates on public lands increased NECB the most by 2100, accounting for 90% of total emissions reduction (Fig. 3 and Tables S5 and S6). Reduced harvest led to NECB increasing earlier than the other strategies (by 2050), suggesting this could be a priority for implementation.

Our afforestation estimates may be too conservative by limiting them to nonforest areas within current forest boundaries and 127,000 ha of irrigated grass cropland. There was a net loss of 367,000 ha of forest area in Oregon and Washington combined from 2001 to 2006 (23), and less than 1% of native habitat remains in the Willamette Valley due to urbanization and agriculture (24). Perhaps more of this area could be afforested.

The spatial variation in the potential for each mitigation option to improve carbon stocks and fluxes shows that the reforestation potential is highest in the Cascade Mountains, where fire and insects occur (Fig. 4). The potential to reduce harvest on public land is highest in the Cascade Mountains, and that to lengthen harvest cycles on private lands is highest in the Coast Range.

Although western Oregon is mesic with little expected change in precipitation, the afforestation cobenefits of increased water availability will be important. Urban demand for water is projected to increase, but agricultural irrigation will continue to consume much more water than urban use (25). Converting 127,000 ha of irrigated grass crops to native forests appears to be a win–win strategy, returning some of the area to forest land, providing habitat and connectivity for forest species, and easing irrigation demand. Because the afforested grass crop represents only 11% of the available grass cropland (1.18 million ha), it is not likely to result in leakage or indirect land use change. The two forest strategies combined are likely to be important contributors to water security.

Cobenefits with biodiversity were not assessed in our study. However, a recent study showed that in the mesic forests, cobenefits with biodiversity of forest species are largest on lands with harvest cycles longer than 80 y, and thus would be most pronounced on private lands (26). We selected 80 y for the harvest cycle mitigation strategy because productivity peaks at 80–125 y in this region, which coincides with the point at which cobenefits with wildlife habitat are substantial.

Habitat loss and climate change are the two greatest threats to biodiversity. Afforestation of areas that are currently grass crops would likely improve the habitat of forest species (27), as about 90% of the forests in these areas were replaced by agriculture. About 45 mammal species are at risk because of range contraction (28). Forests are more efficient at dissipating heat than grass and crop lands, and forest cover gains lead to net surface cooling in all regions south of about 45° latitude in North American and Europe (29). The cooler conditions can buffer climate-sensitive bird populations from approaching their thermal limits and provide more food and nest sites (30). Thus, the mitigation strategies of afforestation, protecting forests on public lands and lengthening harvest cycles to 80–125 y, would likely benefit forest-dependent species.

Oregon has a legislated mandate to reduce emissions, and is considering an offsets program that limits use of offsets to 8% of

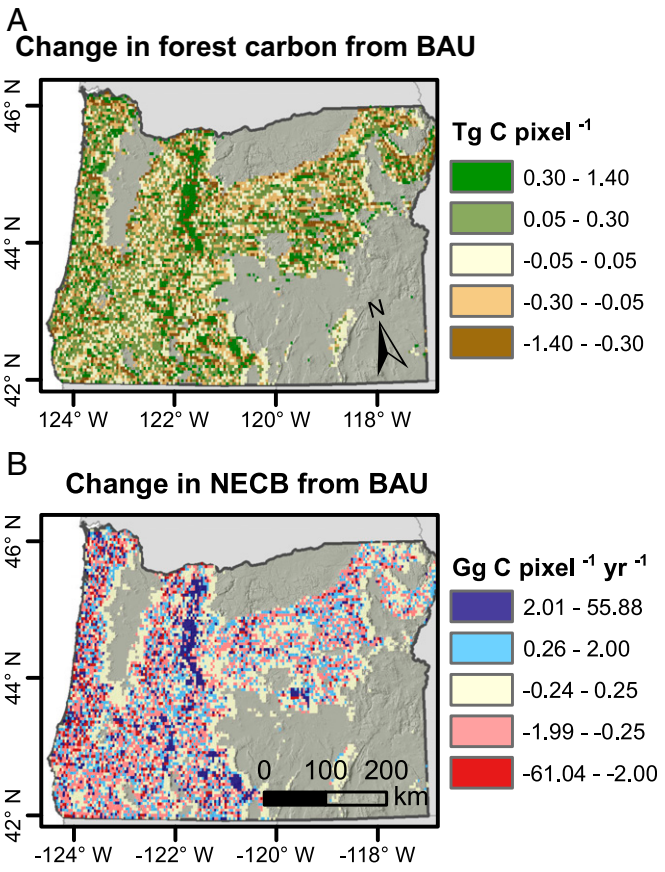


Fig. 4. Spatial patterns of forest carbon stocks and NECB by 2091–2100. The decadal average changes in forest carbon stocks (*A*) and NECB (*B*) due to afforestation, reforestation, protected areas, and lengthened harvest cycles relative to continued BAU forest management (red is increase in NECB) are shown.

the total emissions reduction to ensure that regulated entities substantially reduce their own emissions, similar to California's program (19). An offset becomes a net emissions reduction by increasing the forest carbon sink (NECB). If only 8% of the GHG reduction is allowed for forest offsets, the limits for forest offsets would be 2.1 and 8.4 million metric tCO_2e of total emissions by 2025 and 2050, respectively (Table S6). The combination of afforestation, reforestation, and reduced harvest would provide 13 million metric tCO_2e emissions reductions, and any one of the strategies or a portion of each could be applied. Thus, additionality beyond what would happen without the program is possible.

State-level reporting of GHG emissions includes the agriculture sector, but does not appear to include forest sector emissions, except for industrial fuel (i.e., utility fuel in Table S3) and, potentially, fire emissions. Harvest-related emissions should be quantified, as they are much larger than fire emissions in the western United States. Full accounting of forest sector emissions is necessary to meet climate mitigation goals.

Increased long-term storage in buildings and via product substitution has been suggested as a potential climate mitigation option. Pacific temperate forests can store carbon for many hundreds of years, which is much longer than is expected for buildings that are generally assumed to outlive their usefulness or be replaced within several decades (7). By 2035, about 75% of buildings in the United States will be replaced or renovated, based on new construction, demolition, and renovation trends (31, 32). Recent analysis suggests substitution benefits of using wood versus more fossil fuel-intensive materials have been overestimated by at

least an order of magnitude (33). Our LCA accounts for losses in product substitution stores (PSSs) associated with building life span, and thus are considerably lower than when no losses are assumed (4, 34). While product substitution reduces the overall forest sector emissions, it cannot offset the losses incurred by frequent harvest and losses associated with product transportation, manufacturing, use, disposal, and decay. Methods for calculating substitution benefits should be improved in other regional assessments.

Wood bioenergy production is interpreted as being carbon-neutral by assuming that trees regrow to replace those that burned. However, this does not account for reduced forest carbon stocks that took decades to centuries to sequester, degraded productive capacity, emissions from transportation and the production process, and biogenic/direct emissions at the facility (35). Increased harvest through proposed thinning practices in the region has been shown to elevate emissions for decades to centuries regardless of product end use (36). It is therefore unlikely that increased wood bioenergy production in this region would decrease overall forest sector emissions.

Conclusions

GHG reduction must happen quickly to avoid surpassing a 2 °C increase in temperature since preindustrial times. Alterations in forest management can contribute to increasing the land sink and decreasing emissions by keeping carbon in high biomass forests, extending harvest cycles, reforestation, and afforestation. Forests are carbon-ready and do not require new technologies or infrastructure for immediate mitigation of climate change. Growing forests for bioenergy production competes with forest carbon sequestration and does not reduce emissions in the next decades (10). BECCS requires new technology, and few locations have sufficient geological storage for CO_2 at power facilities with high-productivity forests nearby. Accurate accounting of forest carbon in trees and soils, NECB, and historic harvest rates, combined with transparent quantification of emissions from the wood product process, can ensure realistic reductions in forest sector emissions.

As states and regions take a larger role in implementing climate mitigation steps, robust forest sector assessments are urgently needed. Our integrated approach of combining observations, an LCA, and high-resolution process modeling (4-km grid vs. typical 200-km grid) of a suite of potential mitigation actions and their effects on forest carbon sequestration and emissions under changing climate and CO_2 provides an analysis framework that can be applied in other temperate regions.

Materials and Methods

Current Stocks and Fluxes. We quantified recent forest carbon stocks and fluxes using a combination of observations from FIA; Landsat products on forest type, land cover, and fire risk; 200 intensive plots in Oregon (37); and a wood decomposition database. Tree biomass was calculated from species-specific allometric equations and ecoregion-specific wood density. We estimated ecosystem carbon stocks, NEP (photosynthesis minus respiration), and NECB (NEP minus losses due to fire or harvest) using a mass-balance approach (36, 38) (Table 1 and *SI Materials and Methods*). Fire emissions were computed from the Monitoring Trends in Burn Severity database, biomass data, and region-specific combustion factors (15, 39) (*SI Materials and Methods*).

Future Projections and Model Description. Carbon stocks and NEP were quantified to the years 2025, 2050, and 2100 using CLM4.5 with physiological parameters for 10 major forest species, initial forest biomass (36), and future climate and atmospheric carbon dioxide as input (Institut Pierre Simon Laplace climate system model downscaled to 4 km × 4 km, representative concentration pathway 8.5). CLM4.5 uses 3-h climate data, ecophysiological characteristics, site physical characteristics, and site history to estimate the daily fluxes of carbon, nitrogen, and water between the atmosphere, plant state variables, and litter and soil state variables. Model components are biogeophysics, hydrological cycle, and biogeochemistry. This model version does not include a dynamic vegetation model to simulate resilience and establishment following disturbance. However, the effect of regeneration lags on forest carbon is not particularly strong for the long disturbance intervals in this study (40). Our plant functional type (PFT) parameterization for 10 major forest species rather than one significantly improves carbon modeling in the region (41).

Forest Management and Land Use Change Scenarios. Harvest cycles, reforestation, and afforestation were simulated to the year 2100. Carbon stocks and NEP were predicted for the current harvest cycle of 45 y compared with simulations extending it to 80 y. Reforestation potential was simulated over areas that recently suffered mortality from harvest, fire, and 12 species of beetles (13). We assumed the same vegetation regrew to the maximum potential, which is expected with the combination of natural regeneration and planting that commonly occurs after these events. Future BAU harvest files were constructed using current harvest rates, where county-specific average harvest and the actual amounts per ownership were used to guide grid cell selection. This resulted in the majority of harvest occurring on private land (70%) and in the mesic ecoregions. Beetle outbreaks were implemented using a modified mortality rate of the lodgepole pine PFT with 0.1% y^{-1} biomass mortality by 2100.

For afforestation potential, we identified areas that are within forest boundaries that are not currently forest and areas that are currently grass crops. We assumed no competition with conversion of irrigated grass crops to urban growth, given Oregon's land use laws for developing within urban growth boundaries. A separate study suggested that, on average, about 17% of all irrigated agricultural crops in the Willamette Valley could be converted to urban area under future climate; however, because 20% of total cropland is grass seed, it suggests little competition with urban growth (25).

Landsat observations (12,500 scenes) were processed to map changes in land cover from 1984 to 2012. Land cover types were separated with an unsupervised K-means clustering approach. Land cover classes were assigned to an existing forest type map (42). The CropScape Cropland Data Layer (CDL 2015, https://nassgeodata.gmu.edu/CropScape/) was used to distinguish nonforage grass crops from other grasses. For afforestation, we selected grass cropland with a minimum soil water-holding capacity of 150 mm and minimum precipitation of 500 mm that can support trees (43).

Afforestation Cobenefits. Modeled irrigation demand of grass seed crops under future climate conditions was previously conducted with hydrology and agricultural models, where ET is a function of climate, crop type, crop growth state, and soil-holding capacity (20) (Table S7). The simulations produced total land area, ET, and irrigation demand for each cover type. Current grass seed crop irrigation in the Willamette Valley is 413 billion $m^3 \cdot y^{-1}$ for 238,679 ha and is projected to be 412 and 405 billion m^3 in 2050 and 2100 (20) (Table S7). We used annual output from the simulations to estimate irrigation demand per unit area of grass seed crops (1.73, 1.75, and 1.84 million $m^3 \cdot ha^{-1}$ in 2015, 2050, and 2100, respectively), and applied it to the mapped irrigated crop area that met conditions necessary to support forests (Table S7).

LCA. Decomposition of wood through the product cycle was computed using an LCA (8, 10). Carbon emissions to the atmosphere from harvest were calculated annually over the time frame of the analysis (2001–2015). The net carbon emissions equal NECB plus total harvest minus wood lost during manufacturing and wood decomposed over time from product use. Wood industry fossil fuel emissions were computed for harvest, transportation, and manufacturing processes. Carbon credit was calculated for wood product storage, substitution, and internal mill recycling of wood losses for bioenergy.

Products were divided into sawtimber, pulpwood, and wood and paper products using published coefficients (44). Long-term and short-term products were assumed to decay at 2% and 10% per year, respectively (45). For product substitution, we focused on manufacturing for long-term structures (building life span >30 y). Because it is not clear when product substitution started in the Pacific Northwest, we evaluated it starting in 1970 since use of concrete and steel for housing was uncommon before 1965. The displacement value for product substitution was assumed to be 2.1 Mg fossil C/Mg C wood use in long-term structures (46), and although it likely fluctuates over time, we assumed it was constant. We accounted for losses in product substitution associated with building replacement (33) using a loss rate of 2% per year (33), but ignored leakage related to fossil C use by other sectors, which may result in more substitution benefit than will actually occur.

The general assumption for modern buildings, including cross-laminate timber, is they will outlive their usefulness and be replaced in about 30 y (7). By 2035, ~75% of buildings in the United States will be replaced or renovated, based on new construction, demolition, and renovation trends, resulting in threefold as many buildings as there are now [2005 baseline (31, 32)]. The loss of

the PSS is therefore PSS multiplied by the proportion of buildings lost per year (2% per year).

To compare the NECB equivalence to emissions, we calculated forest sector and energy sector emissions separately. Energy sector emissions ["in-boundary" state-quantified emissions by the Oregon Global Warming Commission (14)] include those from transportation, residential and commercial buildings, industry, and agriculture. The forest sector emissions are cradle-to-grave annual carbon emissions from harvest and product emissions, transportation, and utility fuels (Table S3). Forest sector utility fuels were subtracted from energy sector emissions to avoid double counting.

Uncertainty Estimates. For the observation-based analysis, Monte Carlo simulations were used to conduct an uncertainty analysis with the mean and SDs for NPP and Rh calculated using several approaches (36) (*SI Materials and Methods*). Uncertainty in NECB was calculated as the combined uncertainty of NEP, fire emissions (10%), harvest emissions (7%), and land cover estimates (10%) using the propagation of error approach. Uncertainty in CLM4.5 model simulations and LCA were quantified by combining the uncertainty in the observations used to evaluate the model, the uncertainty in input datasets (e.g., remote sensing), and the uncertainty in the LCA coefficients (41).

Model input data for physiological parameters and model evaluation data on stocks and fluxes are available online (37).

ACKNOWLEDGMENTS. We thank Dr. Thomas Hilker (deceased) for producing the grass data layer, and Carley Lowe for Fig. 1. This research was supported by the US Department of Energy (Grant DE-SC0012194) and Agriculture and Food Research Initiative of the US Department of Agriculture National Institute of Food and Agriculture (Grants 2013-67003-20652, 2014-67003-22065, and 2014-35100-22066) for our North American Carbon Program studies, "Carbon cycle dynamics within Oregon's urban-suburban-forested-agricultural landscapes," and "Forest die-off, climate change, and human intervention in western North America."

1. Canadell JG, Raupach MR (2008) Managing forests for climate change mitigation. *Science* 320:1456–1457.
2. Holtsmark B (2013) The outcome is in the assumptions: Analyzing the effects on atmospheric CO2 levels of increased use of bioenergy from forest biomass. *Glob Change Biol Bioenergy* 5:467–473.
3. Repo A, Tuomi M, Liski J (2011) Indirect carbon dioxide emissions from producing bioenergy from forest harvest residues. *Glob Change Biol Bioenergy* 3:107–115.
4. Schlamadinger B, Marland G (1996) The role of forest and bioenergy strategies in the global carbon cycle. *Biomass Bioenergy* 10:275–300.
5. Heck V, Gerten D, Lucht W, Popp A (2018) Biomass-based negative emissions difficult to reconcile with planetary boundaries. *Nat Clim Chang* 8:151–155.
6. Field CB, Mach KJ (2017) Rightsizing carbon dioxide removal. *Science* 356:706–707.
7. Tollefson J (2017) The wooden skyscrapers that could help to cool the planet. *Nature* 545:280–282.
8. Law BE, Harmon ME (2011) Forest sector carbon management, measurement and verification, and discussion of policy related to climate change. *Carbon Manag* 2: 73–84.
9. Law BE (2014) Regional analysis of drought and heat impacts on forests: Current and future science directions. *Glob Change Biol* 20:3595–3599.
10. Hudiburg TW, Luyssaert S, Thornton PE, Law BE (2013) Interactive effects of environmental change and management strategies on regional forest carbon emissions. *Environ Sci Technol* 47:13132–13140.
11. Keith H, Mackey BG, Lindenmayer DB (2009) Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proc Natl Acad Sci USA* 106:11635–11640.
12. Law B, Waring R (2015) Carbon implications of current and future effects of drought, fire and management on Pacific Northwest forests. *For Ecol Manage* 355:4–14.
13. Berner LT, Law BE, Meddens AJ, Hicke JA (2017) Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States (2003–2012). *Environ Res Lett* 12:065005.
14. Oregon Global Warming Commission (2017) Biennial Report to the Legislature (Oregon Global Warming Commission, Salem, OR).
15. Campbell J, Donato D, Azuma D, Law B (2007) Pyrogenic carbon emission from a large wildfire in Oregon, United States. *J Geophys Res Biogeosci* 112:G04014.
16. King AW, Hayes DJ, Huntzinger DN, West TO, Post WM (2012) North American carbon dioxide sources and sinks: Magnitude, attribution, and uncertainty. *Front Ecol Environ* 10:512–519.
17. Wilson BT, Woodall CW, Griffith DM (2013) Imputing forest carbon stock estimates from inventory plots to a nationally continuous coverage. *Carbon Balance Manag* 8:1.
18. Reilly MJ, et al. (2017) Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). *Ecosphere* 8:e01695.
19. Anderson CM, Field CB, Mach KJ (2017) Forest offsets partner climate-change mitigation with conservation. *Front Ecol Environ* 15:359–365.
20. Willamette Water 2100 Explorer (2017) Assessing water futures under alternative climate and management scenarios: Agricultural water demand, crop and irrigation decisions. Available at explorer.bee.oregonstate.edu/Topic/WW2100/AgSummaries.aspx. Accessed November 13, 2017.
21. Hudiburg T, et al. (2009) Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. *Ecol Appl* 19:163–180.
22. Bonan GB, Doney SC (2018) Climate, ecosystems, and planetary futures: The challenge to predict life in Earth system models. *Science* 359:eaam8328.
23. Riitters KH, Wickham JD (2012) Decline of forest interior conditions in the conterminous United States. *Sci Rep* 2:653.
24. Noss RF, LaRoe ET, Scott JM (1995) *Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation* (US Department of the Interior, National Biological Service, Washington, DC).
25. Jaeger W, Plantinga A, Langpap C, Bigelow D, Moore K (2017) *Water, Economics and Climate Change in the Willamette Basin* (Oregon State University Extension Service, Corvallis, OR).
26. Kline JD, et al. (2016) Evaluating carbon storage, timber harvest, and habitat possibilities for a Western Cascades (USA) forest landscape. *Ecol Appl* 26:2044–2059.
27. Matthews S, O'Connor R, Plantinga AJ (2002) Quantifying the impacts on biodiversity of policies for carbon sequestration in forests. *Ecol Econ* 40:71–87.
28. Arnold S, Kagan J, Taylor B (2000) Summary of current status of Oregon's biodiversity. *Oregon State of the Environment Report* (Oregon Progress Board, Salem, OR), pp 121–126.
29. Bright RM, et al. (2017) Local temperature response to land cover and management change driven by non-radiative processes. *Nat Clim Chang* 7:296–302.
30. Betts M, Phalan B, Frey S, Rousseau J, Yang Z (2017) Old-growth forests buffer climate-sensitive bird populations from warming. *Diversity Distrib*, 10.1111/ddi.12688.
31. Architecture 2030(2017) The 2030 Challenge. Available at architecture2030.org. Accessed October 23, 2017.
32. Oliver CD, Nassar NT, Lippke BR, McCarter JB (2014) Carbon, fossil fuel, and biodiversity mitigation with wood and forests. *J Sustain For* 33:248–275.
33. Harmon ME, Moreno A, Domingo JB (2009) Effects of partial harvest on the carbon stores in Douglas-fir/western hemlock forests: A simulation study. *Ecosystems (N Y)* 12:777–791.
34. Lippke B, et al. (2011) Life cycle impacts of forest management and wood utilization on carbon mitigation: Knowns and unknowns. *Carbon Manag* 2:303–333.
35. Gunn JS, Ganz DJ, Keeton WS (2011) Biogenic vs. geologic carbon emissions and forest biomass energy production. *GCB Bioenergy* 4:239–242.
36. Hudiburg TW, Law BE, Wirth C, Luyssaert S (2011) Regional carbon dioxide implications of forest bioenergy production. *Nat Clim Chang* 1:419–423.
37. Law BE, Berner LT (2015) *NACP TERRA-PNW: Forest Plant Traits, NPP, Biomass, and Soil Properties, 1999-2014* (ORNL DAAC, Oak Ridge, TN).
38. Law BE, Hudiburg TW, Luyssaert S (2013) Thinning effects on forest productivity: Consequences of preserving old forests and mitigating impacts of fire and drought. *Plant Ecol Divers* 6:73–85.
39. Meigs G, Donato D, Campbell J, Martin J, Law B (2009) Forest fire impacts on carbon uptake, storage, and emission: The role of burn severity in the Eastern Cascades, Oregon. *Ecosystems (N Y)* 12:1246–1267.
40. Harmon ME, Marks B (2002) Effects of silvicultural practices on carbon stores in Douglas-fir western hemlock forests in the Pacific Northwest, USA: Results from a simulation model. *Can J For Res* 32:863–877.
41. Hudiburg TW, Law BE, Thornton PE (2013) Evaluation and improvement of the community land model (CLM4) in Oregon forests. *Biogeosciences* 10:453–470.
42. Ruefenacht B, et al. (2008) Conterminous U.S. and Alaska forest type mapping using forest inventory and analysis data. *Photogramm Eng Remote Sens* 74:1379–1388.
43. Peterman W, Bachelet D, Ferschweiler K, Sheehan T (2014) Soil depth affects simulated carbon and water in the MC2 dynamic global vegetation model. *Ecol Modell* 294:84–93.
44. Smith JE, Heath L, Skog KE, Birdsey R (2006) Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States (US Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA), General Technical Report NE-343.
45. Harmon ME, Harmon JM, Ferrell WK, Brooks D (1996) Modeling carbon stores in Oregon and Washington forest products: 1900–1992. *Clim Change* 33:521–550.
46. Sathre R, O'Connor J (2010) Meta-analysis of greenhouse gas displacement factors of wood product substitution. *Environ Sci Policy* 13:104–114.

frontiers | Frontiers in Forests and Global Change

TYPE Original Research
PUBLISHED 05 December 2022
DOI 10.3389/ffgc.2022.1028401

Check for updates

OPEN ACCESS

EDITED BY
Brendan George Mackey,
Griffith University, Australia

REVIEWED BY
Alfredo Di Filippo,
University of Tuscia, Italy
Andreas Fichtner,
Leuphana University Lüneburg,
Germany

*CORRESPONDENCE
Beverly E. Law
bev.law@oregonstate.edu

SPECIALTY SECTION
This article was submitted to Forest Management, a section of the journal Frontiers in Forests and Global Change

RECEIVED 26 August 2022
ACCEPTED 17 November 2022
PUBLISHED 05 December 2022

CITATION
Law BE, Berner LT, Mildrexler DJ, Bloemers RO and Ripple WJ (2022) Strategic reserves in Oregon's forests for biodiversity, water, and carbon to mitigate and adapt to climate change.
Front. For. Glob. Change 5:1028401.
doi: 10.3389/ffgc.2022.1028401

COPYRIGHT
© 2022 Law, Berner, Mildrexler, Bloemers and Ripple. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

Strategic reserves in Oregon's forests for biodiversity, water, and carbon to mitigate and adapt to climate change

Beverly E. Law[1]*, Logan T. Berner[2], David J. Mildrexler[3], Ralph O. Bloemers[4] and William J. Ripple[1,2,5]

[1]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, United States, [2]EcoSpatial Services L.L.C., Flagstaff, AZ, United States, [3]Eastern Oregon Legacy Lands, Joseph, OR, United States, [4]Green Oregon Alliance, Portland, OR, United States, [5]Conservation Biology Institute, Corvallis, OR, United States

Creating strategic forest reserves is essential for stemming the loss of biodiversity and contributing to climate mitigation and adaptation. Meeting preservation targets of 30% protection by 2030, and 50% by 2050 would lead to greater protection of animal taxa and tree species habitat, carbon stocks and accumulation, and forests that are important sources of drinking water. Here, we develop a regional framework to specifically identify at a fine resolution (30 m) high priority forestlands for preservation in Oregon, USA. We include a resilience metric that represents connectivity and topographic diversity, and identify areas within each ecoregion that are ranked high priority for carbon, biodiversity, resilience and drinking water. Oregon has less than 10% of its forestlands protected at the highest levels, yet its temperate forests are among those with the highest carbon densities in the world. Reserves for surface drinking water sources and forest habitat for birds, mammals, amphibians, and reptiles could increase to 50–70% protection at the highest levels by 2050. Protected aboveground biomass carbon could triple to 635 teragrams of carbon by 2050. The ownership of the high preservation priority lands for carbon and biodiversity is primarily federal (67% by 2050) followed by private (28% by 2050), with much less in the other ownerships. Forest reserves could be established on federal lands through executive action, regulation and rule-making, while private landowners could be incentivized to store more carbon, limit harvest in certain areas and transfer ownership to land trusts. Protecting mature and old forests on federal lands fulfills an urgent need for protection and provides a low-cost way to simultaneously meet national and international goals. This study provides a flexible, dynamic framework for identifying areas that are high priority to protect for climate mitigation and adaptation at regional and sub-regional scales.

KEYWORDS

forests, carbon, biodiversity, drinking water, resilience, climate mitigation, adaptation

Introduction

Immediate and effective action is essential to address accelerated warming, water shortages and biodiversity losses, which includes animals, plants, and ecosystems (Pörtner et al., 2021). Biodiversity loss, degradation and transformation of ecosystems are already worse than predicted due to past global warming and will continue to escalate with increased warming (IPCC, 2022). Safeguarding biodiversity and ecosystem services depend on effective "conservation of about 30–50% of Earth's land, freshwater and ocean areas, including currently near-natural ecosystems" (IPCC, 2022).

In the conterminous United States, only 6.1% of forestland is protected at the highest level, with 0.2% in strict nature reserves to protect biodiversity, 4.8% in wilderness areas, and 1.1% in National Parks (Nelson et al., 2020). Some of the responsibility for immediate action to halt biodiversity loss, protect human drinking water supplies, and mitigate climate change rests upon the states and requires cross-jurisdictional coordination across complex multi-ownership boundaries.

Over the western US, we previously prioritized forest areas for protection based on their carbon densities and biodiversity of animal taxa and tree species (Law et al., 2021). The study suggests the Pacific Northwest has a large amount of forest area that should be high priority for protection by 2030 and 2050. Yet, Oregon has the lowest percentage (10%) of its forest area permanently protected in the eleven western US states. This shortfall called for a closer examination of available ecological data and policy considerations.

Oregon is positioned to take significant actions to meet the protection targets, as it has more than 12 million hectares of forestland, with some of the highest carbon densities in the world (Hudiburg et al., 2009; Law et al., 2018). Oregon relies on mountain watersheds and rivers for a large portion of the drinking water supply. Identifying important areas for conservation at the local scale may require finer spatial data than our western US study (Law et al., 2021), and consideration of different facets of biodiversity, from species richness to the importance of species with small ranges (Pollock et al., 2017), and consideration of all land ownerships to formulate appropriate policy actions. Here, we refined our regional framework to identify forest areas within Oregon for permanent protections that, if preserved, would stem further biodiversity loss, protect drinking water supplies at their sources, prevent carbon dioxide emissions from forest conversion, and safeguard natural carbon stocks and accumulation. We focus on the following questions:

(1) How much of Oregon's land and forestland is currently protected by ecoregion?
(2) Which forestlands could be strategically preserved under 30 × 30 and 50 × 50 within each ecoregion based on forest carbon, biodiversity and/or climate resilience?
(3) Who owns the high preservation priority forestlands?
(4) How would reaching 30 × 30 or 50 × 50 affect protection of species habitat, current forest carbon stocks and surface drinking water sources?
(5) What are potential social and cultural effects of preservation actions and how could policies address this?

Here we used fine resolution datasets (30 m), and expanded our analysis from using species richness as a biodiversity metric to include a priority class based on landscape characteristics such as connectivity and topographic diversity as a resilience metric (Carroll et al., 2018). Stable land characteristics that increase diversity and resilience are not likely to change with climate change (Lawler et al., 2013). We applied the priority ranking within each ecoregion to address the importance of distributing protections across the diversity of ecoregions (Dinerstein et al., 2017; Law et al., 2021).

Our study demonstrated that Oregon has high carbon density forests that also have high biodiversity and connectivity for species movement. When these characteristics were prioritized within each ecoregion, it identified sufficient forestland to meet both the 30% protection by 2030 and 50% by 2050 targets that are important nationally and internationally. Our study did not consider the effects of livestock grazing, but this topic was recently investigated in Oregon and across the American West (Ripple et al., 2022).

Materials and methods

Study region

The study region is Oregon, USA, with a total land area of about 25.06 Mha, of which 12.45 Mha (∼49.7%) is forested (**Figure 1**). Oregon has strong climatic gradients from the Pacific coast to the inland high desert, and multiple mountain ranges that have their own climatic gradients associated with aspect and elevation. Because of this variation, we chose to identify areas with relative potential for protection within each ecoregion. Oregon has nine Environmental Protection Agency (EPA) level 3 ecoregions (Omernik and Griffith, 2014) ranging from temperate mesic forests in the Coast Range and West Cascades ecoregions to semi-arid East Cascades and high biodiversity forests of the Klamath Mountains to interior mixed-conifer forests of the Blue Mountains. Ecoregions are defined by seasonal temperature, precipitation, soil properties, and vegetation types. Three of the eleven ecoregions have little to no forest, including the Columbia Plateau, Northern Basin and Range, and Snake River Plain. Soils range from the high nitrogen and high soil water holding capacity of the Coast Range ecoregion to volcanic soils in the semi-arid East Cascades,

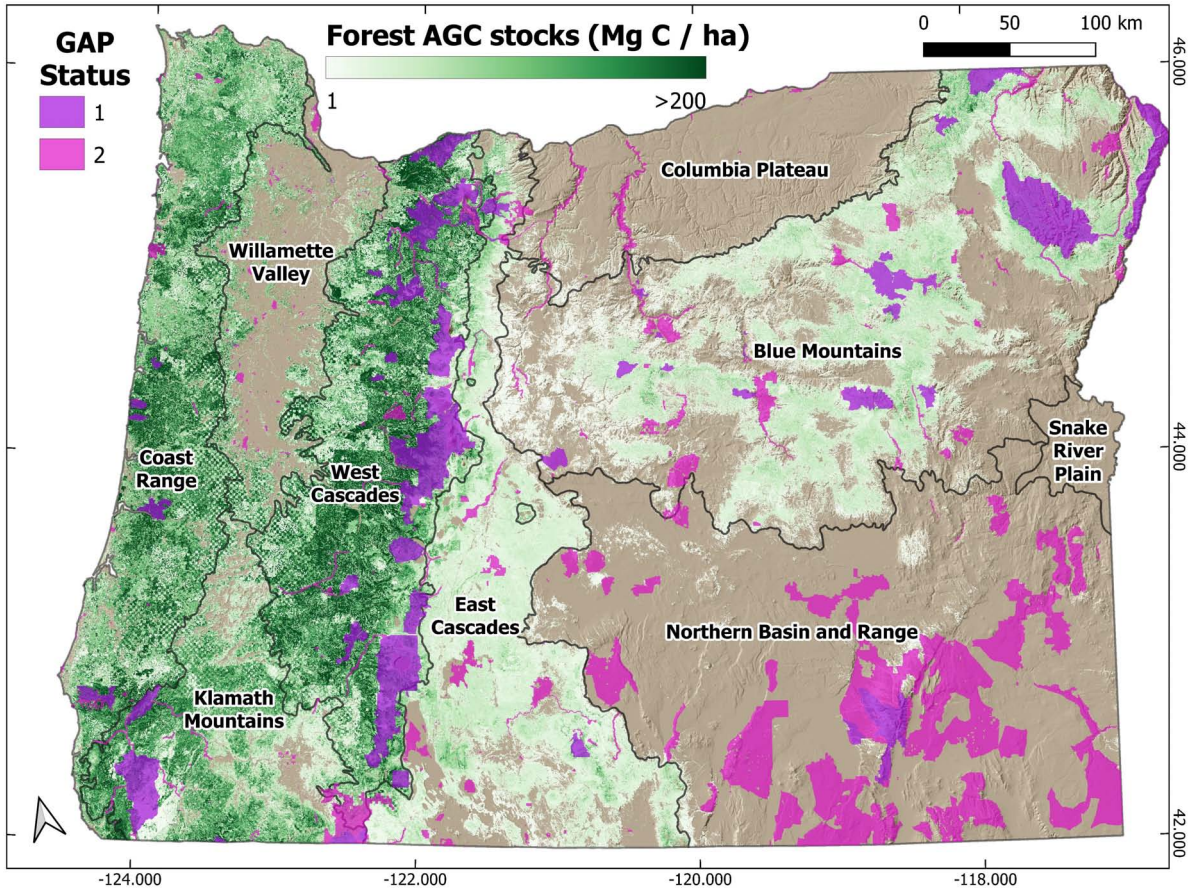


FIGURE 1
Current protected lands and forest aboveground carbon stocks across Oregon. Protected lands depicted here are assigned GAP Analysis Project (GAP) Status 1 or 2 by the Protected Areas Database of the United States (PAD-US v. 2.1) (USGS GAP, 2020) and include both forestlands and non-forestlands. These statuses characterize areas with permanent protection from anthropogenic conversion of natural land cover. Forest aboveground carbon stocks (Mg C ha^{-1}) in 2017 were spatially modeled from inventory measurements, satellite remote sensing, and environmental data (Landscape Ecology Modeling Mapping and Analysis (Lemma) Team, 2020).

affecting productivity. The study region provides a range of conditions that might be expected at much larger scales.

The forests in the region experienced intensive harvesting across public and private lands from the early 1900s through the late 1980s. Implementation of the Northwest Forest Plan (NWFP) in the wetter western portion of Oregon, Washington, and Northern California to protect sensitive aquatic and terrestrial species and habitat in old-growth forests resulted in an 82% decrease in timber harvest on public forestlands. These protections also benefited other ecosystem services like watershed protection (Frissell, 2013) and increased forest carbon accumulation on public lands. Prior to implementation of the NWFP, both public and private forests were about equal net carbon sources (Turner et al., 2011). Between 1990 and 2007, net carbon accumulation on public lands, even after accounting for fires and harvest, was 8 times that on private lands where intensive harvest of young tree plantations continued (Turner et al., 2011; Law et al., 2022). This demonstrates how forest carbon increases when harvest on public lands is limited for biodiversity and water protection. In the drier eastern forests, a set of rules were adopted around the same time to protect sensitive species, older trees and aquatic life, but these rules were rolled back by the US Forest Servic (2021).

Data processing

We analyzed the current extent, future opportunities, and benefits of forest preservation across Oregon using existing spatial datasets related to live tree aboveground carbon stocks, biodiversity, climate resilience, disturbance, and other factors. These spatial datasets were mapped at 30 m to 90 m spatial resolution and thus well suited to inform local to regional forest management decisions (Hansen et al., 2013; USGS GAP, 2018). Therefore, we conducted our spatial analysis at moderately high (30 m) spatial resolution using a common grid in an Albers

Equal Area projection. We analyzed and visualized data using the open-source software R (version 4.0) (R Core Team, 2021) with the libraries *terra* (Hijmans, 2022), *raster* (Hijmans, 2019), *sf* (Pebesma, 2018), *data.table* (Dowle and Srinivasan, 2021), and *ggplot2* (Wickham, 2016). We created the maps using open-source software QGIS (v3.20; R Core Team, 2021).

Current and additional protection to meet targets

We determined the current extent of protected lands across Oregon using the Protected Areas Database of the United States (PAD-US version 2.1) that is the official national inventory of protected areas. The PAD-US is a geospatial database created by the United States Geological Survey (USGS) GAP Analysis Project (GAP) that includes information on the spatial extent and protective status of public and private lands across the nation (USGS GAP, 2020). Protective status is characterized by GAP status codes that describe management intent to preserve biodiversity following guidelines from the International Union for the Conservation of Nature (IUCN). The highest protective statuses are GAP 1 and 2, which are for lands that have management plans to maintain the natural state of ecosystems and include permanent protection from human activities that cause land cover conversion. GAP 1 typically aligns with IUCN Categories Ia, Ib, and II, whereas GAP 2 aligns with IUCN Categories III through VI. We clipped the PAD-US shapefile to the boundaries of Oregon and then gridded the GAP status codes at 30 m resolution. Lands can have multiple GAP status codes when under multiple forms of management, in which case we used the lowest GAP status code. We then computed the total land and forest area with permanent protection (GAP 1 or 2) in each ecoregion, as well as how much additional area would be required to protect 30 and 50% of total land and forest area in each ecoregion.

Prioritizing forest protection using preservation targets

To strategically meet the 30 × 30 and 50 × 50 preservation targets in each of Oregon's ecoregions, we jointly and singularly prioritized forestlands for protection using carbon, biodiversity, and climate resilience metrics (*sensu* Law et al., 2021). For each prioritization metric, we computed the percentile rank (0–100%) of every grid cell compared to all other grid cells in the ecoregion. We then computed each grid cell's overall forest preservation priority rank by reranking the sum of its live tree aboveground carbon stocks, biodiversity, and climate resilience ranks. We identified the highest ranked currently unprotected forestlands that could be strategically protected (GAP 1 or 2) to meet each preservation target with the prioritization metrics.

For the carbon priority ranking, we focused on live tree aboveground carbon stocks (AGC). Tree AGC stocks in Oregon's forests typically account for 41 to 55% of total ecosystem carbon and are a focus for climate change mitigation because of their sensitivity to forest management activities. Tree AGC stocks have been mapped across Oregon's forestlands for the year 2017 using forest inventory, satellite, and environmental datasets (Landscape Ecology Modeling Mapping and Analysis (Lemma) Team, 2020). Specifically, tree AGC stocks were mapped for all live trees ≥2.5 cm diameter at breast height that occurred in areas that had or could potentially have at least 10% tree cover (Landscape Ecology Modeling Mapping and Analysis (Lemma) Team, 2020). To account for impacts of recent stand-replacing disturbances (e.g., wildfires, logging), we identified areas where forest loss occurred from 2017 to 2020 using the most recently available Global Forest Change dataset derived from 30 m resolution Landsat satellite data (Hansen et al., 2013). We set tree AGC stocks to zero in any grid cell where forest loss was observed during this period, and assumed the disturbances did not cause a permanent transition to non-forest.

For the biodiversity priority ranking, we used terrestrial vertebrate species (hereafter animal) richness by taxa and tree species richness. Current potential habitat distribution of 1,718 animal species was mapped by the USGS at 30 m resolution across the contiguous U.S. using geospatial predictors (USGS GAP, 2018). This included potential habitat for amphibian, bird, mammal, and reptile species found in the region. These habitat maps do not include stopover habitats for migratory species. Furthermore, we characterized the current potential habitat distribution of 89 tree species across Oregon based on the presence or absence of live tree basal area mapped statewide at 30 m resolution using forest inventory, satellite, and environmental datasets (Landscape Ecology Modeling Mapping and Analysis (Lemma) Team, 2020). For each species that occurred in Oregon, we masked out habitat on non-forestlands, which resulted in our analysis including 544 animal species and 89 tree species. We then estimated species richness for each taxon by counting the number of species with habitat in each forested grid cell. For each grid cell, we (1) derived an animal priority rank based on the ranked sum of the four animal taxa ranks and then (2) derived the biodiversity rank by reranking the sum of the animal and tree priority rank.

For the climate resilience ranking, we used a metric of terrestrial landscape resilience that incorporated geophysical and topo-climatic diversity and landscape permeability (Buttrick et al., 2015). Landscape resilience refers to the capacity of a landscape or ecoregion to maintain biological diversity and ecological function despite climate change. As the climate continues to warm, biodiversity and ecological function are more likely to be maintained in landscapes that are topographically complex and permeable to movement of animals and plants. Complex topography provides corridors

and microsites where species can move in response to climate change while a landscape free of barriers (i.e., highly permeable) allows species to take advantage of different microclimates. We used the terrestrial landscape resilience dataset (90 m resolution) produced for the Pacific Northwest USA by The Nature Conservancy (Buttrick et al., 2015). The topo-climatic diversity metric incorporated a heat-load index computed from a digital elevation model and topographic index as a metric of relative variation in water availability. Permeability is a measure of the hardness of barriers, connectedness of natural cover, and arrangement of land uses. More details are in Buttrick et al. (2015).

To select areas with the highest priority for preservation that could meet the 30 × 30 and 50 × 50 targets, forestlands within each ecoregion were ranked by carbon, biodiversity, and/or climate resilience metrics. We used pixel by pixel prioritization ranking rather than neighborhood average for adding spatial structure to the prioritization. The highest ranked forests were then combined with areas currently protected at GAP 1 or 2 until each preservation target was reached. We then assessed who owns these high-preservation priority forestlands, as well as potential effects of increased forest preservation for carbon, biodiversity, and drinking water.

Ownership of high preservation priority forests

Forestland ownership across the state was assessed using the Oregon Department of Forestry (ODF) data representing forest ownership conditions in 2015. The ownership classes in this spatial dataset include Federal, Tribal, State, Local, Private, and Industrial. We examined current ownership of forestlands, as well as ownership of forestlands that we identified as high priority for preservation.

Assessing effects of forest preservation on carbon, biodiversity, and water

We assessed current protection of forest carbon, biodiversity, and surface drinking water across Oregon, as well as potential protection of these ecosystem services if each preservation target was met. To help Oregon's public water systems and communities, the Department of Environmental Quality identified and mapped public surface drinking water source areas across the state, including rivers, streams and lakes (Oregon Department of Environmental Quality [DEQ], 2019). We used these data in our analysis. First, we quantified the amount of tree AGC stocks, animal and tree species' habitat, and surface drinking water source areas that are currently protected (GAP 1 or 2) across forestlands in Oregon. Next, we quantified potential protection of these ecosystem services if the 30 × 30 and 50 × 50 preservation targets were met. We focused particularly on forestlands that could be jointly prioritized for preservation using carbon, biodiversity, and climate resilience metrics. Given the importance of protecting the habitat that sustains threatened and endangered (T&E) species, we summarized current and potential habitat protection for animal species that are currently listed by Oregon and/or the federal government. A list of current T&E species is maintained by the Oregon Department of Fish and Wildlife (2021). We excluded from analysis (1) T&E fish, sea turtles, shore birds, and marine mammals; (2) animal species with only distinct population segments listed as T&E [e.g., Pacific marten (*Martes caurina*)]; and (3) the streaked horned lark (*Eremophila alpestris strigata*) because habitat data were not available.

Results

Current protected forests

Oregon has 12.45 Mha of forestland of which 1.23 Mha is protected at GAP 1 or 2 levels, less than 10% of the forested area (**Figure 1** and **Table 1**). The largest protected forest area is in the mesic West Cascades (0.55 Mha) followed by the Blue Mountains in eastern Oregon (0.32 Mha) and Klamath Mountains in southwestern Oregon (0.13 Mha). Oregon's portion of the Coast Range with its heavily forested temperate rainforests is primarily in industrial ownership and managed as tree plantations and, therefore, it holds the smallest portion of forestland that is permanently protected (3%, 0.06 Mha). When the Washington to California portions of the Coast Range are included, it increases to 10%. Similarly, the full Blue Mountains ecoregion that extends into southeast Washington has 10% of its forestland permanently protected (0.48 Mha) (Law et al., 2021).

High priority areas for preservation of carbon and/or biodiversity

The forest preservation rankings for carbon and/or biodiversity at GAP 1 or 2 status levels are widely distributed across the forested ecoregions (**Figures 2B,C**; **Supplementary Figures 1–6**). However, the climate resilience rank highlights large areas within the ecoregions with larger landscape features that are important for resilience (**Figure 2D**), such as the topography of mountain ranges in southwest Oregon, the Coast Range, Cascades, and Blue Mountains in the northeast.

To reach 30% protection in each forested ecoregion by 2030, an additional 2.5 Mha (20.1% of forest area) would need to be protected in less than 10 years (**Table 1**). To reach the 50% target, a total of 5 Mha (40.1%) would need to be protected by 2050, most of which is in the Blue Mountains, followed by East and West Cascades and the Coast Range (**Figure 3**).

TABLE 1 Current extent of all forestlands, protected forestlands, and additional forestlands needed to meet preservation targets for each ecoregion in Oregon.

								Additions needed to meet preservation targets							
								All lands				Forest			
	All lands	Protected lands		All forest		Protected forest		30% target		50% target		30% target		50% target	
Ecoregion	Mha	Mha	%	Mha	%	Mha	%	Mha	%	Mha	%	Mha	%	Mha	%
Blue Mountains	6.20	0.55	8.9	3.42	55.2	0.32	9.4	1.3	21.1	2.5	41.1	0.7	20.6	1.4	40.6
West Cascades	2.90	0.61	21	2.72	93.8	0.55	20.2	0.3	9.0	0.8	29.0	0.3	9.8	0.8	29.8
Coast Range	2.34	0.06	2.6	2.01	85.9	0.06	3.0	0.6	27.4	1.1	47.4	0.5	27.0	0.9	47.0
Columbia Plateau	1.75	0.04	2.3	0.09	5.1	0.00	0.0	0.5	27.7	0.8	47.7	0.0	30.0	0.0	50.0
East Cascades	2.73	0.14	5.1	2.13	78.0	0.09	4.2	0.7	24.9	1.2	44.9	0.5	25.8	1.0	45.8
Klamath Mountains	1.56	0.14	9.0	1.34	85.9	0.13	9.7	0.3	21.0	0.6	41.0	0.3	20.3	0.5	40.3
N. Basin and Range	5.95	1.34	22.5	0.25	4.2	0.08	32.0	0.4	7.5	1.6	27.5	0.0	−2.0	0.0	18.0
Snake River Plain	0.26	0.00	0.0	0.00	0.0	0.00	0.0	0.1	30.0	0.1	50.0	0.0	30.0	0.0	50.0
Willamette Valley	1.37	0.03	2.2	0.49	35.8	0.01	2.0	0.4	27.8	0.7	47.8	0.1	28.0	0.2	48.0
Oregon	25.06	2.91	11.6	12.45	49.7	1.23	9.9	4.6	18.4	9.6	38.4	2.5	20.1	5	40.1

Forestlands are considered currently protected if GAP 1 or 2 (IUCN categories Ia-VI).

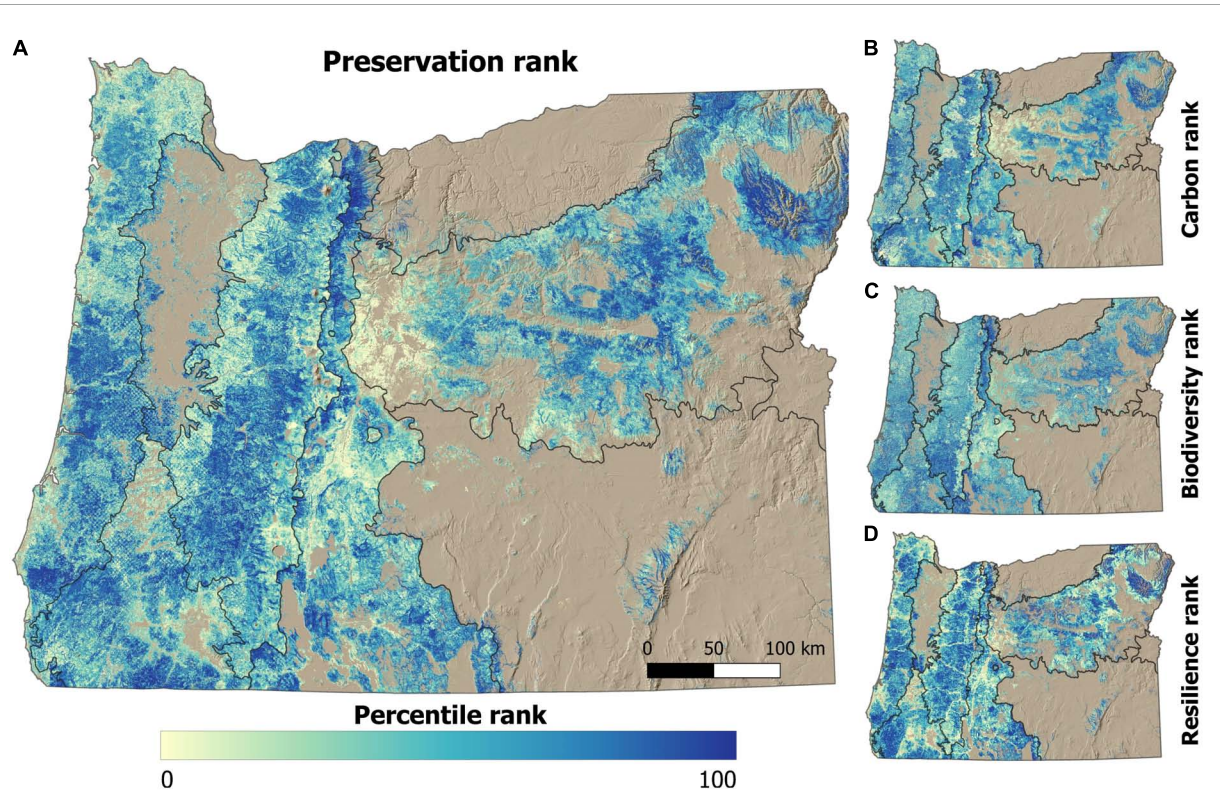


FIGURE 2
Oregon forest preservation, carbon, biodiversity, and climate resilience priority rankings. **(A)** Forest preservation priority ranks were derived from **(B)** carbon, **(C)** biodiversity, and **(D)** climate resilience priority ranks within each ecoregion. Forest carbon ranks were based on tree aboveground carbon stocks (AGC) stocks. Forest biodiversity ranks incorporate species richness of amphibians, birds, mammals, reptiles, and trees. Climate resilience priority ranks incorporated topoclimatic diversity and landscape connectivity.

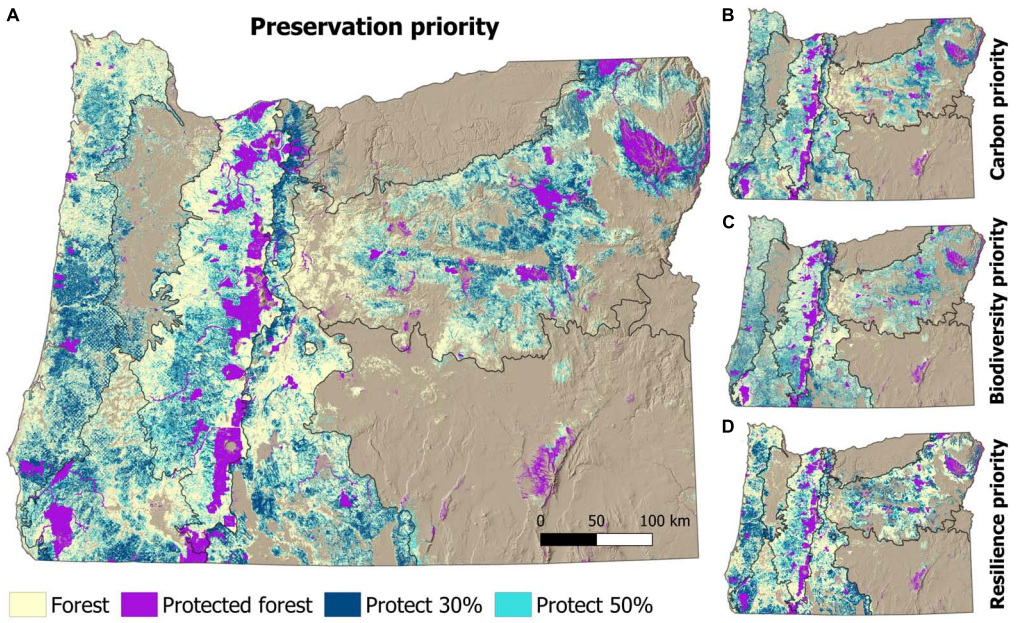


FIGURE 3
Forestlands prioritized to meet preservation targets across Oregon. Preservation targets include protecting 30 and 50% of each ecoregion's forestlands. To identify preservation targets, the current extent of forest protection was determined for each ecoregion and then the highest ranked unprotected forestlands were sequentially added to the protected area network until each preservation target was met. **(A)** Forest preservation priority targets are shown, as are the **(B)** carbon, **(C)** biodiversity, and **(D)** climate resilience priority targets.

We chose four areas for closer examination as examples of potential co-benefits and synergies with existing public lands (**Figure 4**).

The Coast Range ecoregion stretches along the coasts of Washington, Oregon, and northern California. The low elevation mountains (~1000 m) generally have deep soils with high soil water holding capacity and frequent fog that keeps vapor pressure deficits relatively low, resulting in a longer period of photosynthesis. The Coast Range contains two of the tallest conifer species in the world–Coast Douglas-fir (*Pseudotsuga menziesii var. menziesii*) and Sitka spruce (*Picea sitchensis*). These cool, temperate, moist forests can achieve higher biomass carbon density than tropical forests (Law et al., 2018). It is also the most intensively logged ecoregion. Within the areas we identified as high priority for both carbon and biodiversity are the Devil's Staircase Wilderness and the 32,375 ha Elliott State Research Forest (**Figure 4**). Both areas have a large portion of mature and old forests. Together, the ESRF reserves in Conservation Research Watersheds and adjacent Devil's Staircase Wilderness Area represent 26,404 ha of protected reserve (3.8% of Coast Range forestland), the largest in the Oregon Coast Range. The Devil's Staircase Wilderness was designated in 2019, and could be expanded to a larger area with connectivity corridors on BLM and State forestlands. The 83,000-acre Elliott State Forest was established as Oregon's first state forest in 1930. By 2020, half of it had been clearcut and planted. In 2020, the Elliott State Research Forest (ESRF) was established following an attempt to privatize the area for industrial management. The Research Forest has strong public support for conservation values including protection of mature and older forests, and threatened and endangered species (northern spotted owl, marbled murrelet, and Oregon Coast coho). Approximately 61% of the Elliott is identified as a reserve to meet state conservation goals, including 13,759 contiguous hectares, and another 5,870 ha of reserves located in harvest areas "protecting older trees and critical species habitat" (Oregon Division of State Lands, 2021; College of Forestry, 2022). To meet IUCN rules and national goals, at least 75% of the ESRF needs to be protected as strict reserves (IUCN, 2013).

The Klamath Mountains ecoregion is very diverse in climate, topography and plant and animal species. This area extends from southwestern Oregon into northern California where high priority forestlands provide connectivity between several large protected Wilderness Areas (Law et al., 2021). The most diverse forest flora in western North America (Whittaker, 1960) is found here, with more than 3,500 plant species, partly due to its steep climatic and topo-edaphic gradients. Plant communities range from temperate rain forests to moist inland forests, oak forests and savannas, and high elevation forests. The Kalmiopsis and Wild Rogue Wilderness Areas are in the Klamath Mountains, and each one presents potential for expansion (**Figure 4**). The Kalmiopsis was designated an Area of Global Botanical Significance by the IUCN, one of only seven in the United States. The area experienced the large Biscuit Fire

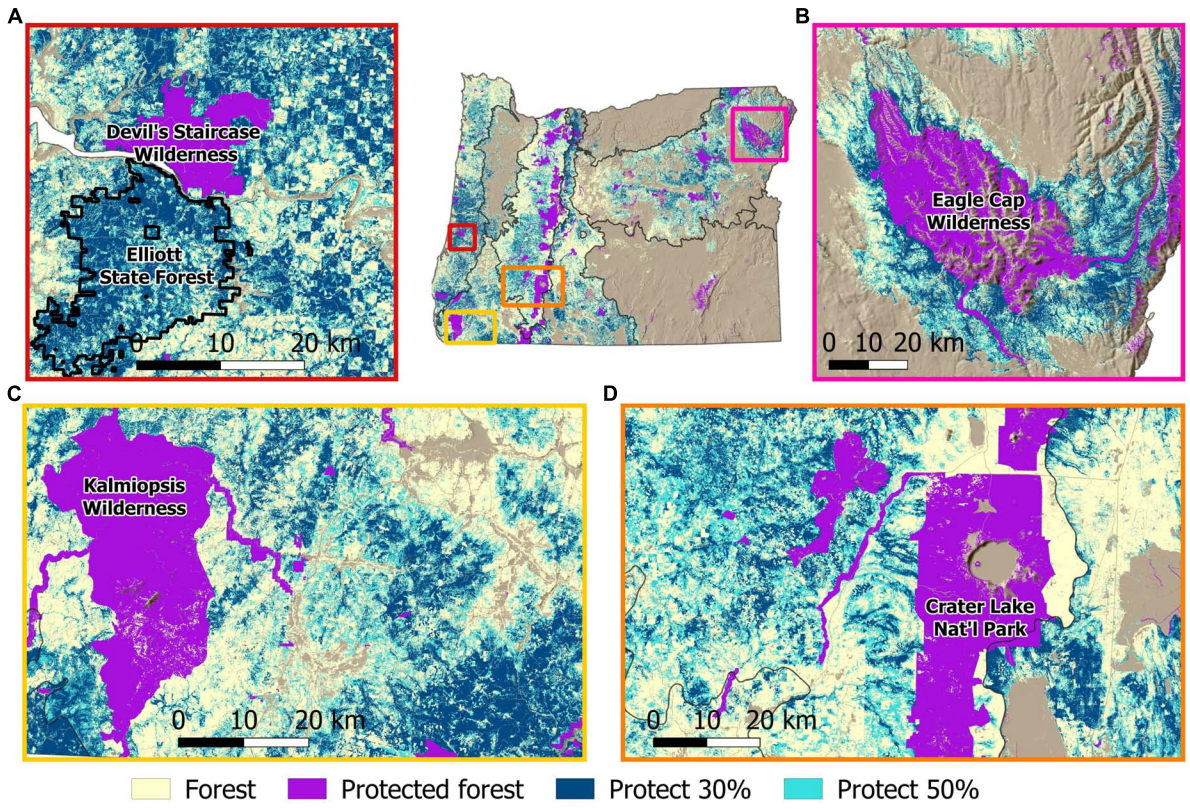


FIGURE 4
Close-up examples of forestlands prioritized to meet preservation targets in Oregon. Examples include forestlands around the **(A)** Devil's Staircase Wilderness and Elliot State Forest in the Coast Range, **(B)** Eagle Cap Wilderness in the Blue Mountains, **(C)** Kalmiopsis Wilderness in the Klamath Mountains, and **(D)** Crater Lake National Park in the Cascade Mountains. In these examples, forestlands were jointly prioritized using carbon, biodiversity, and climate resilience metrics.

in 2002, but has been slowly recovering its carbon stocks as conifer regeneration continued and woody biomass increased in the 10 years after the fire (Donato et al., 2015). The proposed Wild Rogue Wilderness would protect the Zane Grey Roadless Area, the largest forested BLM roadless area in southern Oregon and northern California.

The West Cascades ecoregion has a moist temperate climate that supports high productivity coniferous forests that are also intensively managed for logging. High-elevation forests along the Cascades Crest have received more protection including Crater Lake National Park, Oregon's only National Park (Figure 4). Crater Lake and surrounding forestlands include significant expansion opportunities of its protected area boundaries to include multiple rivers and elevating the protection of species (GAP 1 or 2) to become part of the strategic reserves system. The Crater Lake Wilderness Proposal would designate 219,744 hectares (2,197 km^2) of intact roadless forestlands as Wilderness on National Forest and National Park lands in a conservation area.

The Blue Mountains ecoregion contains a complex of mountain ranges interspersed with valleys stretching from the Cascades in the west to the Rocky Mountains in the east. This is the largest ecoregion in Oregon and has the largest Wilderness area in the state. The area supports diverse and abundant native fish and wildlife populations and has a significant portion of the region's remaining road-free wildlands. The forest types have fire-adaptive traits related to the wildfire regimes in this ecoregion, with ponderosa pine dominated forests in the south and a greater mix of dry, moist and cold forest types in the north due to receiving more moisture through the Columbia River Gorge. The Eagle Cap Wilderness (Figure 4) is surrounded by roadless areas and presents expansion opportunities that would help secure connectivity in a crucial wildlife corridor with large Wilderness areas in the Rocky Mountains.

Land ownership of high priority areas

In 2015, Oregon forestlands were primarily owned by the federal government (59%), private entities (31%), and industry (7%), whereas little was owned by state, local, or tribal governments (0–3%; Table 2). However, forest ownership widely varied among ecoregions. The federal government

owned 66–77% of forestlands in the Blue Mountains, East and West Cascades, and Northern Basin, with these four ecoregions together accounting for 80% of federal forestlands statewide. Conversely, private or industrial owners held 57–92% of forestlands in the Coast Range, Columbia Plateau, Snake River Plain, and Willamette Valley, though these ecoregions together made up only 35% of private and industrial forestlands statewide because, with the exception of the Coast Range, these ecoregions are minimally forested. In terms of total forest area, private ownership was concentrated in the Blue Mountains and Coast Range, which respectively, accounted for 30 and 20% of private forestlands statewide. Similarly, industrial ownership was concentrated in the Coast Range and West Cascades, which respectively, accounted for 46 and 36% of all industrial forestlands statewide. The notable checkerboard pattern of forest carbon stocks and preservation priorities in the Coast Range (**Figures 1–3**) reflects differences in forest management between public and private ownership.

The ownership of the high preservation priority forestlands for carbon and biodiversity is primarily federal (72% by 2030, 67% by 2050) followed by private (20% by 2030 and 25% by 2050), with much less in the other ownerships (**Figure 5**). The additional federal lands needed to meet the high preservation priority targets adds up to 1.75 Mha by 2030 and 3.3 Mha by 2050 (**Table 1** and **Figure 5**). Prioritizing biodiversity increases the percentages on private lands (**Figure 5**, right frame).

There are large differences among ecoregions in the ownership of high priority forestlands (**Figure 6**). For example, 80 to >90% of high priority forestlands are federally owned in the Cascade, Klamath, and Blue Mountains, whereas about 80% are privately owned in the Willamette Valley. In ecoregions with very little forestlands (Willamette Valley, Snake River, and Columbia Plateau), most high priority areas are privately owned. The highest population density is in the Willamette Valley and the other two ecoregions are drier. In the Coast Range, 60% of high priority forestlands are on federal lands, and 15% are on Tribally owned lands, the highest in the State.

Forest habitat, carbon, and drinking water if protected

Meeting the forest preservation targets would substantially increase protection of tree carbon stocks, animal and tree species' habitat, and surface drinking water source areas. Tree AGC stocks in all of Oregon's forests is 905 Tg C (**Table 3**). Currently, only 12% of Oregon's tree AGC stocks (104 Tg C) are in protected areas, mostly in the West Cascades (65 Tg C), followed by the Blue Mountains (13.5 Tg C) and Coast Range (10.9 Tg C). If the 30 and 50% forest preservation targets were met, then protected tree AGC stocks would total 405 and 635 Tg C (**Table 3**). The West Cascades and Coast Range would account for about 60% of the additional protected carbon stocks.

For most of the considered animal taxa and tree species, only a small percentage of their forest habitat is currently protected. Merely 6 and 14% of animal and tree species have at least 30% of their forest habitat currently protected. Moreover, the median percentage of forest habitat currently protected ranges from 8 to 12% among amphibian, bird, mammal, and reptile species and is 10% among tree species (**Figure 7A**). If the 30 and 50% forest preservation targets were met, then the median amount of forest habitat protected would be 27–42 and 45–63% among animal taxa, respectively, and reach 41 and 67% among tree species (**Figure 7B**).

Meeting these forest preservation targets would substantially increase forest habitat protection for threatened and endangered (T&E) species and other species of interest (**Table 4**). For example, only 8% of marbled murrelet (*Brachyramphus marmoratus*) and spotted owl (*Strix occidentalis*) forest habitat is currently protected, yet 36–44% would be protected if the 30% forest preservation target was met. Similarly, forest habitat protection for Canada lynx (*Lynx canadensis*) would increase from 12 to 40%, while it would increase from 34 to 55% for wolverines (*Gulo gulo*). Important non-T&E species such as wolves (*Canis lupus*) and beavers (*Castor canadensis*) would see forest habitat protection increase from 35 to 59% and from 10 to 40%, respectively, if this preservation target was met. These wolf and beaver habitat targets would help fulfill a recent proposal for rewilding the American West (Ripple et al., 2022). The additional habitat that could be protected by 2030 and 2050 increases dramatically for most of these species when forestlands are jointly prioritized based on carbon, biodiversity and climate resilience, which includes connectivity for animal movement.

Forestlands account for 78% (4.14 Mha) of the 5.3 Mha of surface drinking water source areas across Oregon, yet only 9% (0.37 Mha) of these forestlands are currently protected at GAP 1 or 2 levels (**Table 5**). This would increase to 27% by 2030 and 48% by 2050 if the high priority areas for carbon, biodiversity and resilience are protected (GAP 1 or 2). Most of the currently protected surface water source areas and the areas suitable for potential increases in protection are in the West Cascades, though protection of surface water sources areas would also increase notably in the Blue Mountains, Klamath Mountains, and Coast Range (**Figure 8**).

Discussion

Regional considerations for protecting carbon, biodiversity, and water

The IPCC AR6 (2022) states that "maintaining the resilience of biodiversity and ecosystem services at a global scale depends on effective and equitable conservation of approximately 30–50% of Earth's land, freshwater and ocean

TABLE 2 Current forestland ownership and management within each ecoregion and overall for Oregon.

Ecoregion	Ownership land management					
	Federal	State	Tribal	Local	Private	Industrial
Blue Mountains	2.26 (66%)	0.02 (1%)	0.02 (0%)	0.00 (0%)	1.14 (33%)	0.00 (0%)
West Cascades	2.11 (77%)	0.03 (1%)	0.00 (0%)	0.01 (0%)	0.30 (11%)	0.30 (11%)
Coast Range	0.61 (29%)	0.26 (13%)	0.01 (0%)	0.02 (1%)	0.79 (38%)	0.39 (19%)
Columbia Plateau	0.01 (14%)	0.00 (1%)	0.00 (1%)	0.00 (0%)	0.08 (84%)	0.00 (0%)
East Cascades	1.42 (67%)	0.05 (2%)	0.00 (0%)	0.01 (0%)	0.61 (28%)	0.04 (2%)
Klamath Mountains	0.79 (58%)	0.01 (1%)	0.00 (0%)	0.00 (0%)	0.55 (41%)	0.00 (0%)
Northern Basin and Range	0.18 (71%)	0.01 (4%)	0.00 (0%)	0.00 (0%)	0.06 (25%)	0.00 (0%)
Snake River Plain	0.00 (6%)	0.00 (1%)	0.00 (0%)	0.00 (0%)	0.00 (92%)	0.00 (0%)
Willamette Valley	0.04 (8%)	0.01 (2%)	0.00 (0%)	0.01 (1%)	0.33 (66%)	0.11 (22%)
Oregon	7.43 (59%)	0.40 (3%)	0.03 (0%)	0.05 (0%)	3.86 (31%)	0.84 (7%)

The extent of forestland in each category is given in million hectares (Mha) and as a percentage of total forestland within each ecoregion. Ownership land management data from the Oregon Department of Forestry (2015).

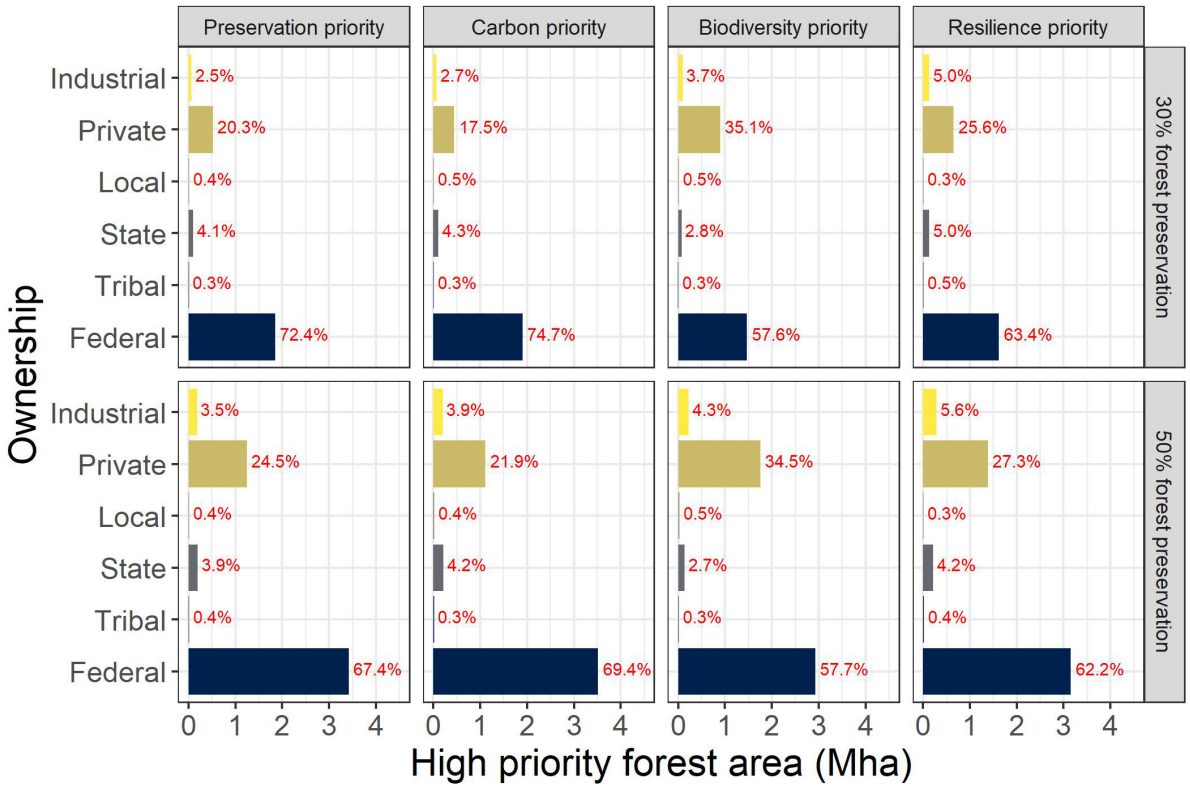


FIGURE 5
Land ownership of high priority forest areas to protect in Oregon to meet preservation targets. Ownership is summarized for each preservation target (rows) and priority (columns). Land ownership data from Oregon Department of Forestry (2015).

areas, including currently near-natural ecosystems." This acknowledges the multiple lines of evidence that maintaining ecological integrity of biodiversity is essential for addressing climate change effectively.

Accordingly, our analysis prioritizes areas within ecoregions to ensure biodiversity losses are reduced, or even enhanced in some areas through natural recovery of species and reintroductions, across the range of ecosystems. This approach also benefits carbon for climate mitigation, protects water availability and increases other ecosystem services.

A global application of the ecoregion approach found that temperate broadleaf, mixed, and conifer forests could achieve

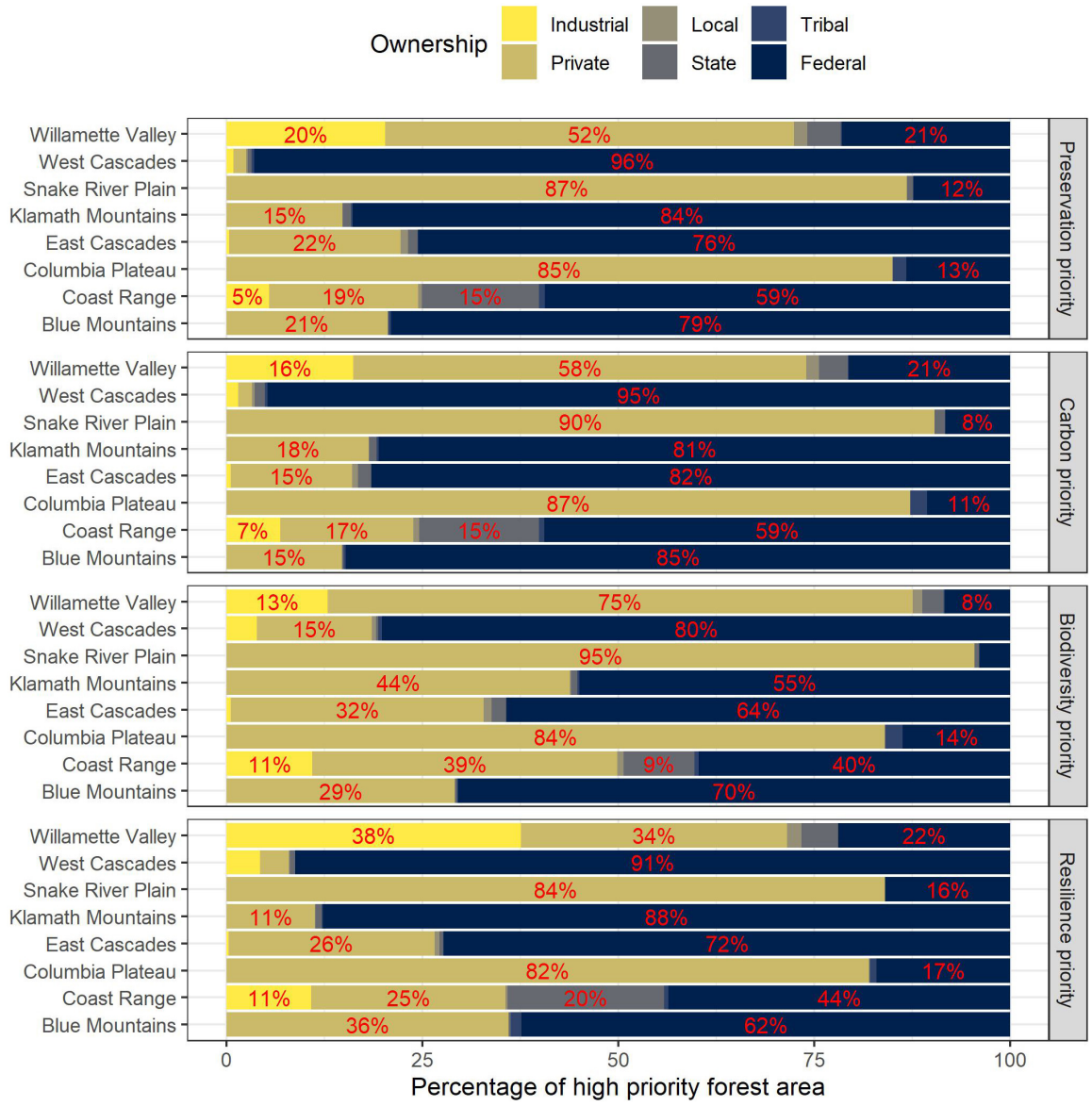


FIGURE 6
Land ownership of high priority forest areas to protect to reach 30% preservation for each ecoregion in Oregon. Ownership is summarized for each preservation priority **(rows)**. Land ownership data from Oregon Department of Forestry (2015).

protection of half of the global forest area, and the majority of the ecoregions are categorized as "imperiled" or "could recover" (Dinerstein et al., 2017). This emphasizes the need for protection.

Here, we found that the current 1.3 Mha protected as GAP 1 or GAP 2 status would increase to 2.5 Mha by 2030 and 5 Mha by 2050 to meet the preservation targets. Federal lands account for the majority of the protected area needed, which would provide more permanence. Protecting high carbon priority forests from timber harvest (GAP 1) is critical to dampen the accelerating anthropogenic carbon dioxide emissions.

Mitigation strategies need to explicitly protect existing old-growth forests, and allow mature secondary forests to regrow to their carbon capacity. For climate mitigation using natural climate solutions, effectiveness is based on the time that a unit of biomass carbon is resident in a forest ecosystem stock and thus kept out of the atmosphere (Körner, 2017; Mackey et al., 2020). Oregon's wet coastal forests have among the highest carbon residence times of any forests in the western USA (Berner et al., 2017). The large and old trees dominate forest carbon in temperate and tropical forests, and can maintain large carbon stocks and accumulation for centuries (Luyssaert et al., 2008; Hudiburg et al., 2009).

TABLE 3 Current tree aboveground carbon (AGC) stocks in each ecoregion's forests, protected forests, and forests that would be protected by meeting preservation targets using joint prioritization.

	All forest	Unprotected forest		Protected forest		Forestland preservation target			
						30% protection		50% protection	
Ecoregion	Tg C	Tg C	%	Tg C	%	Tg C	%	Tg C	%
Blue Mountains	110.8	97.2	88	13.5	12	53.0	48	79.1	71
West Cascades	323.6	258.6	80	65	20	125.7	39	220.7	68
Coast Range	240.3	229.4	95	10.9	5	117.9	49	171.9	72
Columbia Plateau	1.5	1.5	94	0.1	6	0.9	58	1.2	79
East Cascades	73.8	69.4	94	4.4	6	35.8	48	50.1	68
Klamath Mountains	112.9	103.5	92	9.4	8	50.6	45	80.7	71
N. Basin and Range*	1.7	1.3	75	0.4	25	–	–	1.0	60
Snake River Plain	< 0.1	< 0.1	99	< 0.1	1	< 0.1	36	< 0.1	56
Willamette Valley	40.3	39.7	98	0.7	2	20.7	51	30	75
Oregon	904.9	800.5	88	104.4	12	405.1	45	634.8	70

*32% of forestlands in the Northern Basin and Range ecoregion are currently protected, thus summaries of tree AGC stock protection were not computed for the 30% forest preservation target. Each category includes tree AGC stocks in teragrams (10^{12} g or million metric tons) of carbon and as the percentage of the ecoregion's total tree AGC stocks. Tree AGC stocks protected by meeting each preservation target include the stocks in current protected forests. Tree AGC stocks are considered currently protected if they occur on forestlands as GAP 1 or 2 status.

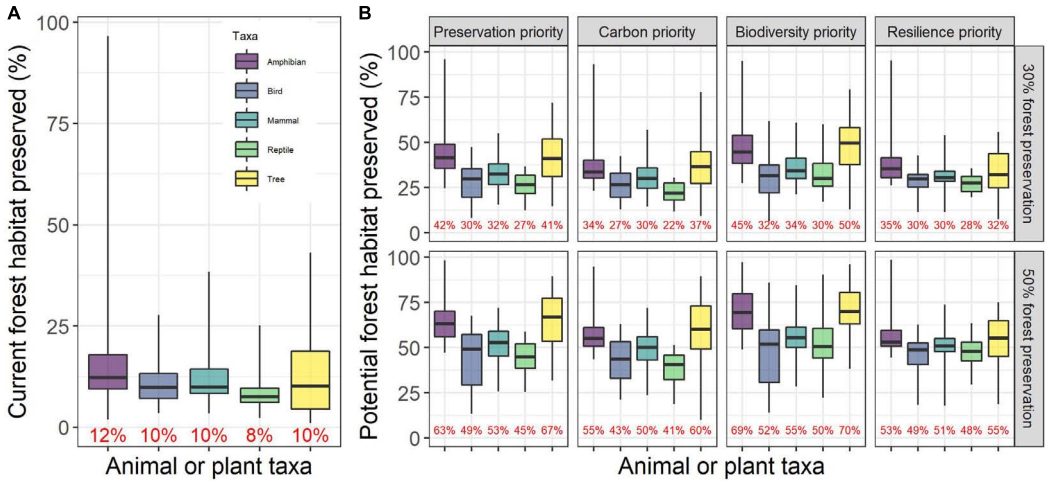


FIGURE 7
Current and potential protection of animal taxa and tree species forest habitat across Oregon. The percentage of each species' forest habitat that **(A)** is currently protected and **(B)** would be protected by meeting preservation targets based on each priority. The median percentage of current and potential protected species habitat is provided for each taxon (red text). Boxplots depict medians (intra-box lines), 25th–75th percentiles (box edges), and 5th to 95th percentiles (whiskers). Animal and tree species habitat data were from the USGS GAP (2018) and Landscape Ecology Modeling Mapping and Analysis (Lemma) Team (2020), respectively.

Oregon inventory data show that stand ages reach beyond 1,000 years, and public lands have far more stands older than 200 years than private lands do (Hudiburg et al., 2009). Mean and maximum live biomass are also higher on public lands. The maximum mean trend of biomass within each ecoregion occurred by the age of 300 years in the Coast Range to 430 years in the West Cascades and 600+years in the Klamath Mountains, and biomass continued to increase beyond these ages (Hudiburg et al., 2009). Ecoregions with the highest ecosystem carbon density in vegetation and soils are the Coast Range, West Cascades, and Klamath Mountains (330, 318 and 316 Mg C ha^{-1}, respectively), with 55% of it in live tree carbon (180, 175, 173 Mg C ha^{-1}) (Law et al., 2018). Oregon's forest carbon stocks could almost double in the absence of disturbance (Hudiburg et al., 2009). These trends are influenced by harvest intensities, particularly in the Coast Range where the temperate rainforests have so little forestland protected, yet they are among the highest carbon dense forests in the world (**Table 1**).

TABLE 4 Current and potential habitat protection for animal species listed as threatened (T) or endangered (E) by the state of Oregon.

Common name	Scientific name	State (Federal) status	Forest habitat (km^2)	Forest habitat protected (%)		
				Current	30% protected	50% protected
Oregon spotted frog	*Rana pretiosa*	T	507	17	42	65
Marbled murrelet	*Brachyramphus marmoratus*	E (T)	14,913	8	44	65
Northern spotted owl	*Strix occidentalis caurina*	T (T)	39,379	8	36	59
Canada lynx	*Lynx canadensis*	T	16,211	12	40	62
Kit fox	*Vulpes macrotis*	T	295	25	26	32
Washington ground squirrel	*Urocitellus washingtoni*	E	1	4	27	41
Wolverine	*Gulo gulo*	T	791	34	55	71

Several of these species are also listed by the federal government. Each species includes the amount of forest habitat that is currently protected (GAP 1 or 2), as well as how much would be protected by reaching the 30 and 50% preservation targets when jointly prioritizing forestlands based on carbon, biodiversity, and climate resilience metrics. Information on listing status was from the Oregon Department of Fish and Wildlife as revised October 2021.

TABLE 5 Surface drinking water source areas for public water systems in each ecoregion's forests, protected forests, and forests that would be protected by meeting preservation targets using joint prioritization.

Ecoregion	All lands	All forest		Protected forest		Preservation target			
						30% protection		50% protection	
	Mha	Mha	%	Mha	%	Mha	%	Mha	%
Blue Mountains	0.26	0.18	70	0.02	12	0.09	48	0.13	70
Coast Range	0.77	0.7	91	0.00	1	0.18	26	0.32	46
Columbia Plateau	0.13	0.01	6	0.00	1	0.00	48	0.00	64
East Cascades	0.01	0.01	92	0.00	7	0.01	68	0.01	81
Klamath Mountains	0.81	0.65	80	0.02	2	0.12	19	0.25	38
N. Basin and Range	0.00	0.00	0	0.00	0	0.00	0	0.00	0
Snake River Plain	0.02	0.00	0	0.00	0	0.00	27	0.00	55
West Cascades	2.28	2.2	97	0.33	15	0.59	27	1.09	50
Willamette Valley	1.03	0.39	38	0.01	1	0.12	30	0.20	50
Oregon	5.30	4.14	78	0.37	9	1.11	27	2.00	48

Joint prioritization was based on forest carbon, biodiversity, and climate resilience metrics. Surface drinking water source areas are considered currently protected if they occur on forestlands as GAP 1 or 2 status. Surface drinking water source areas were mapped by the Oregon Department of Environmental Quality (DEQ) (updated 2019).

Although we did not simulate changes in forest carbon and accumulation under future climate, our previous studies showed that preserving 50% of high priority forests by 2050 would triple the amount of carbon accumulation compared to current levels over the western United States (Law et al., 2021), accounting for projected climate effects including CO_2 enhancement of photosynthesis constrained by nitrogen and carbon losses from forest fires. Because we prioritized relatively high carbon density within each forested ecoregion in our current study, the carbon accumulation is probably lower than if priorities were only in the ecoregions with the highest net accumulation (average of 1.4 compared to 4 to 8 Mg C ha^{-1} yr^{-1}; Law et al., 2013).

A global study assumed an average accumulation rate of 0.14 MgC ha^{-1} yr^{-1} for boreal and temperate forests over the next decades (Griscom et al., 2017). Our estimate for natural forest management in Oregon is almost ten times the global value. We also found that limiting harvest to half of current levels on public lands and doubling harvest cycles to 80 years on private lands was three times more effective as a land use strategy than replanting and reforestation after cutting within current forest boundaries in Oregon (Law et al., 2018). The global study presents different results, highlighting the need for consistent approaches for national, regional and state-level analysis to refine estimates of forest carbon benefits.

There is concern that protecting areas that are vulnerable to increased drought and fire will be ineffective, however, species diversity, and threatened and endangered species still need habitat, refugia and connectivity with other protected areas. Wildfires tend to be patchy, and a majority of trees survive low to mixed-severity fires (Halofsky et al., 2011) that can be critical habitat, and burned forests still retain the vast majority of their carbon (Hudiburg et al., 2009; Law et al., 2018). When very few populations of a given species exist, the potential to recolonize areas with strong site fidelity is needed.

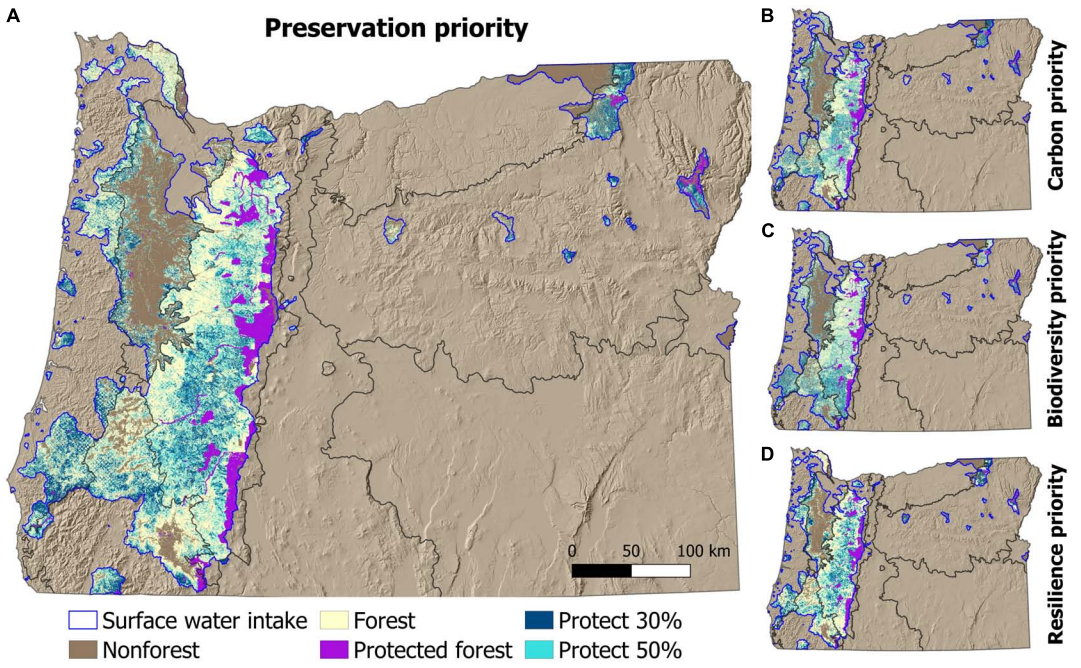


FIGURE 8
Current and potential protection of surface drinking water source areas in forestlands across Oregon. Potential protection is shown for the **(A)** forest preservation priority targets, as well as for **(B)** carbon, **(C)** biodiversity, and **(D)** climate resilience priority targets. Surface drinking water source area data were from the Oregon Department of Environmental Quality (Oregon Department of Environmental Quality [DEQ], 2019).

The conservation of habitat suitability is necessary even if it is currently unoccupied by those populations (Merkle et al., 2022). Moreover, transboundary assessment of priority areas for preservation and connectivity is essential, as well as collaborative development of implementation plans that transcend political boundaries (Noss et al., 2012; Law et al., 2021).

Across the western U.S., federal forestlands are the dominant source of clean drinking water, and private forestlands are the most likely to experience land use change and impacts on water supplies (Liu et al., 2021). In western Oregon, where human population is concentrated and projected to continue growing rapidly, communities depend on drinking water from both private and federal forestlands. While there is concern about the impacts of wildfire on drinking water sources, forestlands tend to be adapted to these periodic disturbances and recover with minimal interventions. However, repeated harvesting, road networks and application of pesticides can expose aquatic systems to chronic stressors that continuously reduce water quantity and degrade water quality (e.g., soil erosion, sediment load, higher stream temperature) (Rieman et al., 2003; Karr et al., 2004).

As warming increases, mountain snowpack is expected to melt earlier in spring, which reduces drinking water supplies (Evan and Eisenman, 2021). The Cascade Mountains are expected to be among the most vulnerable mountain ranges because of their mild climate where even small temperature increases will result in precipitation falling as rain rather than snow, further reducing snowpack accumulation and increasing melt. This ecoregion is the largest area currently protecting forest drinking water sources at GAP 1 or 2 status and it is critical for additional preservation area for protection of habitat, biodiversity, and carbon. Protecting clean drinking water sources from extractions (mining, logging) is cost effective and essential, as loss of forest cover or conversion to plantations has been shown to reduce water supplies by up to 50% as compared to mature forests (Segura et al., 2020). Logging is still occurring in Oregon watersheds that feed surface water and replenish groundwater sources of drinking water.

In the drier Klamath and Blue Mountains ecoregions, dependence of water supplies on sufficient accumulated winter snowpack is amplified due to less rainfall. The mountains serve as crucial water collection sources for these areas. Mountains receive far more moisture than the lower elevation valleys and canyons that they eventually supply with water. As snow melts, it recharges soil water to support ecosystems through seasonally dry summers. The slow transfer of water sustains water supplies and maintains summer stream flows that in turn support high levels of biodiversity in aquatic and riparian systems. Mountain water is also of major importance to agriculture. In these seasonally dry forests, protecting forested watersheds will be crucial to the long-term water security of the region.

Older forests in Oregon's watersheds exhibit greater water retention and improved late summer stream flows compared to managed plantations (Segura et al., 2020). Intact forests also tend to harbor more large and old trees, bolstering carbon stores and biodiversity services that large trees provide (Lutz et al., 2018; Plumtre et al., 2021). As warming increases, protecting the integrity of these intact forested watersheds would help sustain valuable ecosystem services, including a clean, reliable supply of water. Oregon's largest protected area, the Eagle Cap Wilderness, demonstrates the tremendous value of a largely protected forested mountain range for providing a reliable source of clean water to the ecosystems and communities of northeast Oregon.

Some ecoregions will see declines and even biome shifts as warming continues, but this is somewhat counteracted by the positive effect of atmospheric CO_2 on photosynthesis and lengthened growing seasons in the wetter ecoregions. The effects of increasing atmospheric CO_2 will continue in spite of reaching greenhouse gas reduction targets because surface temperatures will not immediately return to previous levels and may persist for a millennium or more (Solomon et al., 2009). While strategic forest reserves for climate mitigation and adaptation by plants and animals may face near-term challenges, the urgency and benefits of protecting landscapes for community and ecosystem values is nonetheless very high as the world moves to transition away from fossil fuel pollution.

The diversity of ecoregions and forest communities within Oregon also suggests that systems will respond differently to warming across the region. Even within forest types, individual species have unique adaptations and vulnerability thresholds. In Oregon's Coast Range, conversion of diverse conifer systems to Douglas-fir plantations has increased vulnerability to Swiss Needle Cast disease (Shaw et al., 2021), and climatic change may further exacerbate this vulnerability (Mildrexler et al., 2019). Moreover, young industrial plantations show a higher incidence of high severity fires, almost twice as many as on public lands (Levine et al., 2022). In other ecosystems, disturbance-induced shifts may facilitate changes in species composition, including shifts toward communities better adapted to changing climatic conditions. Taken as a whole, Oregon's exceptional ecosystem diversity will help buffer its forests against large-scale shifts in ecosystems.

Improving measurement, reporting and verification

To initiate strategic reserves, consistent guidelines, definitions, and accounting rules need to be established. Similar to international requirements for monitoring, reporting and verification (MRV; Ellis and Moarif, 2015), there is a need to upgrade our measurement systems as recommended in national and international reports (e.g., Law et al., 2008; Ciais et al., 2014). Consistent, current metrics will help refine locations for reserves, establish baseline conditions, and monitor changes in plant and animal species, forest carbon and other metrics of condition. Updated metrics will also ensure reliability in protection agreements.

An executive order issued by President Biden in 2022 recognized the importance of mature and old-growth forests in limiting climate change and makes their conservation a national policy.[1] The land management agencies are tasked with defining mature and old. Carbon per unit area ground (carbon density) is an essential climate variable for mitigation, and can be used to distinguish mature from young forests. Carbon density is computed from tree diameter and height and can be used to identify the inflection point at which the increase following stand-replacing disturbance begins to slow for a tree community within ecoregion. In addition, tree diameter and height are useful to infer site fertility and could be used to scale forest carbon potential in different environments. When assessing the mitigation potential of forests in a region, we must consider that carbon density and removal rates are strongly variable with edaphoclimatic conditions, even within the same forest type. Young forests have low carbon density compared to mature and old (Hudiburg et al., 2009). Age alone is not a good metric because it is not measured well in most regions or is approximated from tree diameter. Furthermore, age is a good indicator of the time since the last stand-replacing disturbance only in early successional stands with pioneer tree species. In late-successional stands with shade-tolerant trees (i.e., long suppression phases), maximum tree age is not necessarily related to disturbance. Long-term repeated measurements of ecosystems across the landscape/ecoregion provide a much more precise picture of carbon dynamics, like the repeated direct measurements of diameter and height in federal inventories (Forest Inventory and Analysis [FIA], 2014). In addition, these measurements are used to produce a metric of structural diversity that is important for biodiversity.

Coordination among federal, state and international programs are needed for consistency of repeated measurements, reporting, and verification. To inform strategic assessments and decision making, spatial datasets must represent environmental conditions consistently across the country at moderate to high spatial resolution (30–250 m) and must be updated at least every 5-year (e.g., for the federally mandated National Climate Assessment produced every 4 years), and include:

- Processed inventory data that use height and dbh in improved algorithms for estimating aboveground biomass carbon.

1 https://www.federalregister.gov/documents/2022/04/27/2022-09138/strengthening-the-nations-forests-communities-and-local-economies

- More frequent maps of forest area, forest type, forest carbon stocks, forest age (young, mature, and old) and spatial estimates of uncertainty for each product.
- Consistent and repeated measurements of plant and animal species richness and habitat quality in a measurement system that is co-located or coincides with the forest inventory, and data reporting to a central database.
- Habitat connectivity data products.
- Ecosystem model projections of future forest carbon dynamics and vulnerabilities to drought, fire, and insects under various climate scenarios (transition model projection from research oriented to operational oriented analysis).

Socioeconomic and policy challenges and solutions

To some extent, forest management priorities on national forests have changed from timber harvest and maximizing wood production to conservation and adaptation to climate change (USDA Forest Service, 2022). These changes are well aligned with strategic forest reserves that can serve as focal areas of ecological integrity and genetic diversity that benefit adjacent areas (Greater Protected Areas). As our western US and Oregon analyses show, achieving protected area targets is a practical goal and does not require all federal forestlands. Many areas will remain outside protected areas, but these forests will experience long-term benefits from increased proximity to protected landscapes.

Forest ownership by public real estate investment trusts (REITs) and timber investment management organizations (TIMOs) have the goal of maximizing return on investment. In Canada and the United States, 60% of the timberland area owned by the top ten entities was in REITs in 2015. Over the past 40 years, as much as 304,000 hectares of Oregon's non-industrial forest ownership has transferred to forest industries by buyouts and mergers, now dominated by a few industrial owners in each county (Willer, 2021). As of 2020, at least 40% of private forest lands are owned by investment companies as public or private REITs whose forestland portfolio is managed by TIMOs. The industry consists of investors or owners and corporate management that serves them, and it often subcontracts harvest, transport, reforestation and pesticide chemical application. Forest operations are compartmentalized. While REITs and TIMOs seek to monetize the value of timber harvest, they also have been involved in projects that monetize ecosystem services, carbon sequestration, and, in some cases, a land use change from forestry to development. Integrated forest companies own forestland and mills and they, on the other hand, depend on a consistent, predictable supply of wood. They view limits on harvest for ecosystem values as an encumbrance that impacts the bottom line. REITs, TIMOs and integrated forest product companies own the bulk of private forests in Oregon, but there are approximately 1.49 million hectares of family owned non-industrial forests that are enjoyed for privacy, wildlife, scenic values, water and, to a far lesser extent, harvest.

Currently, there is little incentive to manage private forestlands for ecosystem resilience to climate change impacts, biodiversity or carbon storage, and industrial management has resulted in significant losses of habitat and biodiversity and carbon stocks, and degraded water systems. Oregon's private forests laws have lagged behind those in California and Washington for decades, and recent changes adopted in 2022 focus primarily on changes for threatened and endangered fish species, not climate mitigation, terrestrial biodiversity or drinking water supplies.

Land trusts have played a role in protecting Oregon's private forestlands, yet their coverage area is growing but not yet substantial. With significant funding, land trusts could play a greater and important role in securing high-priority private forest lands from development and harvest. Land trusts typically use conservation easements to protect key private lands from extractive management and to protect certain values in perpetuity. This analysis provides a framework to spatially examine the value of private forestlands and prioritize efforts for the greatest climate mitigation and biodiversity protection benefits.

To sustainably achieve climate and conservation goals, projects must not lead to more emissions from deforestation and forest degradation (Nolan et al., 2021). To do so and be included in meeting preservation targets, lands should be protected at GAP 1 or GAP 2 status (IUCN 1a to VI). Roadless areas that are not currently inventoried should be inventoried to determine if they qualify.

Projects have to demonstrate permanence of protected forest carbon, and account for leakage and additionality. Regular assessment of permanence, leakage and additionality is essential for forest offsets programs to ensure there is not over-crediting (Anderegg et al., 2020). Moreover, carbon accounting among projects is needed to understand their contributions to meeting climate goals. Permanence can be addressed by requiring a portion of the credits (e.g., 20%) be set aside as a buffer in case natural disturbances occur in the project area (wildfire, beetle kill; Anderson et al., 2017). Leakage means that protecting one area of forest could result in cutting elsewhere, even in another country, and currently there is no international program to track it. Leakage could be addressed by assuming leakage exists and providing only partial credit for projects. Although a regulatory pathway is the typical approach to constraining what qualifies for meeting the intended goal with a minimum of unintended consequences, the requirement of additionality can hinder success in protecting private and indigenous forestlands. Additionality means one has to demonstrate that the climate benefits of preserving forests would not have occurred without the project. An option is to have science-based verification of proposed projects before they are approved, and if a proposed

project cannot protect the whole area, then provide partial credit for the areas that are most likely to be protected with permanence. Accounting and incentives could be applied to ensure the protection targets are met at local to national scales. Offsets are just one of a number of ways (and not the best way from a climate mitigation perspective) in which forest ecosystem carbon removals from the atmosphere and accumulated carbon stocks can be used, accounted for, and forest stewards rewarded.

Conclusion

The most important action Oregon can take to mitigate climate change, reduce biodiversity losses, and protect watersheds for drinking water is to set aside existing forests. Reforestation or afforestation can be done too, but it takes decades for young trees to mature into net carbon sinks. Planting young trees will not result in much additional storage within the time forest carbon stocks need to increase in order to contribute to emission reduction and global warming targets.

The approach developed by Law et al. (2021) demonstrated the value of coupling forest carbon and biodiversity metrics into a spatially continuous prioritization framework that can be applied across large, diverse forested regions. Here, we improved the approach by adding a resilience metric that represents connectivity and topographic diversity, and used finer resolution (30 m) and more recent data to better resolve within-state variability in carbon, drinking water sources, and biodiversity and resilience metrics. An ecoregion-based approach along with resilience-based metrics will ensure species and habitat are protected and connected so that species can move to areas where they can survive and thrive as climate change intensifies.

The analysis identifies the potential for a well distributed forest reserve network within Oregon that captures unique ecological facets by ecoregion to achieve targets for protecting 30% of forests by 2030 and 50% by 2050. Protecting forest carbon, watersheds, and biodiversity are universally important priorities regionally, nationally and globally, and our framework could be applied in other regions for mitigation and adaptation to climate change.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: The forest prioritization dataset generated for this study will be publicly archived with PANGAEA (https://www.pangaea.de/). Further, the following existing dataset were analyzed for this study. Forest structure and composition data were from the Landscape Ecology Modeling Mapping and Analysis (Lemma) Team (https://lemma.forestry.oregonstate.edu/data). Forest disturbance data were from University of Maryland's Global Forest Change dataset (https://earthengine.google.com/). Protected Area data were from the United States Geological Survey GAP Analysis program (https://doi.org/10.5066/P92QM3NT), as were species habitat maps (https://doi.org/10.5066/F7V122T2). Forest land management data were from the Oregon Department of Forestry (https://spatialdata.oregonexplorer.info/). Surface drinking water source data were from the Oregon Department of Environmental Quality (https://www.oregon.gov/deq/wq/programs/Pages/DWP-Maps.aspx).

Author contributions

BL: conceptualization the project. BL and LB: investigation and writing – original draft preparation. LB: data analysis and visualization. BL, LB, DM, WR, and RB: writing – review and editing. All authors have read and agreed to the published version of the manuscript.

Funding

RB was supported by the Oregon Community Foundation.

Acknowledgments

The authors thank Mary Wood and Doug Quirk from U Oregon and Polly Buotte from UC-Berkeley for reviewing an early draft.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.1028401/full#supplementary-material

References

Anderegg, W. R., Trugman, A. T., Badgley, G., Anderson, C. M., Bartuska, A., Ciais, P., et al. (2020). Climate-driven risks to the climate mitigation potential of forests. *Science* 368:6497. doi: 10.1126/science.aaz7005

Anderson, C. M., Field, C. B., and Mach, K. J. (2017). Forest offsets partner climate-change mitigationwith conservation. *Front. Ecol. Environ.* 15:359–365. doi: 10.1002/fee.1515

Berner, L. T., Law, B. E., and Hudiburg, T. W. (2017). Water availability limits tree productivity, carbon stocks, and carbon residence time in mature forests across the western US. *Biogeosciences* 14, 365–378.

Buttrick, S., Popper, K., Schindel, M., McRae, B., Unnasch, B., Jones, A., et al. (2015). *Conserving nature's stage: Identifying resilient terrestrial landscapes in the Pacific Northwest*. Portland, OR: The Nature Conservancy.

Carroll, C., Parks, S. A., Dobrowski, S. Z., and Roberts, D. R. (2018). Climatic, topographic, and anthropogenic factors determine connectivity between current and future climate analogs in North America. *Glob. Change Biol.* 24, 5318–5331. doi: 10.1111/gcb.14373

Ciais, P., Dolman, A. J., Bombelli, A., Duren, R., Peregon, A., Rayner, P. J., et al. (2014). Current systematic carbon-cycle observations and needs for implementing a policy-relevant carbon observation system. *Biogeoscience* 11, 3547–3602. doi: 10.5194/bg-11-3547-2014

College of Forestry (2022). *Elliott state research forest, forest management plan*. 390.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., et al. (2017). An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* 67, 534–545. doi: 10.1093/biosci/bix014

Donato, D. C., Campbell, J. L., and Fontaine, J. B. (2015). *Ten years after the biscuit fire: Evaluating vegetation succession and post-fire management effects. Final Report JFSP*. Olympia, WA: Washington State Department of Natural Resources.

Dowle, M., and Srinivasan, A. (2021). *data.table: Extension of 'data.frame'. R package version 1.14.2*. Available online at: https://CRAN.R-project.org/package=data.table

Ellis, J., and Moarif, S. (2015). *Identifying and addressing gaps in the UNFCCC reporting framework, OECD/IEA climate change expert group papers, no. 2015/07*. Paris: OECD Publishing. doi: 10.1787/5jm56w6f918n-en

Evan, A., and Eisenman, I. (2021). A mechanism for regional variations in snowpack melt under rising temperature. *Nat. Clim. Change* 11, 326–330. doi: 10.1038/s41558-021-00996-w

Forest Inventory and Analysis (2014). *The forest inventory and analysis database: Database description and user guide version 6.0.1 for phase 3*. Washington, DC: U.S. Department of Agriculture, Forest Service.

Frissell, C. A. (2013). *Aquatic resource protections in the northwest forest plan: Evaluating potential consequences of proposed riparian reserve reductions for clean water, streams and fish*. Corvallis, OR: Report prepared for the Coast Range Association.

Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., et al. (2017). Natural climate solutions. *Proc. Natl. Acad. Sci. U.S.A.* 114, 11645–11650.

Halofsky, J. E., Donato, D. C., Hibbs, D. E., Campbell, J. L., Donaghy Cannon, M., Fontaine, J. B., et al. (2011). Mixed-severity fire regimes: Lessons and hypotheses from the Klamath-Siskiyou Ecoregion. *Ecosphere* 2, 1–19. doi: 10.1890/ES10-00184.1

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., et al. (2013). High-resolution global maps of 21st-century forest cover change. *Science* 342:850. doi: 10.1126/science1244693

Hijmans, R. J. (2019). *raster: Geographic analysis and modeling. R package Version 3.0-12*. Available online at: http://CRAN.R-project.org/package=raster

Hijmans, R. J. (2022). *terra: Spatial data analysis. R package Version 1.5-21*. Available online at: https://CRAN.Rproject.org/package=terra

Hudiburg, T., Law, B. E., Turner, D. P., Campbell, J. L., Donato, D. C., and Duane, M. (2009). Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. *Ecol. Appl.* 19, 163–180. doi: 10.1890/07-2006.1

IPCC (2022). "Climate change 2022: Impacts, adaptation, and vulnerability. Contribution of working group ii to the sixth assessment report of the intergovernmental panel on climate change," in *Summary for policymakers*, eds H.-O. Pörtner, D. C. Roberts, E. S. Poloczanska, K. Mintenbeck, M. Tignor, A. Alegría, et al. (Cambridge: Cambridge University Press).

IUCN (2013). "IUCN WCPA best practice guidance on recognising protected areas and assigning management categories and governance types," in *Best practice protected area guidelines series no. 21*, ed. N. Dudley (Gland: IUCN).

Karr, J. R., Rhodes, J. J., Minshall, G. W., Hauer, F. R., Beschta, R. L., Frissell, C. A., et al. (2004). The effects of postfire salvage logging on aquatic ecosystems in the American West. *Bioscience* 54, 1029–1033. doi: 10.1641/0006-35682004054[1029:TEOPSL]2.0CO;2

Körner, C. (2017). A matter of tree longevity. *Science* 355, 130–131. doi: 10.1126/science.aal2449

Landscape Ecology Modeling Mapping and Analysis (Lemma) Team (2020). *Gradient nearest neighbor (GNN) raster dataset (version 2020.01). Modeled forest vegetation data using direct gradient analysis and nearest neighbor imputation*. Available online at: https://lemma.forestry.oregonstate.edu/data

Law, B. E., Arkebauer, T., Campbell, J. L., Chen, J., Sun, O., Schwartz, M., et al. (2008). *Terrestrial carbon observations: Protocols for vegetation sampling and data submission. Report 55, global terrestrial observing system*. Rome: FAO, 87.

Law, B. E., Berner, L. T., Buotte, P. C., Mildrexler, D. J., and Ripple, W. J. (2021). Strategic forest reserves can protect biodiversity in the western United States and mitigate climate change. *Nat. Commun. Earth Environ.* 2:254. doi: 10.1038/s43247-021-00326-0

Law, B. E., Hudiburg, T. W., Berner, L. T., Kent, J. J., Buotte, P. C., and Harmon, M. E. (2018). Land use strategies to mitigate climate change in carbon dense temperate forests. *Proc. Natl. Acad. Sci. U.S.A.* 115, 3663–3668. doi: 10.1073/pnas.1720064115

Law, B. E., Hudiburg, T., and Luyssaert, S. (2013). Thinning effects on forest productivity: Consequences of preserving old forests and mitigating impacts of fire and drought. *Plant Ecol. Divers.* 6, 73–85. doi: 10.1080/17550874.2012.679013

Law, B. E., Moomaw, W. R., Hudiburg, T. W., Schlesinger, W. H., Sterman, J. D., and Woodwell, G. W. (2022). Creating strategic reserves to protect forest carbon and reduce biodiversity losses in the United States. *Land* 11:721. doi: 10.3390/land11050721

Lawler, J. J., Ruesch, A., Olden, J. D., and McRae, B. H. (2013). Projected climate-driven faunal movement routes. *Ecol. Lett.* 16, 1014–1022. doi: 10.1111/ele.12132

Levine, J. I., Collins, B. M., Steel, J. L., de Valpine, P., and Stevens, S. L. (2022). High incidence of higher severity fire in and near industrially managed forests. *Front. Ecol. Environ.* 20:397–404. doi: 10.1002/fee.2499

Liu, N., Caldwell, P. V., Dobbs, G. R., Miniat, C. F., Bolstad, P. V., Nelson, S. A., et al. (2021). Forested lands dominate drinking water supply in the conterminous United States. *Environ. Res. Lett.* 16:084008. doi: 10.1088/1748-9326/ac09b0

Lutz, J. A., Furniss, T. J., Johnson, D. J., Davies, S. J., Allen, D., Alonso, A., et al. (2018). Global importance of large-diameter trees. *Glob. Ecol. Biogeogr.* 27, 849–864. doi: 10.1111/geb.12747

Luyssaert, S., Schulze, E. D., Börner, A., Knohl, A., Hessenmöller, D., Law, B. E., et al. (2008). Old-growth forests as global carbon sinks. *Nature* 455, 213–215. doi: 10.1038/nature07276

Mackey, B., Kormos, C. F., Keith, H., Moomaw, W. R., Houghton, R. A., Mittermeier, R. A., et al. (2020). Understanding the importance of primary tropical forest protection as a mitigation strategy. Mitigation adaptation strat. *Glob. Change* 25, 763–787.

Merkle, J. A., Abrahms, B., Armstrong, J. B., Sawyer, J., Costa, D. P., and Chalfoun, A. D. (2022). Site fidelity as a maladaptive behavior in the anthropocene. *Front. Ecol. Environ.* 20:187–194. doi: 10.1002/fee.2456

Mildrexler, D. J., Shaw, D. C., and Cohen, W. B. (2019). Short-term climate trends and the Swiss needle cast epidemic in Oregon's public and private coastal forestlands. *For. Ecol. Manag.* 432, 501–513. doi: 10.1016/j.foreco.2018.09.025

Nelson, M. D., Riitters, K. H., Coulston, J. W., Domke, G. M., Greenfield, E. J., Langner, L. L., et al. (2020). *Defining the United States land base: A technical document supporting the USDA forest service 2020 RPA assessment*. General Technical Reports NRS–191. Madison, WI: USDA Forest Service, Northern Research Station. doi: 10.2737/NRS-GTR-191

Nolan, C. J., Field, C. B., and Mach, K. J. (2021). Constraints and enablers for increasing carbon storage in the terrestrial biosphere. *Nat. Rev. Earth Environ.* 2, 436–446. doi: 10.1038/s43017-021-00166-8

Noss, R. F., Dobson, A. P., Baldwin, R., Beier, P., Davis, C. R., DellaSala, D. A., et al. (2012). Bolder thinking for conservation. *Conserv. Biol.* 26:1. doi: 10.1111/j.1523-1739.2011.01738.x

Omernik, J. M., and Griffith, G. E. (2014). Ecoregions of the conterminous United States: Evolution of a hierarchical spatial framework. *Environ. Manag.* 54, 1249–1266. doi: 10.1007/s00267-014-0364-1

Oregon Department of Environmental Quality [DEQ] (2019). *Surface water drinking water source areas in Oregon dataset*. Available online at: https://www.oregon.gov/deq/wq/programs/Pages/DWP-Maps.aspx (accessed June 9, 2022).

Oregon Department of Fish and Wildlife (2021). *Threatened, endangered, and candidate fish and wildlife species [Online]*. Available online at: https://www.dfw.state.or.us/wildlife/diversity/species/threatened_endangered_candidate_list.asp (accessed June 2022).

Oregon Department of Forestry (2015). *Oregon land management – 2015*. Available online at: https://spatialdata.oregonexplorer.info/geoportal/ (accessed February 2022).

Oregon Division of State Lands (2021). *Elliott state research forest habitat conservation plan*. 234.

Pebesma, E. J. (2018). Simple features for R: Standardized support for spatial vector data. *R. J.* 10, 439–446.

Plumtre, A. J., Baisero, D., Belote, R. T., Vázquez-Domínguez, E., Faurby, S., Jędrzejewski, W., et al. (2021). Where might we find ecologically intact communities? *Front. For. Glob. Change* 4:626635. doi: 10.3389/ffgc.2021.626635

Pollock, L. J., Thuiller, W., and Jetts, W. (2017). Large conservation gains possible for global biodiversity facets. *Nature* 546, 141–144. doi: 10.1038/nature22368

Pörtner, H. –O., Sholes, R. J., Agard, J., Archer, E., Arneth, A., Bai, X., et al. (2021). *IPBES-IPCC co-sponsored workshop report on biodiversity and climate change*. Bonn: IPBES and IPCC. doi: 10.5281/zenodo.4782538

Qgis Org (2021). *QGIS geographic information system*. QGIS Association. Available online at: http://www.qgis.org

R Core Team (2021). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Rieman, B. E., Lee, D., Burns, D., Gresswell, R., Young, M., Stowell, R., et al. (2003). Status of native fishes in the western United States and issues for fire and fuels management. *For. Ecol. Manage.* 178, 197–211. doi: 10.1016/S0378-1127(03)00062-8

Ripple, W. J., Wolf, C., Phillips, M. K., Beschta, R. L., Vucetich, J. A., Kauffman, B., et al. (2022). Rewilding the American West. *Bioscience* 72, 931–935. doi: 10.1093/biosci/biac069

Segura, C., Bladon, K. D., Hatten, J. A., Jones, J. A., Hale, V. C., and Ice, G. G. (2020). Long-term effects of forest harvesting on summer low flow deficits in the coast range of Oregon. *J. Hydrol.* 585:124749. doi: 10.1016/j.jhydrol.2020.124749

Shaw, D. C., Ritóková, G., Lan, Y.-H., Mainwaring, D. B., Russo, A., Comeleo, R., et al. (2021). Persistence of the swiss needle cast outbreak in oregon coastal douglas-fir and new insights from research and monitoring. *J. For.* 119, 407–421. doi: 10.1093/jfore/fvab011

Solomon, S., Plattner, G.-K., Knutti, R., and Friedlingstein, P. (2009). Irreversible climate change due to carbon dioxide emissions. *Proc. Nat. Acad. Sci. U.S.A.* 106, 1704–1709. doi: 10.1073/pnas.0812721106

Turner, D. P., Ritts, W. D., Yang, Z., Kennedy, R. E., Cohen, W. B., Duane, M. V., et al. (2011). Decadal trends in net ecosystem production and net ecosystem carbon balance for a regional socioecological system. *For. Ecol. Manage.* 262, 1318–1325. doi: 10.1016/j.foreco.2011.06.034

US Forest Servic (2021). *Forest plans amendment. Forest management direction for large diameter trees in eastern oregon and southeastern washington. Environmental assessment*. Portland, OR: USDA, Forest Service, Pacific Northwest Region.

USDA Forest Service (2022). *USDA forest service climate adaptation plan*. Available online at: https://www.usda.gov/sites/default/files/documents/4_NRE_FS_ClimateAdaptationPlan_2022.pdf (accessed August 19, 2022).

USGS GAP (2018). *Gap analysis project species habitat maps CONUS_2001*. Reston, VA: U.S. Geological Survey. doi: 10.5066/F7V122T2

USGS GAP (2020). *Protected areas database of the United States (PAD-US) 2.1: U.S. geological survey data release*. Reston, VA: U.S. Geological Survey. doi: 10.5066/P92QM3NT

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains. *Ecol. Monogr.* 30, 279–338. doi: 10.2307/1943563

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer-Verlang.

Willer, C. (2021). *Climate and Oregon's industrial forests: A green new deal proposal*. Oregon, OR: Coast Range Association, 50.

Version of Record: https://www.sciencedirect.com/science/article/pii/S0378112721006873
Manuscript_387a7dbd12cb1eb063d5f2b0209b57bd

The importance of Indigenous cultural burning in forested regions of the Pacific West, USA

Jonathan W. Long[a*], 1731 Research Park Dr. Davis, CA 95618, United States

Frank K. Lake[a], 1700 Bayview Drive Arcata CA 95521, United States

Ron W. Goode[b], 13396 Tollhouse Rd., Clovis CA 93619, United States

[a]USDA Forest Service, Pacific Southwest Research Station

[b]North Fork Mono Tribe

***Corresponding author, Jonathan.w.long@usda.gov**

Submitted for special issue, **"Restoration of Cultural Values in Forested Landscapes."**

© 2021 published by Elsevier. This manuscript is made available under the Elsevier user license
https://www.elsevier.com/open-access/userlicense/1.0/

Abstract

Indigenous communities in the Pacific West of North America have long depended on fire to steward their environments, and they are increasingly asserting the importance of cultural burning to achieve goals for ecological and social restoration. We synthesized literature regarding objectives and effects of cultural burning in this region within an ecosystem services framework. Much scholarly literature focuses on why various species harvested from burned areas were important historically, while tribes and recent research increasingly stress the benefits of contemporary cultural burning for a wide range of ecological and cultural benefits. These tribal values generally align with broader ecological restoration objectives, although Indigenous practitioners espouse holistic views on the benefits of burning rather than focusing narrowly on fuel reduction and wildfire mitigation. While government agencies are motivated to treat more and larger areas to reduce fire risk (expanding pace and scale), tribal practitioners have tended to burn comparatively small areas at one time, and cumulatively due to various constraints. However, they would like to burn more widely and frequently to promote resilience to wildfire and drought; conserve biocultural diversity, maintain traditional knowledge and spiritual values; and provide material goods such as foods, medicines, and fiber materials. Much of the experimental research on the effects of cultural burning has been conducted as graduate research and has tended to look at single burns (sometimes agency prescribed burns or wildfires rather than tribally-led cultural burns) for short periods in very limited contexts. Such studies have found that treatments often promote desirable plant qualities, including reduced incidence of pests and structural qualities that facilitate weaving and other crafts. However, effects on understory plant diversity, wildlife, fruit production, parasites, and other key aspects of resource quality have been more difficult to evaluate due to complex interactions and scale considerations. Expanding long-term tribal collaboratives, including designating cultural management areas with

frequent burning, would help to understand the potential to achieve ecocultural restoration objectives.

Keywords: ecosystem services, Indigenous stewardship, cultural burning, fire ecology, forest management, socioeconomic values, prescribed burning, wildland fire, American Indians

1. Introduction

Indigenous communities in the Pacific West of North America have long depended on fire to steward their environments (Boyd, 1999; Turner, 1999; Anderson, 2009; Lightfoot and Parrish, 2009; Anderson, 2018). Indigenous communities in this region have expressed their interest in reasserting their traditional fire stewardship practices (Goode *et al.*, 2018; Clark *et al.*, 2021). Federal and state agencies have sought to increase their engagement with tribes and other Indigenous organizations to support restoration, including collaboratives such as the Western Klamath Restoration Partnership (Kelly *et al.*, 2019). Consequently, there is heightened interest in how Indigenous approaches to burning can integrate with broader ecosystem restoration policies and investments.

1.1. Calls for increased use of fire

Scientists and land managers have increasingly called for greater use of fire, including both prescribed and naturally-ignited fires, to expand the "pace and scale" of restoration and promote resilience of social-ecological systems (Kolden, 2019; McWethy *et al.*, 2019; Spies *et al.*, 2019). These calls have become stronger as uncharacteristically large and severe wildfires have become more common (Miller and Safford, 2012; Miller *et al.*, 2012; Reilly *et al.*, 2017), and disruptive to ecological and social values, including public health (O'Dell *et al.*, 2019) and cultural resources (Welch, 2012). National forests in this region have initiated the process of revising their land management plans to expand the role of intentional fire (Spies *et al.*, 2019), while the

State of California has committed to sweeping new initiatives (Forest Management Task Force, 2021) that include support for tribal cultural burning. However, significant policy obstacles, including liability concerns and air quality regulations, may hinder these efforts (Clark *et al.*, 2021).

1.2. Intent and scope of this review

In this paper we review and synthesize publications about Indigenous use of fire in the Pacific West in the present-day United States to explain its importance to tribal communities, its utility in advancing social and ecological well-being now and in the future, and key implications for research and management. Our review concentrates on the forested regions of Northern California and southern Oregon, which is a center stage for Indigenous burning, including being the place where the Indigenous Peoples Burning Network (http://www.conservationgateway.org/ConservationPractices/FireLandscapes/Pages/IPBN.aspx) was founded. However, we also reference studies from the wider region of Western North America that are associated with frequent fire regimes.

We considered a variety of sources, including previously published review articles and synthesis reports, publications derived from social science research including interviews and ethnographies, articles and theses that report findings from monitoring/observational studies, as well as recent reports produced by and for tribal entities that have a policy orientation (Sloan and Hostler, 2014; Goode *et al.*, 2018; Tribe, 2019; Clark *et al.*, 2021). Older academic publications often focus on historical practices and intentions described by cultural practitioners to non-Indigenous researchers (e.g., Stewart 2002), while more recent documents help to understand contemporary needs and constraints often as part of tribal collaborative efforts. Our approach complements a recent review of Indigenous fire management across the globe whose scope was

limited to articles published in peer-reviewed journals since 2000 to reflect contemporary knowledge (Nikolakis and Roberts, 2020). Older literature and tribal reports can highlight objectives that are pertinent to our region, but which may not be well-represented in recent peer-reviewed articles.

We begin by briefly summarizing debates over the past importance of Indigenous burning and the implications for addressing contemporary challenges. Next, we consider how an ecosystem services framework can help to identify important benefits of cultural burning, while also acknowledging how such classification could also misrepresent more holistic tribal perspectives. We then consider implications for management and research. Throughout the paper, we include figures that illustrate examples of contemporary Indigenous burning and their associated targets.

1.3. Evolving debates over the past influence of Indigenous burning

After modern land management institutions in the U.S. were established over a century ago, some land managers decried Indigenous burning, then derided by some as "Paiute forestry", as harmful to forests (Harley, 1918; Greeley, 2000). Early U.S. Government records include derogatory references to "old superstitious Indians" (Crouse, 1902), "renegades" (Harley, 1918), and the "hand of the incendiary" with "selfish and malicious motives" (Lake, 2007) (p. 273). Over the past century, academics have debated the importance of Indigenous burning versus climate on fire regimes. Whitlock and Knox (2002) provided a review for the Pacific Northwest that considered paleoecological evidence over thousands of years and historical accounts and which highlighted the extensive influences in the Willamette Valley of Oregon. Focusing on ethnoecology research in the same region, Boyd (1999) highlighted regional features associated with fire use, including huckleberry patches, ponderosa pine forests, oak woodlands, and prairies. Other scientists have contended that the influence of Indigenous burning in the Pacific

West was confined to localized areas around settlements (Vale, 2002). These claims have been challenged by researchers who have found evidence that changes in fire regimes coincide with interruption of Indigenous practices (Fry and Stephens, 2006; Skinner *et al.*, 2009; Taylor *et al.*, 2016; Metlen *et al.*, 2018). They have also been challenged by other researchers who have engaged directly with Indigenous communities to document their use of fire (Anderson, 2009; Lake, 2013; Anderson, 2018). Recent research using paleoecological reconstruction and landscape modeling found that Indigenous burning shaped the environment, including promoting oaks, over large areas around meadow sites in the southern Sierra Nevada (Klimaszewski-Patterson and Mensing, 2020).

Debates over the influence of Indigenous burning have occurred in other regions of North America, leading some scientists to note how conventional paleoecology approaches may fail to recognize the influence of Indigenous burning. For example, Oswald *et al.* (2020b) recently synthesized paleoecological research and historical documents and concluded that "Native people did not use fire to shape New England's landscape" (Oswald *et al.*, 2020a) and that fire was not an appropriate management tool in that region. That work generated several responses that explained why the effects of Indigenous burning may be difficult to resolve at landscape scales and why it is important to carefully consider such evidence and Indigenous knowledge (Abrams and Nowacki, 2020; Leonard *et al.*, 2020; Roos, 2020).

Recent studies in other regions, many of which have involved partnerships with Tribes, have also documented legacies of Indigenous burning. In a study in the Northern Great Plans that involved the Blackfeet Nation, Roos *et al.* (2018) concluded that small groups of Indigenous bison hunters were using fire in response to favorable climate conditions, thereby enhancing climate impacts in ways that might be difficult to distinguish from Indigenous burning. A study in the high plateaus

of Utah using archaeological data and modeling found that fire activity was more strongly correlated with ancient Indigenous farming-foraging systems than the climate factors that dominate more recent wildfire activity (Carter *et al.*, 2021). In the Jemez Mountains of the Southwest, a recent study by Roos *et al.* (2021), which involved several tribes in the region, documented the ecological influence of patchy Indigenous burning and wood collection around an ancestral Jemez community. This work added to research by Liebmann *et al.* (2016), who provided fine-grained evidence of the impacts of Spanish colonization on Native Jemez populations and the indirect changes on fire regimes and forest regeneration. These recent studies contrast with older ecological research in the Southwest that discounted Indigenous influence on fire regimes and instead emphasized the influence of lightning (Allen, 2002).

This evolving science demonstrates the importance of engaging with tribes to interpret records and understand implications of research. In many of the more recent publications that were informed by collaborations with Indigenous peoples, researchers have noted that methods need to be sensitive to the finer-scale, more subtle signatures of Indigenous burning (Lake, 2013; Roos *et al.*, 2019). We return to research issues later in this paper, while turning our focus to understanding how and why Indigenous burning can help confront present and future social and ecological challenges.

1.4. Definition and objectives of cultural burning

Cultural burning has been recently defined by Clark *et al.* (2021) as the "purposeful use of fire by a cultural group (e.g., family unit, Tribe, clan/moiety, society) for a variety of purposes and outcomes" (p. 3). Other terms such as Indigenous fire management (Nikolakis and Roberts, 2020), Indigenous burning, and Indigenous stewardship encompass cultural burning. Practitioners note that cultural burns are generally preceded by extensive site preparation and

148 followed by monitoring and additional cultural practices as part of a land stewardship tradition.
149 Agency-led prescribed burns may be informed by cultural practitioners to achieve cultural
150 objectives (Fig. 1). However, cultural burners contend that typical agency-led prescribed burns
151 tend to be more focused on reducing fuels and avoiding canopy mortality, while relying more on
152 climatological metrics, constructed fire lines, and suppression technology (Marks-Block and
153 Tripp, 2021).

154



Figure 1: A prescribed burn project led by a crew from Greenville Rancheria, with guidance from elders, to promote beargrass (*Xerophyllum tenax*) near Canyon Dam on the Plumas National Forest. Photo by Reina Rogers.

155 Scholars have previously catalogued the many objectives of cultural burning. Williams (1994)
156 condensed 70 different reasons for Indigenous burning documented by Lewis (1973) into 11
157 categories (Table 1). A recent review of international burning across temperate and tropical
158 biomes around the work identified 18 categories of objectives (Trauernicht et al., 2015) (Table
159 1). Recent reviews from chaparral ecosystems in California (Anderson and Rosenthal, 2015;
160 Anderson and Keeley, 2018) identify particular organisms that were targeted in Indigenous
161 burning, while then explaining how those practices support social engagement and ecosystem-
162 level functions.

163 *1.5. Present-day priorities*

164 Priorities for cultural burning have shifted in response to the present-day challenges facing tribal
165 communities. A recent article reported that tribes in British Columbia had goals of strengthening
166 cultural connection and well-being, restoring the health of the land, and respecting traditional
167 laws (Nikolakis *et al.*, 2020). Another recent review from British Columbia (Lewis *et al.*, 2018)
168 found that cultural burning continues to follow traditional rationales, but that debris control and
169 hazard abatement have become more predominant while foodstuff amelioration has become less
170 predominant. Recent reports in California directed toward policy change (Goode *et al.*, 2018;
171 Clark *et al.*, 2021) focus on present-day needs and intentions that emphasize social values
172 including the right to burn and cultural integrity, as well as material benefits and community
173 safety. Such forward-looking approaches are an expression of tribal adaptive capacity and self-
174 determination (Mauer, 2020).

2. Ecosystem services frameworks

2.1. Millenium Ecosystem Assessment framework and revisions

Ecosystem services are commonly defined as benefits that ecosystems provide to people, or more precisely as those *functions* of ecosystems that benefit humans (Kremen, 2005). Scholars have noted that humans have to make some investment (for example, harvest and processing) to convert the services into actual benefits (Willot *et al.*, 2019). The United Nations' Millennium Ecosystem Assessment (MEA) featured a function-based typology that included "provisioning", "regulating", and "cultural" services that directly affect people, as well as the "supporting services" that maintain the system (Patterson, 2014). Scholars have tried to update these frameworks to avoid problems such as double counting by not using a supporting services category (Willot *et al.*, 2019). Despite these issues, ES frameworks like the MEA are increasingly structuring agency land management planning, including revision of national forest plans in the U.S. (Armatas *et al.*, 2018), as well as international vulnerability assessments of forest and communities (Paudyal *et al.*, 2015; Long and Steel, 2020). Consequently, an ecosystem services framework may be useful in relating values important to tribes to these institutional processes. In Table 1, we crosswalk these categories to ones previously suggested in reviews of Indigenous burning with different spatial scopes, while acknowledging that objectives often relate to multiple kinds of services.

2.2. Services for ecosystems and other modifications to better reflect Indigenous worldviews

While applying an ecosystem services framework, we recognize that its utilitarian emphasis may conflict with worldviews commonly held by Indigenous people. Applications of the framework often emphasize services that are amenable to economic valuation (Binder *et al.*, 2017); however, for many cultural ecosystem services, quantification and monetization may be difficult or objectionable (Fish *et al.*, 2016). Indigenous communities often maintain more holistic,

reciprocity-based philosophies, which reflect a deontological, or duty-based, framework (Whyte, 2018). This philosophy of stewardship has been described as "reciprocal restoration" (Kimmerer, 2011), a "caretaker responsibility" (Deur, 2009), and "human services for ecosystems" (Lake, 2021). Members of Indigenous communities have emphasized both benefits and a sense of duty as motivations for cultural burning (Deur and Turner, 2005; Strass, 2010). Many Indigenous practitioners view cultural burning as fulfilling their stewardship responsibilities to the land, while suggesting that such practices will in turn benefit the people who depend on those ecosystems (Kimmerer and Lake, 2001). Therefore, frameworks that emphasize measurable goods and ends may reinforce consumerism and fail to appreciate the importance of maintaining proper ways of living and the well-being of whole systems to Indigenous peoples.

Researchers have proposed alternative frameworks for examining cultural services, especially to better integrate Indigenous perspectives (Fish *et al.*, 2016; Mucioki *et al.*, in press). The MEA and other frameworks apply the term "cultural ecosystem services" only to *non-material* benefits, including aesthetic, spiritual and existence values, in contrast with more tangible services (Fish *et al.*, 2016). However, associating cultural services only with intangible benefits is awkward because material provisions are so critical to maintaining Indigenous cultures. In response, Fish *et al.* (2016) (p. 212) instead defined cultural services as "contributions ecosystems make to human well-being in terms of the identities they help frame, the experiences they help enable and the capabilities they help equip."

2.3. Non-material cultural services

Non-material cultural services are one of the least studied dimensions of Indigenous fire stewardship, but they are particularly important in explaining why Indigenous people assert the need to conduct burning themselves. We discuss several examples of non-material cultural

222 services, while noting that these benefits intersect synergistically with each other and with the
223 physical effects that also support tribal cultures.

224 *2.3.1. Maintenance of lifeways*

225 After living in fire-prone landscapes for millennia, many tribes across the Pacific West have
226 become culturally dependent on fires to obtain benefits from their ecosystems. They developed
227 practices to modify fire regimes that responded to climate and other environmental factors
228 (Anderson, 2005; Eriksen and Hankins, 2014; Lake, 2021). These relationships vary across and
229 among tribes and at different levels of organization, including individuals, families, clans/groups,
230 and villages/towns. Differences among practices are associated with gender, specialized trades
231 (e.g., basketweaver, hunter, food gatherer, regalia maker), and cultural roles (e.g. ceremonial
232 leader, defender of sacred areas) (Lake, 2021). Some uses of fire reported from historical
233 literature (e.g. smoke signaling, felling trees, driving game, economic warfare) have been
234 displaced by adoption of alternative technologies and other social changes. As discussed further
235 under provisioning services, to yield good returns on their investments of labor, Indigenous
236 practitioners target areas that are accessible and expected to be productive (Long *et al.*, 2016).
237 Burning remains important for clearing areas and enhancing resource quality in ways that make
238 it sufficiently worthwhile to invest time in tending and harvest (Anderson, 2018; Long and Lake,
239 2018). Accounts from more than a century ago noted the lack of fire and effects of non-
240 Indigenous forest practices were reducing opportunities for traditional harvest (Editor, 1916;
241 Thompson, 1916).

242 *2.3.2. Transmission of knowledge*

243 Indigenous knowledge is derived from observations of the environment, ecological processes and
244 species life histories and interactions; it is also taught continually as members engage in ritual,

subsistence, and other domestic activities that provide opportunities for intergenerational exchange (Huffman, 2013). When environmental conditions deteriorate in ways that no longer support traditional lifeways, the associated knowledge and social structures are likely to erode (Willette *et al.*, 2016; Norgaard *et al.*, 2017; Long and Lake, 2018). Cultural burns are a mechanism for reversing this erosion, as they draw in members from many tribal communities who share their knowledge of using fire and tending resources while reaffirming shared obligations. Such burns are conducted to create more open and safer areas that facilitate access by elders and youth (Anderson and Rosenthal, 2015). Burning and associated stewardship practices maintain culturally important traditions including intergenerational learning and place-making (LeCompte-Mastenbrook, 2016; Norgaard, 2019).

2.3.3. Ceremonies and spiritual well-being

Cultural use of fire is important for sustaining Indigenous spiritual values, including fulfilling obligations in Tribal belief systems and practices (Eriksen and Hankins, 2014). For example, among the Southern Paiute, "oral history states that the Creator charged them with balancing the land, which is sentient and considered a close relative, at different points in time", and fire is one of the tools they are expected to use to maintain that balance (Spoon et al., 2015). Cultural burns are featured in ceremonies (Kimmerer and Lake, 2001), and they are typically conducted with offerings of ceremonial plants like tobacco (*Nicotiana* spp.), wild celery (*Lomatium* spp.) and sage (*Salvia* spp. and *Artemisia* spp.) and sharing of songs. Many Indigenous practitioners consider fire to be "medicine" for both humans and the land, and traditional medicine persons have a key role in using fire (Norgaard, 2019; Wynecoop *et al.*, 2019; Lake, 2021). Some individuals received special training and acquired knowledge of fire, winds, and responses of dead and living plants to fire. Stewart (2002) described such a chosen individual among the

Karuk Tribe as a "formulist": "When setting a fire, the fire setter said formula (made incantations?) for a big fire, yet one which would do no harm…. Then the formulist blows in all four directions to keep the fire from spreading. The formulist is a fire setter who knows the proper medicine" (p. 277). Today such individuals become recognized as cultural burning specialists and serve in roles comparable to a "burn boss" in agency-led prescribed burns.

Areas that have been used to manage wildfires are often located in places of ceremonial and spiritual importance. For example, fire lookout towers were placed upon sacred peaks, which are often used for making medicines and are associated with weather and fires (Norgaard, 2019), and culturally important plants and sites are located along trails and ridges that have been co-opted for agency wildfire management, chiefly suppression (Fig. 2). These places are culturally significant for many reasons, including having long been sites for gathering ceremonial and medicinal plants and instructing youth in the use of fire, as explained by Karuk Tribal member Charlie Thom: "When they [US Forest Service] first come to this country, they start putting lookouts all over…[Mountain peaks named]…I can't make Indian Doctors without [named Mountain peak]…that we go up there, [via] Indian trail, not other trail, but Indians" (Karuk Tribe and Cultural Solutions, 1999a) (p. 13). Failure to recognize the cultural significance of locations being used for wildfire control could reinforce negative impacts to tribal cultures.



Figure 2: Historical tribal trail (upper right) along a ridge, which was maintained using bulldozers as a fire line within the Red-Salmon Complex, August 2020, Klamath National Forest, near Forks of Salmon, California, USA. Photo by Frank Lake, USDA Forest Service.

2.3.4. Sense of place especially at gathering sites

Indigenous tending and gathering often occurs in places that have enduring organisms and cultural associations. Low-intensity fire regimes help ensure the survival of many legacy, "specimen", or "elder" trees that maintain a sense of place and community well-being (Figs. 3, 4, and 5). For many tribes in the Sierra Nevada and Klamath mountains, sugar pine (*Pinus lambertiana)* groves were managed as tribal family-owned resource sites: "the places where the sugar pines grow are owned by individuals. When it is time to gather the cones, each owner invites his family and friends to come with him, and then, when the cones are gathered, they are divided equally among the relatives and guests" (Schenck and Gifford, 1952)*(p. 378)*. Many open old-growth hardwood forests and woodlands support rare wildlife and distinctive architectures, including broad crowns and low branches (Fig. 4) (Long *et al.*, 2016). Fire suppression has aided conifer encroachment in these areas, resulting in development of narrow-

301 crowned trees with high branches that are less conducive for harvesting nuts (Fig. 5). These
302 examples illustrate the difficulty in segregating cultural services from provisioning services.



303

304 Figure 3: An elder sugar pine (*Pinus lambertiana*) provides special cultural values including sense of
305 place in addition to producing edible seeds. Photo by Frank Lake, USDA Forest Service.



Figure 4: This elder canyon live oak tree (*Quercus chrysolepis*) has a distinctive, low-branching architecture growing within an area of Indigenous use that likely moderated fire regimes and facilitated its endurance. Photo by Michael Hentz, Mid Klamath Watershed Council.



Figure 5: An elder tanoak (*Notholithocarpus densiflorus*) tree at a cultural heritage site in the Western Klamath Restoration Project area, where lack of fire and stand densification have accumulated surface fuels and resulted in a loss of lower tree limbs, both of which limit opportunities for gathering. Photo by Kenny Sauve, Karuk Tribe.

2.4. Material cultural-provisioning services

2.4.1. Plants and fungi used for foods, medicines, and materials

Provision of material benefits, often summarized as foods, medicines, and fibers, remain central objectives of Indigenous burning. Several species of hardwood trees, including tanoak, California black oak (*Quercus kelloggii)*, and giant chinquapin (*Chrysolepis chrysophylla*) and some conifers such as sugar pine are associated with low-moderate fire regimes and yield staple foods for tribes throughout the region (Bowcutt, 2013; Long et al., 2018a). Many tribes rely upon cultural burning to stimulate production of berry-producing shrubs, including huckle-blue-bilberries (*Vaccinium* spp.); geophytes, also known as “root crops” or “Indian potatoes” that

propagate from underground storage organs that are edible; and many seed-producing forbs and grasses (Anderson, 1997; Anderson and Rowney, 1999). Many foods, such as roots and berries, are also regarded as medicines (Lynn *et al.*, 2013) and have prominent roles in ceremonies and celebrations of the annual return of "first foods" (Long *et al.*, 2018b). Mushrooms are another tribal resource that may be promoted by cultural burning (Anderson and Lake, 2013). Some fungi including morels and cap mushrooms commonly produce fruiting bodies following disturbances that include fire, although only a few species appear to depend more exclusively on fire (Pilz *et al.*, 2004; Larson *et al.*, 2016). Declines in many of these species have been attributed to fire exclusion, lack of tribal cultivation, and associated growth of competing vegetation (Anderson and Rowney, 1999).

Tribes have long utilized wood for a variety of purposes, including fuel for heating and material for construction. Large trees, especially redwood (*Sequoia sempervirens*), have long been important for constructing structures, furnishings, and canoes (Thompson, 1916; Huntsinger *et al.*, 1994). Frequent, low-intensity Indigenous burning may have promoted development and retention of old-growth redwood (Stephens and Fry, 2005) and therefore, promoted the supply of large logs needed to support tribal traditions. Access to such logs has made traditional canoes available for ceremonies and jumpstarted economic enterprises such as the Yurok Tribe's recently established redwood canoe tours.

Many plants utilized for weaving materials have traditionally been cultivated through burning and associated horticultural practices (Anderson, 1999, 2005; Lake and Long, 2014). Several kinds of plants have been the subjects of recent collaborative research on burning, including beargrass (*Xerophyllum tenax*) (Shebitz *et al.*, 2009b; Hummel *et al.*, 2012; Hart-Fredeluces *et al.*, 2021), sandbar willow (*Salix exigua*) (Lake, 2007; Ross *et al.*, 2008), and hazel (Marks-

347 Block *et al.*, 2019). Thompson (1916) described how Yurok people "take the greatest care of the
348 hazel nut flats" (p. 29) using fire to stimulate nut production and the vast quantities of young
349 shoots needed for baskets.

350 *2.4.2. Harvest of animals*

351 Cultural burning has long been used to facilitate harvest of wild animals, including large and
352 small animals used for meat, tools, regalia, and other material uses (Long and Lake, 2018).
353 While diets in many communities have shown a reduction in the harvest of wild game (Kuhnlein
354 and Receveur, 1996; Norgaard, 2005), burning to promote game animals remains an objective in
355 tribal plans (Karuk Tribe, 2019). Burns were used both to facilitate hunting and to encourage
356 important forage plants, including bracken fern (*Pteridium aquilinum*) relished by deer in
357 prairies of the Olympic peninsula (Norton, 1979). Burning has also been important for harvest of
358 small animals such as insects; for example, Anderson (1996) noted accounts of burning to
359 harvest grasshoppers. A recent collaborative investigation with Northern Paiute Tribes indicated
360 that bark charring encouraged egg deposition of the pandora moth (*Coloradia pandora*), the
361 larvae of which remain a desired traditional food resource (Slaton *et al.*, 2019). Burning was also
362 important in maintaining accessibility for fishing, "Fishing in small streams possible formerly;
363 now completely choked out by brush" (Stewart, 2002) (p. 282).

364 *2.4.3. Multiple dimensions of material productivity*

365 While material uses are considered more straightforward to observe and quantify than other
366 services, measuring provisioning services associated with cultural burning can be very complex.
367 Many products, including traditional foods, medicines, and regalia, may be passed down, traded
368 or gifted rather than sold in markets; often, only finished products such as baskets are priced
369 rather than the component materials harvested from the forest (Marks-Block *et al.*, 2019).

370 Furthermore, wild-harvested products are valued based upon multi-dimensional, non-
371 standardized qualities that resist simple evaluation based upon quantity. For example, several
372 studies have tried to quantify the criteria used by Indigenous basketweavers, who prize the long,
373 pliable and defect-free shoots or leaves that grow after burns (Lake, 2007; Hummel *et al.*, 2015;
374 Marks-Block *et al.*, 2019). While fruit size is not a common measurement in ecological studies,
375 some practitioners suggest that burning could enhance the size of berries. For example, a cultural
376 facilitator, Wally Morgan (Gitxsan) said, "this place was recently burned, that's why the berries
377 are so juicy and the size of marbles" (Armstrong and Anderson, 2020). In a field study,
378 Wynecoop et al. (2019) reported observing large huckleberries in burned plots. These examples
379 illustrate why commonly measured metrics, such as plant canopy cover and frequency, may not
380 capture the many benefits of cultural burning.

381 *2.4.4. Non-substitutable effects of fire on provisional services*

382 While many of the species mentioned previously can also be promoted by non-fire disturbances,
383 fire is considered both an efficient tool and one that is not well-substituted. For example, smoke
384 can enhance germination of plants such as tobacco and beargrass (Preston and Baldwin, 1999;
385 Shebitz *et al.*, 2009a). Tobacco is a featured product of cultural burning in both historical
386 literature and contemporary projects (Harrington, 1932; Boyd, 1999; Baldy, 2013; Tushingham
387 *et al.*, 2013; Aldern and Goode, 2014). In the Klamath region, tobacco has been sowed into burns
388 by individual cultivators, as described by Lucy Thompson over a century ago (1916). As
389 discussed further below, burning also has distinctive effects in regulating insect pests that reduce
390 quality of forest foods and materials.

2.4.5. Managing fire frequency to enhance provisioning services

Indigenous practitioners have long managed the intensity, frequency, and spatial arrangement of fires to promote provisioning services. Indigenous peoples in the region have long considered how fire severity influences mushroom production and the relationships between fungi and host shrubs and trees of cultural importance (Anderson and Lake, 2013). Native Americans in southwest Oregon sometimes burned hazel shrubs at low intensity to "scorch" and "roast" the nuts on the bush as they were harvested (Pullen, 1996). Many roots crops and basketry plants, including those mentioned above and deergrass (*Muhlenbergia rigens*), were burned frequently (1 to 15 years, but often less than 5 years) to cultivate desired forms and to maintain their abundance in openings (Anderson, 1996). Recent burning is critical for maintaining the supply for weavers (Anderson, 1996). As one elder explained, "you find out the places that burned the year before, because that means next year there will be many good materials waiting for you" (Baldy, 2013). Similarly, groves of nut trees were also burned regularly to clear debris and make it easier to collect and separate good acorns from infertile or infested ones (Lake, 2019). Sierra mountain misery (*Chamaebatia foliolosa*) forms dense foliage that impedes acorn harvest (Anderson, 2005), and experimental research has shown the burning can temporarily reduce its abundance (Kauffman and Martin, 1985). Frequent burning to foster open understory forest conditions and grasslands facilitates the gathering of roots and bulbs (Anderson, 2005; Anderson and Lake, 2016). In a study of multiple prescribed burns in Washington State (Orr, 2014), camas (*Camassia quamash*), an important root crop, was more abundant in recently burned areas while strawberry (*Fragaria virginiana*) was more abundant in less recent burns. In response to such complex temporal dynamics, practitioners vary the timing of burns in forests and account for overstory tree cover to promote desired products. Hazel (*Corylus cornuta var. californica*) yields high quality basketry materials after recent burns under closed canopy conditions (Marks-Block

et al., 2019), but hazel nut production requires more exposure to sun and longer time between fires. In addition to the frequency of burning, the seasonality of burning controls the quantity and quality of hazel shoots for weaving (Marks-Block *et al.*, 2021).

2.5. Regulating and supporting services

We combine both regulatory and supporting services since they are difficult to distinguish and they involve ecological processes such pollination, hydrology, and soil development. While anthropologists have long documented how tribes burned to promote species that afforded material and cultural benefits, the effects of cultural burning on ecosystem functions are not as well documented. One reason is that these broad-scale climate factors are likely to overwhelm the effects of small-scale cultural burns. Reflecting this challenge, the review by Anderson (2018) begins by detailing how Indigenous people have used fire to promote individual species, but ends by considering the likely effects of burning on biodiversity, water, and fire regimes at a landscape scale. Some of these effects on ecological processes have also been suggested by field experiments and/or modeling of prescribed burns and wildfires as proxies for cultural burns.

2.5.1. Species biodiversity

Indigenous practitioners emphasize the importance of supporting the wide variety of species (including plants, animals, and fungi, and often described as "relations") that are connected through complex food webs and interconnected life cycles (Anderson and Lake, 2013; Long *et al.*, 2016). Consistent with that perspective, Bowman and Legge (2016) asserted that restoration of degraded ecosystems needs to focus on the influence of fire management on food webs and biodiversity. Such expansive views contrast with management systems that focus heavily on conserving or mitigating impacts to rare and threatened species (Long *et al.*, 2020).

Burning can enhance localized diversity, especially compared to areas that have been encroached by trees due to fire suppression. For example, Livingston *et al.* (2016) reported more understory species in sites within oak woodlands that had been treated with fire than in encroached sites. Studies of fall cultural burns in chaparral and oak woodlands reported greater abundance and diversity of herpetofauna and small mammals (Hankins, 2009; Hankins, 2013). Another study in blue oak (*Quercus douglasii*) woodland found an increase in native plant species cover, but not in an isolated valley oak (*Quercus lobata*) woodland surrounded by agricultural fields (Hankins, 2015).

Cultural burning practices may target relatively common resources to enhance their quality rather than to simply make them more abundant. They may focus on single species that dominate patches, including sedge *(Carex* spp.) beds, oatgrass (*Danthonia* spp.) meadows, and sandbar willow thickets (Fig. 6). Frequent burning may favor certain plant groups that have fire resistant and resilient traits, such as annual forbs, open bunchgrasses, and rhizomatous and resprouting perennials (Kerns and Day, 2018). Maintenance of fire regimes can also help some vegetation communities to resist invasion by non-native species, including Scotch broom (*Cytisus scoparius*), that can displace native plants (Hamman *et al.*, 2011).



Figure 6: A US Forest Service burner and Yurok tribal member (right), uses a propane torch to burn at sandbar willow at Tishunick, a Karuk village near Orleans, CA, with guidance from a Karuk/Yurok cultural adviser, Laverne Glaze. Photo by Frank Lake, USDA Forest Service.

2.5.2. Ecosystem biodiversity

Cultural burning may augment the diversity of communities within a landscape (Anderson, 2018), particularly at a finer grain than occurs under wildfires (Bowman and Legge, 2016). Recent field studies of wildfires are finding evidence that a diversity of fire characteristics, or "pyrodiversity" supports plant and pollinator diversity by sustaining a wide variety of successional communities and associated nesting habitats (Ponisio *et al.*, 2016). However, field studies of wildfires with varying severities may not account for the diversity associated with frequent, predominantly low-severity cultural burning. In the Pacific Northwest, cultural burning over time can enhance landscape diversity by maintaining rare species associated with open habitats such as prairies (Fig. 7), including western lily (*Lilium occidentale*) (Long *et al.*, 2018b), Howell's triteleia (*Triteleia howellii*) (Douglas and Penny, 2004) and certain butterflies

(Hamman *et al.*, 2011). Frequent fires are important for curbing the encroachment of conifers (Engber *et al.*, 2011) and shrubs into open, herbaceous-dominated or savanna communities. For example, one historical account described such conditions within an area in modern day Mendocino County in northern California (which was recently burned in the enormous August Complex of 2020) "Lassik burned a hell-of-a-lot. [Tribal] Informant said country was kept burned off completely—almost a prairie…. Did not harm oak trees. Kept brush from getting too thick or higher…Indians complain about modern [Government fire] restrictions." (Stewart, 2002) (p. 282). In the Yurok country, Thompson (1916) observed that "our Legends tell when they arrived in Klamath River country, that there were thousands of acres of prairie lands and with all the burning they could do the country has been growing up to timber more and more." (p. 31). Skinner (1995) also attributed the loss of forest openings in the Klamath mountains to fire exclusion, while Lake (2007, 2013) described the landscape as the product of tribally-mediated cultural fire regimes. Tribes today have highlighted the impacts of losing these open grasslands and associated biodiversity (Anderson, 2009; Sloan and Hostler, 2014; Karuk Tribe, 2019). Some initiatives, such as the prescribed burning program in Redwood National Park, reflect these concerns, with research suggesting that the savanna areas of the Little Bald Hills are the legacy of fire stewardship by the Tolowa people (Varner *et al.*, 2012).



Figure 7: Prescribed burn conducted by the Confederated Tribes of Grande Ronde at Champoeg Prairie to curb invasive plants and facilitate future harvest of camas, yampa, tarweed, and other culturally important plants. Photo by Andy Neill, Institute for Applied Ecology.

2.5.3. Pollination

Indigenous traditional knowledge and teachings often relate the interconnectedness between host plants, pollinators, and tribal uses (Charnley and Hummel, 2011; Hill *et al.*, 2019; Underwood, 2020). Many pollinators, including hummingbirds, bees, and butterflies, depend upon resources found in recent fires, including plant flowers, exposed mineral soil patches, and dead wood that serves as nesting burrows. Fire diversity in forests managed with intentional fire can buffer pollinator communities against the scarcity of floral resources during droughts (Ponisio *et al.*, 2016). Declines in several rare butterfly species have been linked to the combination of long-

497 term declines in fire, loss of prairie habitat, and reductions in Indigenous stewardship such as
498 tending of camas, which is an important nectar source (Schultz *et al.*, 2011). The California
499 tortoiseshell butterfly (*Nymphalis californica*) and ceanothus silk moth (*Hyalophora euryalus*)
500 are examples of two culturally important pollinator species that may benefit from cultural
501 burning of shrub areas (Anderson and Keeley, 2018). Some of the field studies of prescribed
502 burns in butterfly habitat have revealed challenges in minimizing potential short-term negative
503 impacts of prescribed burns while restoring the benefits of fire-maintained habitats (Trudeau,
504 1996; Schultz *et al.*, 2011). Such findings point to the value of understanding how to use fires of
505 different intensities and scales to promote multiple objectives.

506 *2.5.4. Regulating pests and diseases*

507 Indigenous people have long used fires to reduce the incidence of pests that degrade nut foods,
508 basketry materials, and berry-producing shrubs (Anderson, 2005; Anderson and Rosenthal,
509 2015). This objective is prominent in early discussion of Indigenous burning in the region
510 (Editor, 1916; Harley, 1918). These pests include filbertweevils (*Curculio* spp.) and filbertworms
511 (*Cydia latiferreana*) in acorns, hazel, chinquapin, and other nuts (Anderson, 2005; Bowcutt,
512 2013; Halpern, 2016). Recent research has illustrated how burning can modulate insect levels in
513 contemporary tanoak groves (Halpern, 2016). Indigenous burners have also asserted that burning
514 can reduce mistletoe (*Phoradendron* spp.) infestations through smoke fumigation (Anderson,
515 2018), and some studies have shown such effects on dwarf mistletoe (*Arceuthobium* ssp.) in
516 pines (Zimmerman and Laven, 1987; Harrington and Hawksworth, 1990). Research has also
517 indicated that burning sandbar willow can reduce insects that render stems unsuitable for
518 weaving (Lake, 2007). Although most of these examples refer to harvested species, pest control
519 was related to general forest health. For example, one individual reported in 1933 that the

520 "smoke kept the bugs down and kept the country healthy" (Stewart, 2002) (p. 283). In a more
521 recent example, Earl Scrub Albury (a Karuk elder) explained that when fir trees were weeping
522 pitch, that indicated a need to burn to rejuvenate the area (Lake, 2007). The introduced Sudden
523 Oak Death pathogen (*Phytophthora ramorum*) has impacted fire-prone coastal forests, including
524 many hardwoods of special cultural importance to tribes. Recent research has suggested that
525 intense wildfires can reduce the incidence of that introduced disease, but with costs to healthy
526 forests and other values (He *et al.*, 2021). Researchers have begun to investigate how tribal
527 stewardship practices including prescribed burning and silviculture to promote large hardwoods
528 may reduce spread of the disease and resulting tanoak mortality (Cobb *et al.*, 2017).

529 *2.5.5. Soil health*

530 Similar to other Indigenous cultures around the world, the relationships among fires, soils,
531 plants, and fungi are recognized by tribes of the Pacific West region (Sillitoe, 1998). The
532 combination of burning with other horticultural practices can increase organic matter, promote
533 soil fertility and aeration, facilitate nutrient cycling, maintain mycorrhizae networks, and
534 generate biochar (a product of incomplete combustion of coarse woody material) (Norton, 1979;
535 Anderson and Rowney, 1999; Anderson and Lake, 2013; Anderson and Lake, 2016). Burning
536 can stimulate growth of various species that support nitrogen-fixation including deerbrush
537 (*Ceanothus* spp.) and lupines (*Lupinus* spp.) (Story, 1974; Anderson and Keeley, 2018). Such
538 plants are often important food sources for rare butterflies (Trudeau, 1996; Goergen and
539 Chambers, 2009; Schultz *et al.*, 2011). Biochar can enhance soil quality in ways that promote
540 plant growth (Lehmann *et al.*, 2006) and consumption of biochar by animals can improve their
541 health (Schmidt *et al.*, 2019). Authors Ron Goode and Frank Lake note that Indigenous

practitioners incorporate charred material into the soil to enhance plant growth and have long observed that animals also use it to rid themselves of parasites.

2.5.6. Enhanced hydrology

Cultural burning has been practiced to reduce vegetation density and increase water availability. Tribes have recognized that burning can increase water levels in springs and meadows that favor many culturally important plants (Anderson and Rosenthal, 2015). Historical research documented an example of this intention on the Trinity River, "He [Indian informant circa 1933] told me that they [Indians] were sure that the burning made the springs run better" (Stewart, 2002) (p. 283). Such hydrologic effects of prescribed burning received attention by pioneering fire researcher Harold Biswell (1999). Research has documented increased water flows in a forested montane watershed that has been managed with extensive use of wildland fire (Boisramé *et al.*, 2019). Furthermore, Indigenous burners indicated that smoke would benefit salmon and other fish by reducing summer water temperatures (Karuk Tribe, 2019). A recent study reported that wildfire smoke had such beneficial effects in the Klamath River valley (David *et al.*, 2018).

2.5.7. Wildfire regulation

A recent global review found that intentional burning to protect resources by preventing high-intensity, destructive fires was common in both ethnographic studies (49%) and all studies (36%) in their analysis (Trauernicht et al., 2015). Within the past century in the Pacific West region, tribal members reported setting fires to inhibit spread of wildfires. For example, Johnny Bennett (Karuk, Forks of Salmon, 1977) said "when the lightning hit they [old Indians] never put it out, push them [fires] back, [Indians] make a fire line, let them go back up the mountain. Take sticks out there, burn up against it" (Karuk Tribe and Cultural Solutions, 1999b) (p. 25). Indigenous

565 burning was conducted to maintain open conditions around villages, harvesting sites, and
566 processing sites, and other favored areas, and to facilitate travel along ridges, riparian areas, and
567 trails between those locations (Boyd, 1999; Lake *et al.*, 2018; Lake and Christianson, 2019) (Fig.
568 2). In the western Sierra Nevada foothills, such dispersed but spatially extensive burning by
569 different tribal communities cultivated a mosaic of fuel conditions that would curtail large
570 wildfires (Anderson and Rosenthal, 2015; Spoon *et al.*, 2015; Anderson and Keeley, 2018),
571 Furthermore, intensive fuelwood gathering, plant pruning and cleaning of areas used for
572 gathering acorn and other resources would have reduced fuel amounts and continuity.

573 Researchers have used modeling and understanding of these spatial patterns to demonstrate that
574 Indigenous burning was a major influence on fire regimes in areas such as the southern Sierra
575 Nevada (Klimaszewski-Patterson *et al.*, 2018). Fire ecology modeling has suggested that
576 reducing fuels within relatively small portions of a landscape, such as 10-20% of a landscape per
577 decade, can greatly moderate extreme fire outcomes in parts of our region (Finney *et al.*, 2007;
578 Collins *et al.*, 2013). Finney *et al.* (2007) suggested that those effects would be achieved with
579 some areas repeatedly treated and others left untreated, that patch size was generally not a key
580 driver of outcomes, and that strategic placement would result in greater benefits. Analysis of
581 historical photography had indicated that high heterogeneity, including areas of very open forests
582 and low fuel continuity, promoted landscape resilience to severe fire (Lydersen and Collins,
583 2018). These findings suggest how widespread application of cultural burning would be
584 consistent with wildfire mitigation efforts.

585 Many tribal resources including homes and infrastructure; ancestral villages, camps, petroglyphs,
586 and sacred sites; and populations of plants used for a range of traditional purposes can be
587 damaged by high-severity fire through both direct consumption and impacts from high heating

588 (Ryan *et al.*, 2012). However, high-severity burn patches were also essential to promoting tribal
589 values, as they often become dominated by shrubs such as hazel, manzanita (*Arctostaphylos*
590 spp.), deerbrush (*Ceanothus* spp.), and gooseberry (*Ribes* spp.) that provide food for wildlife and
591 Indigenous people (Anderson, 2018).

592 Tribal practitioners emphasize that their treatments are not intended to stop fires with stark fuel
593 breaks, but rather to facilitate control of fires and to moderate their intensity and severity.
594 Treatments along ridgelines and in wildlife-urban interface areas have been designed to temper
595 fires while supporting other values, including production of acorns (Harling and Tripp, 2014).
596 This approach is relevant to the wildland fire management strategies of developing Potentially
597 Operational Delineation Units (PODs), which are bounded by linear control features, such as
598 trails (Fig. 8), within which fires can be managed (Wei *et al.*, 2019).



Figure 8: This large tanoak tree featured an archaeological site along a historical trail being used as a containment line during the Somes Fire on the Six Rivers National Forest, near Somes Bar, California, USA. Photo courtesy of USDA Forest Service.

3. Implications for management and research

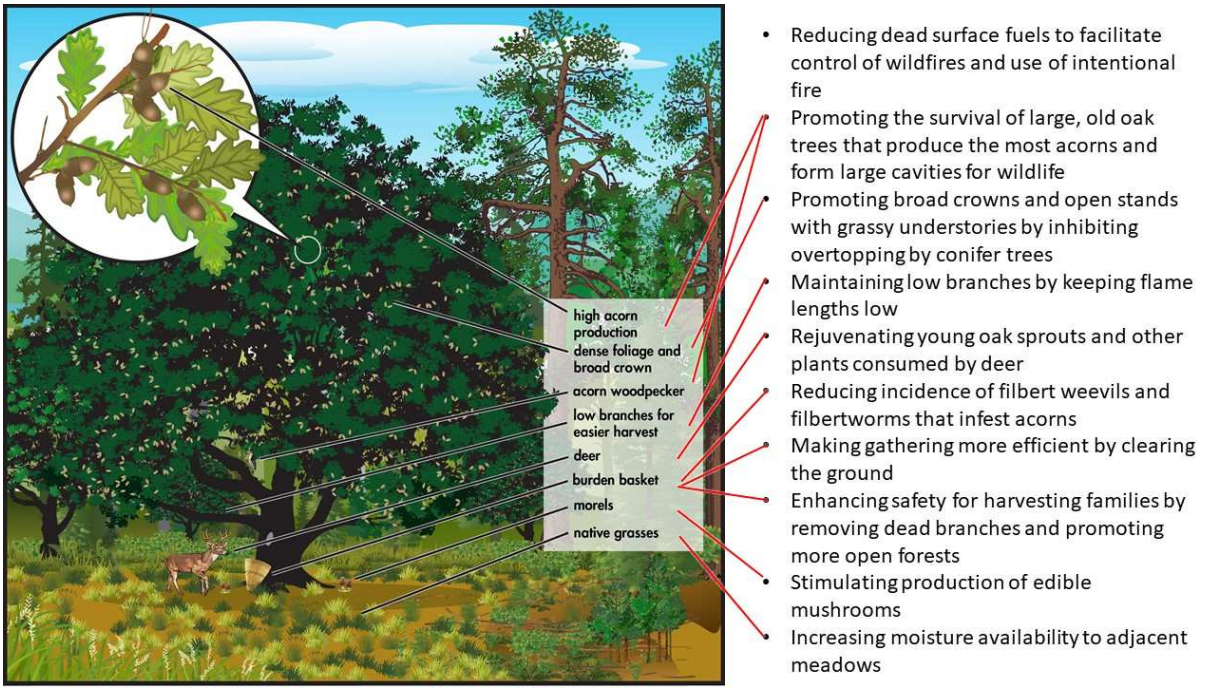
3.1. Recognizing the many ecological and social benefits of cultural burning

Indigenous communities have repeatedly championed the importance of burning as a means of restoring ecosystems and revitalizing their cultures (Anderson, 2009; Sloan and Hostler, 2014; Goode *et al.*, 2018; Karuk Tribe, 2019; Clark *et al.*, 2021). A goal of restoring reference fire regimes, including Indigenous influence, is guiding prescribed burning programs (Thornburgh *et al.*, 2000) and remains a topic of great importance for research (Varner and Jules, 2017). The

610 ecosystem services framework may help to highlight the many positive aspects of fire in ways
611 that can advance burgeoning forest restoration initiatives. Practitioners contrast their holistic
612 approach with strategies that focus on reducing fuels and wildfire impacts. Cultural burning is
613 intended to reduce fuels and rejuvenate and reconfigure shrubs and other understory plants, but
614 not to eliminate them. Indigenous practitioners acknowledge both the benefits and risks
615 associated with vegetation. Despite the salience of cultural burning to tribal communities and to
616 broader restoration outcomes, recent strategy documents paid little attention to the subject. For
617 example, the National Cohesive Wildland Fire Management Strategy does not specifically
618 address tribal interests in using fire (Wildland Fire Leadership Council, 2014). Related academic
619 works proposing strategies to promote more resilient socioecological systems (Abrams *et al.*,
620 2015; Schoennagel *et al.*, 2017) similarly do not discuss Indigenous fire stewardship. These
621 omissions may in part reflect an ingrained emphasis on combating the negative, destructive
622 aspects of wildfires, in contrast to more holistic tribal frameworks.

623 *3.1.1. Holistic understanding of overlapping benefits for social-ecological well-being*
624 Indigenous burners use fire with multiple, overlapping benefits in mind (Anderson and Keeley,
625 2018). For example, burning hazel underneath a canopy of hardwood trees may reduce nuisance
626 diseases and pests, generate stems used for basketry or tools, stimulate flowering for pollinators,
627 enhance nut quality and abundance, enhance browse and forage for game animals, increase
628 hunting efficiency, and reduce risks of severe fire (Marks-Block *et al.*, 2019). Tribal practitioners
629 tune the tending and burning regimes to promote a desired mix of benefits. For example, the
630 Karuk Tribe has prioritized treatments to reduce fuels and threats of wildfire in community areas,
631 while promoting hazel sticks and retaining mature yew and dogwood (Diver, 2016; Karuk Tribe,
632 2019). Within California black oak groves, cultural burning similarly has a multiplicity of effects

633 that promote conditions that support tribal harvest and many other ecosystem services (Fig. 9)
634 (Long *et al.*, 2016). Species like Pacific fisher (*Pekania pennanti*), California condor
635 (*Gymnogyps californianus*), and pileated woodpecker (*Dryocopus pileatus*) are valued in terms
636 of material uses of their fur or feathers, their supporting roles (e.g., predation, cavity excavation),
637 and their roles in stories and ceremonies (Jordan, 2015; Long and Lake, 2018; Karuk Tribe,
638 2019). These multiple benefits cross ecosystem service categories and make it more challenging
639 to evaluate the cumulative benefits of treatments because they involve many effects at different
640 scales. Furthermore, categorizing services may obscure the conjoined nature of socio-ecological
641 values. Previous scholars have noted that culture, ecology and place are inextricably woven
642 together (Berkes, 2012), which complicates efforts to understand changes in community systems
643 (Tremblay *et al.*, 2020).



644

645 Figure 9: Relationships between various objectives of cultural burning and conditions desired by tribes
646 for black oak ecosystems.

In the Klamath region, community-based research has revealed how suppression of cultural burning and other Indigenous stewardship practices led to declines in diet and social well-being (Norgaard, 2019). Understanding how to use fire to restore culturally important resources helps young people to understand both the ecology of their homelands, and their own place within their communities (Norgaard *et al.*, 2017; Norgaard, 2019). Such approaches could shift Indigenous practitioners from being considered "outlaws" or malicious arsonists and turn them into "valued food service employees" (Sowerwine *et al.*, 2019). Such reframing moves the discussion about the need for cultural burning beyond narrow evaluations of ecological conditions and into a broader examination of socio-ecological well-being.

Indigenous peoples also burn to stimulate growth of various plants with medicinal values, although research on this topic is likely to be limited by concerns over protecting sensitive information regarding their use and location. An example of a medicinal plant appearing following a recent early spring cultural burn is Pacific sanicle (*Sanicula crassicaulis*) (Fig. 10). Researchers have reported on its historical use to treat snakebite (Barrett and Gifford, 1933), its use as food by Indigenous people (Anderson and Keeley, 2018), and its value for bees (Wray and Elle, 2017). The plant's ability to store energy in its taproot, intolerance of shade, and association with oak savannas are all traits that explain why it would respond favorably to cultural burning. Indeed, conservationists have identified a decline in Indigenous stewardship as one of the threats to a rare relative in Canada, snakeroot sanicle (*Sanicula arctopoides*) (Zevit and Fairbarns, 2010). Therefore, this plant represents just one of many opportunities to better appreciate the multifaceted effects of cultural burning.



Figure 10: Pacific sanicle (*Sanicula crassicaulis*) emerging between burned swaths in a March 2021 cultural burn near Mariposa, California, USA. Photo by Ron Goode.

3.1.2. Promoting diverse fire mosaics

Indigenous practitioners seek to cultivate a diversity of conditions within a patchy arrangement to ensure that surrounding lands maintain sustainable supplies for current and future needs. These arrangements consider ecological variation across large landscapes; for example, in the Klamath region, tribes cultivated huckleberries, bilberries, tanoaks, and black oaks in lower and mid-elevation forests, while relying on blueberries and acorns in more intermixed shrub-dominated patches following higher severity fire at higher elevations (Pullen, 1996). When staggered across watersheds, elevation ranges, and time, treatments promote food production,

679 facilitate harvest, and enhance food security in the face of drought, wildfire, and other
680 disturbances.

681 A strategy that emphasizes cultural burning may contrast with ones that favor treating large areas
682 in ambitious individual projects that require lengthy environmental reviews (or wildfires
683 managed for resource objectives that are not governed by such reviews). It reflects the "small is
684 beautiful" concept, which holds that small groups working locally can achieve better
685 conservation outcomes than large corporate entities (Schumacher, 1985). This concept has been
686 widely incorporated into natural resources management (Lovell *et al.*, 2002). In addition to
687 relying on smaller treatments, a strategy geared toward cultural burning would also require
688 retreating sites more frequently than national forest managers in the Pacific West region have
689 typically achieved (Kolden, 2019; North *et al.*, 2021). In California, despite calls to rely on
690 greater use of fire, there are few examples of restored fire regimes in frequent fire vegetation
691 types outside of a few areas that have experienced managed wildfires for resource objectives
692 (North *et al.*, 2021). However, current tribal plans such as one advanced by the Western Klamath
693 Restoration Partnership emphasize the role of cultural burning, along with greater use of
694 managed wildfires, in protecting communities from the detrimental effects of uncharacteristically
695 large and severe wildfires (Harling and Tripp, 2014). The intent is not to exclude fire from the
696 landscape but to moderate wildfires so they will not damage vast areas and harm communities.

697 *3.2. Addressing challenges between Indigenous objectives and government agency objectives*
698 There appears to be strong alignment between the benefits of cultural burning and agency
699 restoration strategies, but there are some challenges in implementing both and in making them
700 mutually supportive.

3.2.1. Addressing policy constraints on cultural burning

Constraints on prescribed burning, such as air quality regulations and liability concerns, also have constrained cultural burning by Indigenous practitioners (Clark *et al.*, 2021). Other constraints on restoration treatments include concerns for rare wildlife, including spotted owls (*Strix occidentalis*) and Pacific fisher, which have been translated into requirements to maintain higher levels of forest canopy cover than were historically widespread (Lydersen *et al.*, 2019) and to avoid burning during especially sensitive denning, nesting, and breeding periods in the spring (Thompson and Purcell, 2016). Traditional burning was generally a fall or late winter activity, and tribes have sometimes expressed concerns that burning outside of those traditional seasons could be harmful to wildlife (Halpern, 2016). However, contemporary practitioners may desire flexibility to use fire to advance restoration objectives through an adaptive process.

3.2.2. Recognizing that thinning complements, but does not substitute for, cultural burning

Forest management intended to support tribal values has in many cases relied more on thinning than burning (LeCompte-Mastenbrook, 2016). Researchers have found that both tree cutting and fire will likely benefit both biodiversity conservation and fire management in current mixed conifer forests (Abella and Springer, 2015). However, field studies have found larger effects on plant communities from moderate- to high-severity fires than from low-severity prescribed burning (Kerns and Day, 2018), or from canopy thinning treatments followed by prescribed burns. Such responses are especially likely in forests that are highly departed from historical fire regimes—they may require greater and different forms of disturbance to reset their trajectories. However, even where thinning is effective in increasing light, nutrients, and water to understory plants, it may not accomplish other objectives such as pest reduction and desirable growth forms. Moreover, practitioners have reported contexts in which some traditional plants, such as

huckleberry and western redcedar (*Thuja plicata*), are favored by fire but not by mechanical thinning (Wynecoop *et al.*, 2019).

3.2.3. Avoiding negative effects

Prescribed burning has potential for negative effects, and some of those risks could also apply to cultural burning. However, the likelihood of negative outcomes may be greatly reduced due to practices adhered to by cultural practitioners. Any kind of wildland fire has potential to result in other unintended and undesirable effects including escape, consumption of snag habitats, undesired mortality of large trees, and nuisance levels of smoke (Ryan *et al.*, 2013). In general, however, cultural burns may have lower potential for such effects than other kinds of fire for several reasons. First, individual cultural burns are often intended to result in small, patchy, low-moderate severity burns. Second, cultural burning is often practiced as an intergenerational endeavor with both young people and elders. Burning and tending are often planned to enhance safety for family gatherings. When burners purposefully limit their operations to relatively traditional technologies, they have incentives to avoid conducting risky burns. Cultural practitioners tend their burns closely, with attention to effects on understory plants, wildlife, community health, and protecting legacy resources. The small, patchy scale of cultural burning is likely to inhibit the delivery of large quantities of smoke to large populations, especially as compared to wildfires (Long *et al.*, 2018c). Furthermore, the preparation that precedes cultural burns reduces the likelihood that a fire escape or an infestation of invasive plants will occur.

Despite such precautions, reintroduction of indigenous burning may be complicated in areas that have undergone transformations resulting from Euro-American colonization, including invasion by non-native species and increases in accidental ignitions. In such systems, such as chaparral in southern California, some managers and ecologists are concerned that burning too frequently

could negatively impact native vegetation (Keeley and McGinnis, 2007). In an extreme example, a study in Washington state found that five decades of annual burning resulting from artillery fire transformed the dominant vegetation in a prairie from native fescue to non-native grasses; in contrast, prescribed burning on a 3-5 year rotation for two decades reduced cover of most non-native species while inhibiting conifer encroachment on oaks (Tveten and Fonda, 1999). Potential for increases in non-native species following prescribed burning has been reported from a variety of vegetation types in the region, including chaparral and grasslands (Safford and Harrison, 2008), ponderosa pine forest (Keeley and McGinnis, 2007; Kerns and Day, 2018), and riparian areas (Hankins, 2013), although results often vary greatly. The potential for undesirable increases in non-native species is often associated with the existing level of non-natives within or adjacent to the treatment areas. Research in Arizona forests showed that burning in an area with high levels of cheatgrass promoted the invasive, while burning in a native-dominated site did not (McGlone *et al.*, 2012). Hankins, an Indigenous practitioner and scholar, observed a similar dynamic when comparing outcomes following burning in two oak-grasslands sites in the north-central Sacramento Valley (Hankins, 2015). He speculated that reintroducing cultural burning over time could help to gradually restore the native composition.

3.2.4. Explaining the relevance of services

Different categories of services may be associated with different challenges and opportunities for advancing cultural burning. Many of the benefits of cultural burning may be devalued within market-based frameworks; however, the value of some provisioning services can often be more easily quantified in other economic frameworks. For example, researchers have estimated the volume of materials needed to produce products such as baskets that command high prices (Anderson, 2018; Marks-Block *et al.*, 2021). Furthermore, provisioning services may be afforded

special leverage where the federal government recognizes off-reservation tribal rights to gather, fish, and hunt, especially in Washington and Oregon (Bernholz and Weiner, 2008). Because the ability to exercise such rights depends on the availability of resources of suitable quality and quantity, those legal levers could support cultural burning. On the other hand, the effects of burning on provisioning services may be difficult to measure easily since resource quality of root crops, acorns, and shoots may be best evaluated upon harvest by tribal gatherers (Hummel *et al.*, 2015).

Regulating and supporting systems including wildfire protection, water availability, pollination, food webs, biodiversity, carbon sequestration, and soil tilth, have all been a focus of management and research (Nikolakis and Roberts, 2020). However, quantifying such services can be challenging because of the broad spatial and temporal scales needed to understand them. Burning affects a tremendously wide variety of species and their interactions, including not only biomass removal and more complex effects on air, soil, water, food webs, and parasitic and symbiotic associations. This complexity poses substantial challenges in selecting metrics and scales for evaluation. Cultural services are even more challenging to integrate into institutional processes since they tend to be non-quantified, non-fungible, less openly discussed, and yet more contested. For example, court decisions have often denied protection to tribal sacred sites on public lands (Carpenter, 2004). A resistance to explicit co-management lands under current legal interpretations may impede the ability of Indigenous groups to steward specific places on public lands. The concepts of cultural services and services for ecosystems elucidate why Indigenous people want to directly apply fire themselves.

An ecosystem services framework can help to integrate Indigenous perspectives more fully within planning frameworks (Armatas *et al.*, 2018). Such approaches depart from past efforts

that often focused on tribal concerns for archaeological sites (Long *et al.*, 2020). Recognizing the interconnections between ecological and social services can help to identify opportunities to unravel persistent effects of colonialism (Long and Lake, 2018).

3.3. Addressing limitations of paleoecological research

As noted in the introduction, ecologists have explained that methods used to reconstruct environmental histories, including sampling of charcoal deposits in lakes and fire scars on trees, may have poor ability to detect Indigenous influences (Klimaszewski-Patterson *et al.*, 2018; Abrams and Nowacki, 2020). This methodological challenge is acute in areas where fires would be naturally frequent in the absence of human influence (Roos *et al.*, 2019). Tree rings can sometimes help to distinguish wildfires from Indigenous burning based upon time of year, but even they are likely to underrepresent light Indigenous burning (Whitlock *et al.*, 2004). However, analysis of tree-ring records can also be modified to be more sensitive to patchy burning (Roos *et al.*, 2019). Roos *et al.* (2018) explain that Indigenous burning may have either enhanced or buffered climate impacts on fire regimes at different scales, and it is difficult to separate those influences without considering multiple types of evidence. Responding to the exclusion of Indigenous values and knowledge in this field, researchers have called for more transdisciplinary efforts including collaborations with Indigenous experts to interpret paleoecological evidence and to inform contemporary forest management (Lake, 2013; Lightfoot *et al.*, 2013; Leonard *et al.*, 2020).

3.4. Addressing shortcomings of controlled experiments

Many experimental research studies on cultural burning have been set up as relatively short-term investigations, often as part of graduate studies, with limited resources to obtain environmental clearances needed for treatments. While many projects have been conducted in partnership with

816 tribal practitioners (Shebitz, 2006; Lake, 2007; Shebitz *et al.*, 2008; Hankins, 2013; Halpern,
817 2016), they may not have recreated traditional burning regimes due to such external constraints.
818 For example, Halpern (2016) noted that practitioners wanted to study fall burning, but she had to
819 examine spring burns to comply with federal and state prescribed burning regulations. Similarly,
820 environmental review requirements initially constrained Lake (2007) to study relatively small
821 burns using propane torches to evaluate effects of burning on willow shoots (Fig. 6). He later
822 was able to study a larger prescribed burn, which he found to be more effective in controlling
823 insect pests. Meanwhile, a tribal-Forest Service collaborative research study (Wynecoop *et al.*,
824 2019) considered how burning treatments could benefit culturally important plants by comparing
825 areas burned in a wildfire, treated with a combination of mechanical thinning and prescribed fire,
826 or not having been treated within 10 years. While these studies advance our knowledge, they
827 reveal a lack of studies that explicitly incorporate cultural burning practices.

828 The complexity associated with scale and potential shadow effects of treatment are some of the
829 challenges in delineating "treatment" and "control" units. Studies of single burns are not likely to
830 be representative of cultural burning regimes for several reasons. First, the strong influence of
831 precipitation on plant growth makes the effects of burning more difficult to resolve (Hankins,
832 2015). Second, single burns in long-unburned areas may be more intense than would be typical
833 for cultural burns. For example, a recent study of ceramic sherds in an ancient village site in
834 northern New Mexico found that a that a large prescribed burn during mild October weather, but
835 following 119 years of fire exclusion, burned more intensively than any fires in the previous 900
836 years (Roos *et al.*, 2020). Third, fire effects are likely to change as cultural burning is
837 reintroduced, because consumption rates, fuels, and vegetation composition change with

repeated burning (Levine *et al.*, 2020). Establishment of long-term studies could address many of these shortcomings.

3.5. Establishing long-term collaborative studies

Indigenous peoples are rightfully concerned about potential for traditional ecological knowledge to be extracted and used by non-Indigenous contractors or scientists in ways that do not directly advance tribal stewardship and sovereignty (Klenk *et al.*, 2017). Some collaboratives, such as the Western Klamath Restoration Partnership, have enjoyed success in fostering tribal engagement (Kelly *et al.*, 2019). Tribal influence in other collaboratives, including the Dinkey Landscape Collaborative, is less apparent (Butler *et al.*, 2015). Establishing longer-term experimental studies with Indigenous communities would help to better understand effects of cultural burning and other traditional stewardship practices. For example, a research study on former university lands in Missouri revealed how differences in forest composition and structure can develop under contrasting fire regimes, including frequent fires, over 60 years (Knapp *et al.*, 2015). Tribes and land management agencies could similarly explore opportunities to establish stewardship areas that would support long-term investigations of cultural burning. Many research natural areas (and some wilderness areas) in California have experienced a shortage of fires, yet they also discourage "manipulative" vegetation treatments (Coppoletta *et al.*, 2019). Nevertheless, a recent tribal-agency collaboration in the Indiana Summit Research Natural Area demonstrated how traditional practices and return of fire could safeguard cultural resources and facilitate tribal harvesting of pandora moth larvae (Slaton *et al.*, 2019).

4. Conclusions

Rooted in historical practices and traditional values, tribal cultural burning continues to adapt to meet contemporary challenges. Indigenous people are asserting their rights and responsibilities to

burn to maintain their well-being. The overlap between cultural burning and contemporary agency forest management can encourage mutually beneficial outcomes rather than perpetuating the harmful legacy of fire exclusion. The framework of ecosystem services can relate the goals of Indigenous practitioners to government management systems, while expanding awareness of the many diverse benefits of cultural burning beyond its potential to regulate wildfires. The many benefits of cultural burning are the results of a complex web of material/immaterial and direct/indirect effects. This understanding illustrates why the many benefits are difficult to quantify or evaluate with market-based systems. Nevertheless, scientific approaches can be adapted to better detect and measure many of the physical effects, and collaborative efforts can better reveal the benefits of restoring cultural burning both to tribal communities and to wider society. Distinctive ecological communities that have evolved with Indigenous use of frequent fire in the Pacific West region are especially important to study at long-term and broader spatial scales. Expanding long-term tribal collaboratives, including designating Indigenous stewardship areas with frequent burning, would advance our understanding of restoration in forested landscapes.

Acknowledgments

The authors acknowledge the many knowledge keepers whose ideas and support of tribal traditional practices contributed to this research. Support for the preparation of this article was provided by the USDA Forest Service Pacific Southwest Research Station. The findings and conclusions in this manuscript are those of the authors and should not be construed to represent any official determination or policy by the U.S. Government, U.S. Department of Agriculture, or the North Fork Mono Tribe.

Credits: J.L., F.L.: conceptualization, writing, figures, reviewing, and editing. R.G.: conceptualization, reviewing, figures, and editing.

References

Abella, S.R., Springer, J.D., 2015. Effects of tree cutting and fire on understory vegetation in mixed conifer forests. For. Ecol. Manage. 335, 281-299.

Abrams, J.B., Knapp, M., Paveglio, T.B., Ellison, A., Moseley, C., Nielsen-Pincus, M., Carroll, M.S., 2015. Re-envisioning community-wildfire relations in the U.S. West as adaptive governance. Ecol. Soc. 20.

Abrams, M.D., Nowacki, G.J., 2020. Native American imprint in palaeoecology. Nature Sustainability 3, 896-897.

Aldern, J.D., Goode, R.W., 2014. The stories hold water: learning and burning in North Fork Mono homelands. Decolonization: Indigeneity, Education & Society 3.

Allen, C.D., 2002. Lots of lightning and plenty of people: an ecological history of fire in the upland Southwest. In: Vale, T.R. (Ed.), Fire, Native peoples, and the natural landscape. Island Press, Washington DC, pp. 143-193.

Anderson, K., 2009. The Ozette prairies of Olympic National Park: their former Indigenous uses and management. In. USDA Natural Resources Conservation Service, Davis, CA.

Anderson, M.K., 1996. The ethnobotany of deergrass, *Muhlenbergia rigens* (Poaceae): Its uses and fire management by California Indian tribes. Econ. Bot. 50, 409-422.

Anderson, M.K., 1997. From tillage to table: the indigenous cultivation of geophytes for food in California J. Ethnobiol. 17, 149-169.

Anderson, M.K., 1999. The fire, pruning , and coppice management of temperate ecosystems for basketry material by California Indian tribes. Hum. Ecol. 27, 79-113.

906 Anderson, M.K., 2005. Tending the wild: Native American knowledge and the management of
907 California's natural resources. University of California Press, Berkeley, CA, USA.
908 Anderson, M.K., 2018. The use of fire by Native Americans in California. In: van Wagtendonk,
909 J.W., Sugihara, N.G., Stephens, S.L., Thode, A.E., Shaffer, K.E., Fites-Kaufman, J. (Eds.), Fire
910 in California's ecosystems. University of California Press, Berkeley, pp. 381-398.
911 Anderson, M.K., Keeley, J.E., 2018. Native peoples' relationship to the California chaparral. In,
912 Valuing Chaparral. Springer, pp. 79-121.
913 Anderson, M.K., Lake, F.K., 2013. California Indian ethnomycology and associated forest
914 management. J. Ethnobiol. 33, 33-85.
915 Anderson, M.K., Lake, F.K., 2016. Beauty, bounty, and biodiversity: the story of California
916 Indian's relationship with edible native geophytes. Fremontia. 44 (3): 44-51 44, 44-51.
917 Anderson, M.K., Rosenthal, J., 2015. An ethnobiological approach to reconstructing Indigenous
918 fire regimes in the foothill chaparral of the western Sierra Nevada. J. Ethnobiol. 35, 4-36, 33.
919 Anderson, M.K., Rowney, D.L., 1999. The edible plant *Dichelostemma capitatum*: its vegetative
920 reproduction response to different indigenous harvesting regimes in California. Restor. Ecol. 7,
921 231-240.
922 Armatas, C.A., Campbell, R.M., Watson, A.E., Borrie, W.T., Christensen, N., Venn, T.J., 2018.
923 An integrated approach to valuation and tradeoff analysis of ecosystem services for national
924 forest decision-making. Ecosystem services 33, 1-18.
925 Armstrong, C.G., Anderson, E.N., 2020. Ecologies of the Heart. In, Archaeologies of the heart.
926 Springer, pp. 39-58.
927 Baldy, C.R., 2013. Why we gather: traditional gathering in native Northwest California and the
928 future of bio-cultural sovereignty. Ecological Processes 2, 17.

929 Barrett, S., Gifford, E., 1933. Miwok material culture. Bulletin of the Public Museum of the City
930 of Milwaukee 2, 117-376.
931 Berkes, F., 2012. Sacred ecology, New York, New York, USA.
932 Bernholz, C.D., Weiner, R.J., 2008. The Palmer and Stevens "Usual and Accustomed Places"
933 treaties in the opinions of the courts. Government Information Quarterly 25, 778-795.
934 Binder, S., Haight, R.G., Polasky, S., Warziniack, T., Mockrin, M.H., Deal, R.L., Arthaud, G.,
935 2017. Assessment and valuation of forest ecosystem services: state of the science review. In. US
936 Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp.
937 1-47.
938 Biswell, H., 1999. Prescribed burning in California wildlands vegetation management.
939 University of California Press, Berkeley, CA.
940 Boisramé, G.F.S., Thompson, S.E., Tague, C.N., Stephens, S.L., 2019. Restoring a natural fire
941 regime alters the water balance of a Sierra Nevada catchment. Water Resources Research 55,
942 5751-5769.
943 Bowcutt, F., 2013. Tanoak landscapes: Tending a Native American nut tree. Madrono 60, 64-86.
944 Bowman, D.M., Legge, S., 2016. Pyrodiversity—why managing fire in food webs is relevant to
945 restoration ecology. Restor. Ecol. 24, 848-853.
946 Boyd, R., 1999. Indians, fire and the land. Oregon State University Press, Corvallis.
947 Butler, W.H., Monroe, A., McCaffrey, S., 2015. Collaborative implementation for ecological
948 restoration on US public lands: implications for legal context, accountability, and adaptive
949 management. Environ. Manage. 55, 564-577.
950 Carpenter, K.A., 2004. A property rights approach to sacred sites cases: asserting a place for
951 Indians as nonowners. UCLA Law Review 52, 1061.

952 Carter, V.A., Brunelle, A., Power, M.J., DeRose, R.J., Bekker, M.F., Hart, I., Brewer, S.,
953 Spangler, J., Robinson, E., Abbott, M., Maezumi, S.Y., Codding, B.F., 2021. Legacies of
954 Indigenous land use shaped past wildfire regimes in the Basin-Plateau Region, USA. Commun
955 Earth Environ 2, 72.
956 Charnley, S., Hummel, S., 2011. People, plants, and pollinators: the conservation of beargrass
957 ecosystem diversity in the Western United States. The importance of biological interactions in
958 the study of biodiversity.
959 Clark, S.A., Miller, A., Hankins, D.L., 2021. Good fire: current barriers to the expansion of
960 cultural burning and prescribed fire in California and recommended solutions. In. Karuk Tribe,
961 Happy Camp, CA, p. 45 p.
962 Cobb, R.C., Hartsough, P., Ross, N., Klein, J., LaFever, D.H., Frankel, S.J., Rizzo, D.M., 2017.
963 Resiliency or restoration: management of sudden oak death before and after outbreak. Forest
964 Phytophthoras 7, 1-14.
965 Collins, B.M., Kramer, H.A., Menning, K., Dillingham, C., Saah, D., Stine, P.A., Stephens, S.L.,
966 2013. Modeling hazardous fire potential within a completed fuel treatment network in the
967 northern Sierra Nevada. For. Ecol. Manage. 310, 156-166.
968 Coppoletta, M., Safford, H.D., Estes, B.L., Meyer, M.D., Gross, S.E., Merriam, K.E., Butz, R.J.,
969 Molinari, N.A., 2019. Fire regime alteration in natural areas underscores the need to restore a key
970 ecological process. Nat. Areas J. 39, 250-263.
971 Crouse, C.W., 1902. Report of Fort Apache in the annual report of the Commissioner of Indian
972 Affairs to the Secretary of the Interior for the year 1902. In. U.S. Government Printing Office,
973 Washington, D.C., USA, pp. 147–151.

David, A.T., Asarian, J.E., Lake, F.K., 2018. Wildfire smoke cools summer river and stream water temperatures. Water Resources Research 54, 7273-7290.

Deur, D., 2009. “A caretaker responsibility”: Revisiting Klamath and Modoc traditions of plant community management. J. Ethnobiol. 29, 296-322.

Deur, D., Turner, N.J., 2005. Keeping it living: traditions of plant use and cultivation on the Northwest Coast of North America. University of Washington Press.

Diver, S., 2016. Co-management as a catalyst: pathways to post-colonial forestry in the Klamath Basin, California. Hum. Ecol. 44, 533-546.

Douglas, G.W., Penny, J.L., 2004. Conservation evaluation of Howell's Triteleia, Triteleia howellii, an endangered lily in Canada. The Canadian Field-Naturalist 118, 174-178.

Editor, 1916. An Indian’s view of burning, and a reply. California Fish and Game Journal 2, 194–196.

Engber, E.A., Varner, J.M., Arguello, L.A., Sugihara, N.G., 2011. The effects of conifer encroachment and overstory structure on fuels and fire in an oak woodland landscape. Fire Ecol. 7, 32-50.

Eriksen, C., Hankins, D.L., 2014. The retention, revival, and subjugation of indigenous fire knowledge through agency fire fighting in eastern Australia and California. Soc. Nat. Resour. 27, 1288-1303.

Finney, M.A., Seli, R.C., McHugh, C.W., Ager, A.A., Bahro, B., Agee, J.K., 2007. Simulation of long-term landscape-level fuel treatment effects on large wildfires. Int. J. Wildland Fire 16, 712-727.

Fish, R., Church, A., Winter, M., 2016. Conceptualising cultural ecosystem services: A novel framework for research and critical engagement. Ecosystem Services 21, 208-217.

997 Forest Management Task Force, 2021. California's wildfire and forest resilience action plan. In.
998 California Department of Water Resources, Sacramento, CA, p. 45 p.
999 Fry, D.L., Stephens, S.L., 2006. Influence of humans and climate on the fire history of a
1000 ponderosa pine-mixed conifer forest in the southeastern Klamath Mountains, California. For.
1001 Ecol. Manage. 223, 428-438.
1002 Goergen, E.M., Chambers, J.C., 2009. Influence of a native legume on soil N and plant response
1003 following prescribed fire in sagebrush steppe. Int. J. Wildland Fire 18, 665-675.
1004 Goode, R.W., Gaughen, S., Fierro, M., Hankins, D.L., Johnson-Reyes, K., Middleton, B.R., Red
1005 Owl, T., Yonemura, R., Lucero, S., Ganion, J., 2018. Summary Report from Tribal and
1006 Indigenous Communities. In, Fourth Climate Change Assessment. California Governer's Office
1007 of Planning and Research, California Natural Resources Agency, and the California Energy
1008 Commission, Sacramento, CA, p. 69 p.
1009 Greeley, W.B., 2000. "Piute forestry" or the fallacy of light burning. Fire Management Today 60,
1010 21–26.
1011 Halpern, A.A., 2016. Prescribed fire and tanoak (*Notholithocarpus densifolius*) associated
1012 cultural plant resources of the Karuk and Yurok people of California. In, Integrative Biology.
1013 University of California at Berkeley, Berkeley, California, USA, p. 90.
1014 Hamman, S.T., Dunwiddie, P.W., Nuckols, J.L., McKinley, M., 2011. Fire as a restoration tool
1015 in Pacific Northwest prairies and oak woodlands: challenges, successes, and future directions.
1016 Northwest Sci. 85, 317-328.
1017 Hankins, D., 2009. The effects of indigenous prescribed fire on herpetofauna and small
1018 mammals in two Central Valley California riparian ecosystems. The California Geographer 49,
1019 31-50.

1020 Hankins, D.L., 2013. The effects of indigenous prescribed fire on riparian vegetation in central
1021 California. Ecological Processes 2, 1-9.
1022 Hankins, D.L., 2015. Restoring indigenous prescribed fires to California oak woodlands. Gen.
1023 Tech. Rep. PSW-GTR-251. Berkeley, CA: US Department of Agriculture, Forest Service,
1024 Pacific Southwest Research Station: 123-129 251, 123-129.
1025 Harley, F.W., 1918. Letter dated January 30, 1918, from District Ranger F.W. Harley to the
1026 Supervisor of the Klamath National Forest in Yreka, CA. In.
1027 Harling, W., Tripp, W., 2014. Western Klamath Restoration Partnership: a plan for restoring fire
1028 adapted landscapes. In.
1029 Harrington, J.P., 1932. Tobacco among the Karuk Indians of California. US Government
1030 Printing Office.
1031 Harrington, M.G., Hawksworth, F.G., 1990. Interactions of fire and dwarf mistletoe on mortality
1032 of southwestern ponderosa pine. In: Krammes, J.S. (Ed.), Effects of fire management of
1033 Southwestern natural resources. USDA Forest Service, Rocky Mountain Forest and Range
1034 Experiment Station, Fort Collins, CO, pp. 234-240.
1035 Hart-Fredeluces, G.M., Ticktin, T., Lake, F.K., 2021. Simulated Indigenous fire stewardship
1036 increases the population growth rate of an understorey herb. J. Ecol. 109, 1133-1147.
1037 He, Y., Chen, G., Cobb, R.C., Zhao, K., Meentemeyer, R.K., 2021. Forest landscape patterns
1038 shaped by interactions between wildfire and sudden oak death disease. For. Ecol. Manage. 486,
1039 118987.
1040 Hill, R., Nates-Parra, G., Quezada-Euán, J.J.G., Buchori, D., LeBuhn, G., Maués, M.M., Pert,
1041 P.L., Kwapong, P.K., Saeed, S., Breslow, S.J., Carneiro da Cunha, M., Dicks, L.V., Galetto, L.,
1042 Gikungu, M., Howlett, B.G., Imperatriz-Fonseca, V.L., O'B. Lyver, P., Martín-López, B.,

1043 Oteros-Rozas, E., Potts, S.G., Roué, M., 2019. Biocultural approaches to pollinator conservation.
1044 Nature Sustainability 2, 214-222.
1045 Huffman, M.R., 2013. The Many Elements of Traditional Fire Knowledge: Synthesis,
1046 Classification, and Aids to Cross-cultural Problem Solving in Fire-dependent Systems Around
1047 the World. Ecol. Soc. 18.
1048 Hummel, S., Foltz-Jordan, S., Polasky, S., 2012. Natural and cultural history of beargrass
1049 (Xerophyllum tenax). Gen. Tech. Rep. PNW-GTR-864. Portland, OR: US Department of
1050 Agriculture, Forest Service, Pacific Northwest Research Station. 80 p 864.
1051 Hummel, S., Lake, F.K., Watts, A., 2015. Using forest knowledge: How silviculture can benefit
1052 from ecological knowledge systems about beargrass harvesting sites. In. U.S. Department of
1053 Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, p. 9.
1054 Huntsinger, L., McCaffrey, S., Watt, L., Lee, M., 1994. A Yurok forest history. In. Bureau of
1055 Indian Affairs, Sacramento, CA, p. 145 p.
1056 Jordan, T., 2015. Reciprocity & Hupa woodpeckers. In, California Cultures: A monograph series
1057 v. 2. Land of Oaks Institute, Oakland, CA.
1058 Karuk Tribe, 2019. Karuk climate adaptation plan. In: Norgaard, K.M., Tripp, W. (Eds.). Karuk
1059 Tribe, Happy Camp, CA, p. 232 p.
1060 Karuk Tribe and Cultural Solutions, 1999a. Karuk forest management perspectives: interviews
1061 with tribal members, Vol. 2: Appendices. In, Yreka, California, USA.
1062 Karuk Tribe and Cultural Solutions, 1999b. Karuk forest management perspectives: interviews
1063 with Tribal members: Appendix 1. In. Karuk Tribe, Yreka, CA.

1064 Kauffman, J.B., Martin, R., 1985. A preliminary investigation on the feasibility of preharvest
1065 prescribed burning for shrub control. In, Proceedings of The 6th Forest Vegetation Management
1066 Conference, Redding, CA, pp. 89-114.
1067 Keeley, J.E., McGinnis, T.W., 2007. Impact of prescribed fire and other factors on cheatgrass
1068 persistence in a Sierra Nevada ponderosa pine forest. Int. J. Wildland Fire 16, 96-106.
1069 Kelly, E.C., Charnley, S., Pixley, J.T., 2019. Polycentric systems for wildfire governance in the
1070 Western United States. Land use policy 89, 104214.
1071 Kerns, B.K., Day, M.A., 2018. Prescribed fire regimes subtly alter ponderosa pine forest plant
1072 community structure. Ecosphere 9, e02529.
1073 Kimmerer, R., 2011. Restoration and Reciprocity: The Contributions of Traditional Ecological
1074 Knowledge. In: Egan, D., Hjerpe, E.E., Abrams, J. (Eds.), Human Dimensions of Ecological
1075 Restoration: Integrating Science, Nature, and Culture. Island Press/Center for Resource
1076 Economics, Washington, DC, pp. 257-276.
1077 Kimmerer, R.W., Lake, F.K., 2001. The role of indigenous burning in land management. J. For.
1078 99, 36-41.
1079 Klenk, N., Fiume, A., Meehan, K., Gibbes, C., 2017. Local knowledge in climate adaptation
1080 research: Moving knowledge frameworks from extraction to co-production. Wiley
1081 Interdisciplinary Reviews: Climate Change 8, e475.
1082 Klimaszewski-Patterson, A., Mensing, S., 2020. Paleoecological and paleolandscape modeling
1083 support for pre-Columbian burning by Native Americans in the Golden Trout Wilderness Area,
1084 California, USA. Landscape Ecol., 1-20.
1085 Klimaszewski-Patterson, A., Weisberg, P.J., Mensing, S.A., Scheller, R.M., 2018. Using
1086 paleolandscape modeling to investigate the impact of native American–set fires on pre-

1087 columbian forests in the southern Sierra Nevada, California, USA. Annals of the American
1088 Association of Geographers 108, 1635-1654.
1089 Knapp, B.O., Stephan, K., Hubbart, J.A., 2015. Structure and composition of an oak-hickory
1090 forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. For. Ecol. Manage.
1091 344, 95-109.
1092 Kolden, C.A., 2019. We're not doing enough prescribed fire in the western United States to
1093 mitigate wildfire risk. Fire 2, 30.
1094 Kremen, C., 2005. Managing ecosystem services: what do we need to know about their ecology?
1095 Ecol. Lett. 8, 468-479.
1096 Kuhnlein, H.V., Receveur, O., 1996. Dietary change and traditional food systems of indigenous
1097 peoples. Annu. Rev. Nutr. 16, 417-442.
1098 Lake, F.K., 2007. Traditional ecological knowledge to develop and maintain fire regimes in
1099 northwestern California, Klamath-Siskiyou bioregion: management and restoration of culturally
1100 significant habitats. In, Environmental Sciences. Oregon State University, Corvallis, OR, p. 732.
1101 Lake, F.K., 2013. Trails, fires and tribulations: tribal resource management and research issues in
1102 Northern California. Occasion: Interdisciplinary Studies in the Humanities 5, 22 p.
1103 Lake, F.K., 2019. A sustainable future for use of *Notholithocarpus densiflorus* acorns.
1104 International Oaks 30, 283-288.
1105 Lake, F.K., 2021. Indigenous fire stewardship: Federal/Tribal partnerships for wildland fire
1106 research and management. Fire Management Today. 79 (1): 30-39. 79, 30-39.
1107 Lake, F.K., Christianson, A.C., 2019. Indigenous fire stewardship. In: Mazello, S. (Ed.),
1108 Encyclopedia of wildfire and Wildland-Urban Interface (WUI) fires. Springer Nature,
1109 Switzerland.

Lake, F.K., Long, J.W., 2014. Fire and tribal cultural resources. In: Long, J.W., Quinn-Davidson, L.N., Skinner, C.N. (Eds.), Science synthesis to support socioecological resilience in the Sierra Nevada and southern Cascade Range. USDA Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 173-185.

Lake, F.K., Parrotta, J., Giardina, C.P., Davidson-Hunt, I., Uprety, Y., 2018. Integration of Traditional and Western knowledge in forest landscape restoration. In: Mansourian, S., Parrotta, J. (Eds.), Forest landscape restoration: integrated approaches to support effective implementation. Routledge, New York, pp. 198-226.

Larson, A.J., Cansler, C.A., Cowdery, S.G., Hiebert, S., Furniss, T.J., Swanson, M.E., Lutz, J.A., 2016. Post-fire morel (*Morchella*) mushroom abundance, spatial structure, and harvest sustainability. For. Ecol. Manage. 377, 16-25.

LeCompte-Mastenbrook, J.K., 2016. Restoring Coast Salish foods and landscapes: a more-than-human politics of place, history and becoming. In, Anthropology. University of Washington, Seattle, Washington, USA, p. 258 + appendices.

Lehmann, J., Gaunt, J., Rondon, M., 2006. Bio-char sequestration in terrestrial ecosystems – a review. Mitigation and Adaptation Strategies for Global Change 11, 403-427.

Leonard, K., Aldern, J.D., Christianson, A., Ranco, D., Thornbrugh, C., Loring, P.A., Coughlan, M.R., Jones, P., Mancini, J., May, D., Moola, F., Williamson, G.J., Stoof, C.R., 2020. Indigenous conservation practices are not a monolith: Western cultural biases and a lack of engagement with Indigenous experts undermine studies of land stewardship. EcoEvoRxiv (preprint).

1131 Levine, J.I., Collins, B.M., York, R.A., Foster, D.E., Fry, D.L., Stephens, S.L., 2020. Forest
1132 stand and site characteristics influence fuel consumption in repeat prescribed burns. Int. J.
1133 Wildland Fire 29, 148-159.
1134 Lewis, H.T., 1973. Patterns of Indian burning in California: ecology and ethnohistory. Ballena
1135 Press.
1136 Lewis, M., Christianson, A., Spinks, M., 2018. Return to Flame: Reasons for Burning in Lytton
1137 First Nation, British Columbia. J. For. 116, 143-150.
1138 Liebmann, M.J., Farella, J., Roos, C.I., Stack, A., Martini, S., Swetnam, T.W., 2016. Native
1139 American depopulation, reforestation, and fire regimes in the Southwest United States, 1492-
1140 1900 CE. Proceedings of the National Academy of Sciences 113, E696-E704.
1141 Lightfoot, K.G., Cuthrell, R.Q., Striplen, C.J., Hylkema, M.G., 2013. Rethinking the study of
1142 landscape management practices among hunter-gatherers in North America. Amer. Antiq. 78,
1143 285-301.
1144 Lightfoot, K.G., Parrish, O., 2009. California Indians and their environment: an introduction.
1145 Univ. of California Press, Berkeley.
1146 Livingston, A.C., Varner, J.M., Jules, E.S., Kane, J.M., Arguello, L.A., 2016. Prescribed fire and
1147 conifer removal promote positive understorey vegetation responses in oak woodlands. J. Appl.
1148 Ecol. 53, 1604-1612.
1149 Long, J., Gray, A., Lake, F., 2018a. Recent trends in large hardwoods in the Pacific Northwest,
1150 USA. Forests 9, 651.
1151 Long, J.W., Anderson, M.K., Quinn-Davidson, L.N., Goode, R.W., Lake, F.K., Skinner, C.N.,
1152 2016. Restoring California black oak ecosystems to promote tribal values and wildlife. In. U.S.

Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, p. 111 p.

Long, J.W., Lake, F.K., 2018. Escaping social-ecological traps through tribal stewardship on national forest lands in the Pacific Northwest, United States of America. Ecol. Soc. 23.

Long, J.W., Lake, F.K., Goode, R.W., Burnette, B.M., 2020. How traditional tribal perspectives influence ecosystem restoration. Ecopsychology 12, 71-82.

Long, J.W., Lake, F.K., Lynn, K., Viles, C., 2018b. Tribal ecocultural resources and engagement. In: Spies, T., Stine, P., Gravenmier, R., Long, J., Reilly, M. (Eds.), Synthesis of science to inform land management within the Northwest Forest Plan area. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, USA, pp. 851-917.

Long, J.W., Steel, E.A., 2020. Shifting perspectives in assessing socio-environmental vulnerability in the United States and Southeast Asia. Sustainability 12, 2625.

Long, J.W., Tarnay, L.W., North, M.P., 2018c. Aligning smoke management with ecological and public health goals. J. For. 116, 76-86.

Lovell, C., Mandondo, A., Moriarty, P., 2002. The question of scale in integrated natural resource management. Conserv. Ecol. 5.

Lydersen, J.M., Collins, B.M., 2018. Change in Vegetation Patterns Over a Large Forested Landscape Based on Historical and Contemporary Aerial Photography. Ecosystems 21, 1348-1363.

Lydersen, J.M., Collins, B.M., Hunsaker, C.T., 2019. Implementation constraints limit benefits of restoration treatments in mixed-conifer forests. Int. J. Wildland Fire 28, 495-511.

1174 Lynn, K., Daigle, J., Hoffman, J., Lake, F., Michelle, N., Ranco, D., Viles, C., Voggesser, G.,
1175 Williams, P., 2013. The impacts of climate change on tribal traditional foods. Clim. Change 120,
1176 545-556.
1177 Marks-Block, T., Lake, F.K., Bliege Bird, R., Curran, L.M., 2021. Revitalized Karuk and Yurok
1178 cultural burning to enhance California hazelnut for basketweaving in northwestern California,
1179 USA. Fire Ecol. 17, 6.
1180 Marks-Block, T., Lake, F.K., Curran, L.M., 2019. Effects of understory fire management
1181 treatments on California Hazelnut, an ecocultural resource of the Karuk and Yurok Indians in the
1182 Pacific Northwest. For. Ecol. Manage. 450, 117517.
1183 Marks-Block, T., Tripp, W., 2021. Facilitating Prescribed Fire in Northern California through
1184 Indigenous Governance and Interagency Partnerships. Fire 4, 37.
1185 Mauer, K.W., 2020. Unsettling resilience: colonial ecological violence, Indigenous futurisms,
1186 and the restoration of the Elwha River. Rural Sociology, https://doi.org/10.1111/ruso.12365.
1187 McGlone, C.M., Stoddard, M.T., Springer, J.D., Daniels, M.L., Fulé, P.Z., Wallace Covington,
1188 W., 2012. Nonnative species influence vegetative response to ecological restoration: Two forests
1189 with divergent restoration outcomes. For. Ecol. Manage. 285, 195-203.
1190 McWethy, D.B., Schoennagel, T., Higuera, P.E., Krawchuk, M., Harvey, B.J., Metcalf, E.C.,
1191 Schultz, C., Miller, C., Metcalf, A.L., Buma, B., Virapongse, A., Kulig, J.C., Stedman, R.C.,
1192 Ratajczak, Z., Nelson, C.R., Kolden, C., 2019. Rethinking resilience to wildfire. Nature
1193 Sustainability 2, 797–804.
1194 Metlen, K.L., Skinner, C.N., Olson, D.R., Nichols, C., Borgias, D., 2018. Regional and local
1195 controls on historical fire regimes of dry forests and woodlands in the Rogue River Basin,
1196 Oregon, USA. For. Ecol. Manage. 430, 43-58.

1197 Miller, J.D., Safford, H., 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada,
1198 Modoc Plateau, and southern Cascades, California, USA. Fire Ecol. 8, 41-57.
1199 Miller, J.D., Skinner, C.N., Safford, H.D., Knapp, E.E., Ramirez, C.M., 2012. Trends and causes
1200 of severity, size, and number of fires in northwestern California, USA. Ecol. Appl. 22, 184-203.
1201 Mucioki, M., Sowerwine, J., Sarna-Wojcicki, D., Lake, F.K., Bourque, S., in press.
1202 Conceptualizing Indigenous Cultural Ecosystem Services (ICES) and benefits under changing
1203 climate conditions in the Klamath River Basin and their implications for land management and
1204 governance. J. Ethnobiol.
1205 Nikolakis, W., Roberts, E., 2020. Indigenous fire management: a conceptual model from
1206 literature. Ecol. Soc. 25, 11.
1207 Nikolakis, W., Roberts, E., Hotte, N., Ross, R.M., 2020. Goal setting and Indigenous fire
1208 management: a holistic perspective. Int. J. Wildland Fire 29, 974-982.
1209 Norgaard, K.M., 2005. The effects of altered diet on the health of the Karuk people. In.
1210 Norgaard, K.M., 2019. Salmon & acorns feed our people: colonialism, nature, & social action.
1211 Rutgers University Press, New Brunswick.
1212 Norgaard, K.M., Reed, R., Bacon, J., 2017. How environmental decline restructures indigenous
1213 gender practices: what happens to Karuk masculinity when there are no fish? Sociology of Race
1214 and Ethnicity 2332649217706518, 1-16.
1215 North, M.P., York, R.A., Collins, B.M., Hurteau, M.D., Jones, G.M., Knapp, E.E., Kobziar,
1216 L.N., McCann, H., Meyer, M.D., Stephens, S.L., Tompkins, R.E., Tubbesing, C.L., 2021.
1217 Pyrosilviculture needed for landscape resilience of dry Western U.S. forests. J. For. fvab026.
1218 Norton, H.H., 1979. The association between anthropogenic prairies and important food plants in
1219 western Washington. Journal of Northwest Anthropology 13, 175–200.

1220 O'Dell, K., Ford, B., Fischer, E.V., Pierce, J.R., 2019. Contribution of Wildland-Fire Smoke to
1221 US PM2.5 and Its Influence on Recent Trends. Environ. Sci. Technol. 53, 1797-1804.
1222 Orr, A., 2014. The effect of prescribed burning on the abundance of *Fragaria virginiana* (wild
1223 strawberry) and *Camassia quamash* (blue camas) in Glacial Heritage Preserve. In, Salish Sea
1224 Ecosystem Conference.
1225 Oswald, W.W., Foster, D.R., Chilton, E.S., 2020a. Native people did not use fire to shape New
1226 England's landscape. In, The Conversation.
1227 Oswald, W.W., Foster, D.R., Shuman, B.N., Chilton, E.S., Doucette, D.L., Duranleau, D.L.,
1228 2020b. Conservation implications of limited Native American impacts in pre-contact New
1229 England. Nature Sustainability 3, 241-246.
1230 Patterson, T.M., 2014. Ecosystem services. In: Long, J.W., Quinn-Davidson, L.N., Skinner, C.N.
1231 (Eds.), Science synthesis to support socioecological resilience in the Sierra Nevada and southern
1232 Cascade Range. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research
1233 Station, Albany, CA, p. 543–568.
1234 Paudyal, K., Baral, H., Burkhard, B., Bhandari, S.P., Keenan, R.J., 2015. Participatory
1235 assessment and mapping of ecosystem services in a data-poor region: Case study of community-
1236 managed forests in central Nepal. Ecosystem services 13, 81-92.
1237 Pilz, D., Weber, N.S., Carter, M.C., Parks, C.G., Molina, R., 2004. Productivity and diversity of
1238 morel mushrooms in healthy, burned, and insect-damaged forests of northeastern Oregon. For.
1239 Ecol. Manage. 198, 367-386.
1240 Ponisio, L.C., Wilkin, K., M'Gonigle, L.K., Kulhanek, K., Cook, L., Thorp, R., Griswold, T.,
1241 Kremen, C., 2016. Pyrodiversity begets plant–pollinator community diversity. Global Change
1242 Biol. 22, 1794-1808.

1243 Preston, C.A., Baldwin, I.T., 1999. Positive and negative signals regulate germination in the
1244 post-fire annual, Nicotiana attenuata. Ecology 80, 481-494.
1245 Pullen, R.J., 1996. Overview of the environment of native inhabitants of southwestern Oregon,
1246 late prehistoric era. In. USDA Forest Service Rogue River Siskiyou National Forest and USDI
1247 Bureau of Land Management, Medford, OR.
1248 Reilly, M.J., Dunn, C.J., Meigs, G.W., Spies, T.A., Kennedy, R.E., Bailey, J.D., Briggs, K.,
1249 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA
1250 (1985–2010). Ecosphere 8, e01695.
1251 Roos, C.I., 2020. Scale in the study of Indigenous burning. Nature Sustainability 3, 898-899.
1252 Roos, C.I., Rittenour, T.M., Swetnam, T.W., Loehman, R.A., Hollenback, K.L., Liebmann, M.J.,
1253 Rosenstein, D.D., al., e., 2020. Fire suppression impacts on fuels and fire intensity in the western
1254 U.S.: Insights from archaeological luminescence dating in northern New Mexico. Fire 3, 32.
1255 Roos, C.I., Swetnam, T.W., Ferguson, T., Liebmann, M.J., Loehman, R.A., Welch, J.R.,
1256 Margolis, E.Q., Guiterman, C.H., Hockaday, W.C., Aiuvalasit, M.J., 2021. Native American fire
1257 management at an ancient wildland–urban interface in the Southwest United States. Proceedings
1258 of the National Academy of Sciences 118, e2018733118.
1259 Roos, C.I., Williamson, G.J., Bowman, D.M.J.S., 2019. Is Anthropogenic pyrodiversity invisible
1260 in paleofire records? Fire 2, 42.
1261 Roos, C.I., Zedeño, M.N., Hollenback, K.L., 2018. Indigenous impacts on North American Great
1262 Plains fire regimes of the past millennium. Proceedings of the National Academy of Sciences
1263 115, 8143-8148.
1264 Ross, J., Brawley, S., Lowrey, J., Hankins, D.L., 2008. Creating common ground: a collaborative
1265 approach to environmental reclamation and cultural preservation. In: Wilmsen, C., Elmendorf,

W., Fisher, L., Ross, J., Sarathy, B., Wells, G. (Eds.), Partnerships for empowerment: participatory research for community-based natural resource management. Earthscan, London, UK, pp. 105-126.

Ryan, K.C., Jones, A.T., Koerner, C.L., Lee, K.M., 2012. Wildland fire in ecosystems: effects of fire on cultural resources and archaeology. In. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, p. 224.

Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. 11, e15-e24.

Safford, H.D., Harrison, S., 2008. The effects of fire on serpentine vegetation and implications for management. In: Narog, M.G., tech. coord. (Ed.), Managing fire and fuels in the remaining wildlands and open spaces of the southwestern United States. USDA Forest Service, Albany, CA, pp. 321-327.

Schenck, S.M., Gifford, E.W., 1952. Karok ethnobotany. University of California Anthropological Records 13, 377-392.

Schmidt, H.-P., Hagemann, N., Draper, K., Kammann, C., 2019. The use of biochar in animal feeding. PeerJ 7, e7373.

Schoennagel, T., Balch, J.K., Brenkert-Smith, H., Dennison, P.E., Harvey, B.J., Krawchuk, M.A., Mietkiewicz, N., Morgan, P., Moritz, M.A., Rasker, R., Turner, M.G., Whitlock, C., 2017. Adapt to more wildfire in western North American forests as climate changes. Proceedings of the National Academy of Sciences of the United States of America 114, 4582-4590.

Schultz, C.B., Henry, E., Carleton, A., Hicks, T., Thomas, R., Potter, A., Collins, M., Linders, M., Fimbel, C., Black, S., 2011. Conservation of prairie-oak butterflies in Oregon, Washington, and British Columbia. Northwest Sci. 85, 361-388.

Schumacher, E.F., 1985. Small is beautiful. Rowohlt Taschenbuch Verlag.

Shebitz, D.J., 2006. The historical role and current restoration applications of fire in maintaining beargrass (Xerophyllum tenax (Pursh) Nutt.) habitat on the Olympic Peninsula, Washington State. University of Washington.

Shebitz, D.J., Ewing, K., Gutierrez, J., 2009a. Preliminary observations of using smoke-water to increase low-elevation beargrass *Xerophyllum tenax* germination. Native plants journal 10, 13-20.

Shebitz, D.J., Reichard, S.H., Dunwiddie, P.W., 2009b. Ecological and cultural significance of burning beargrass habitat on the Olympic Peninsula, Washington. Ecol. Restor. 27, 306-319.

Shebitz, D.J., Reichard, S.H., Woubneh, W., 2008. Beargrass (*Xerophyllum tenax*) the Olympic Peninsula, Washington: Autecology and population status. Northwest Sci. 82, 128-140.

Sillitoe, P., 1998. Knowing the land: soil and land resource evaluation and indigenous knowledge. Soil use and Management 14, 188-193.

Skinner, C.N., 1995. Change in spatial characteristics of forest openings in the Klamath Mountains of northwestern California, USA. Landscape Ecol. 10, 219-228.

Skinner, C.N., Abbott, C.S., Fry, D.L., Stephens, S.L., Taylor, A.H., Trouet, V., 2009. Human and climatic influences on fire occurrence in California's North Coast Range, USA. Fire Ecol. 5, 73-96.

Slaton, M.R., Holmquist, J.G., Meyer, M., Andrews, R., Beidl, J., 2019. Traditional Ecological Knowledge Used in Forest Restoration Benefits Natural and Cultural Resources: The Intersection between Pandora Moths, Jeffrey Pine, People, and Fire. Nat. Areas J. 39, 461-471, 411.

1311 Sloan, K., Hostler, J., 2014. Utilizing Yurok traditional ecological knowledge to inform climate
1312 change priorities. In. Yurok Tribe Environmental Program, Klamath, CA, p. 29.
1313 Sowerwine, J., Sarna-Wojcicki, D., Mucioki, M., Hillman, L., Lake, F.K., Friedman, E., 2019.
1314 Enhancing food sovereignty: A five-year collaborative tribal-university research and extension
1315 project in California and Oregon. Journal of Agriculture, Food Systems, and Community
1316 Development 9.
1317 Spies, T.A., Long, J.W., Charnley, S., Hessburg, P.F., Marcot, B.G., Reeves, G.H., Lesmeister,
1318 D.B., Reilly, M.J., Cerveny, L.K., Stine, P.A., Raphael, M.G., 2019. Twenty-five years of the
1319 Northwest Forest Plan: what have we learned? Front. Ecol. Environ. 17, 511-520.
1320 Spoon, J., Arnold, R., Lefler, B.J., Milton, C., 2015. Nuwuvi (Southern Paiute), Shifting Fire
1321 Regimes, and the Carpenter One Fire in the Spring Mountains National Recreation Area,
1322 Nevada. J. Ethnobiol. 35, 85-110.
1323 Stephens, S.L., Fry, D.L., 2005. Fire history in coast redwood stands in the northeastern Santa
1324 Cruz Mountains, California. Fire Ecol. 1, 2-19.
1325 Stewart, O.C., 2002. Forgotten fires: Native Americans and the transient wilderness. University
1326 of Oklahoma Press.
1327 Story, M.T., 1974. Nitrogen fixation by *Ceanothus fendleri* and *Lupinus argenteus* as a function
1328 of parent material and vegetal cover. In. University of Arizona, Tucson, AZ, p. 69.
1329 Strass, K., 2010. Huckleberry harvesting of the Salish and Kootenai of the Flathead Reservation.
1330 In. University of Notre Dame, Dept. of Biology,, Land O'Lakes, WI, p. 26.
1331 Taylor, A.H., Trouet, V., Skinner, C.N., Stephens, S., 2016. Socioecological transitions trigger
1332 fire regime shifts and modulate fire–climate interactions in the Sierra Nevada, USA, 1600–2015
1333 CE. Proc. Natl. Acad. Sci. USA 113, 13684-13689.

1334 Thompson, C.M., Purcell, K.L., 2016. Conditions inside fisher dens during prescribed fires; what
1335 is the risk posed by spring underburns? For. Ecol. Manage. 359, 156-161.
1336 Thompson, L., 1916. To the American Indian: reminiscences of a Yurok woman. Cummins Print
1337 Shop, Eureka, CA.
1338 Thornburgh, D.A., Noss, R.F., Angelides, D.P., Olson, C.M., Euphrat, F., Welsh, H., 2000.
1339 Managing redwoods. In: Noss, R.F. (Ed.), The redwood forest: history, ecology, and
1340 conservation of the coast redwoods. Island Press, Covelo, CA, pp. 229-261.
1341 Trauernicht, C., Brook, B.W., Murphy, B.P., Williamson, G.J., Bowman, D.M.J.S., 2015. Local
1342 and global pyrogeographic evidence that indigenous fire management creates pyrodiversity.
1343 Ecology and Evolution 5, 1908-1918.
1344 Tremblay, R., Landry-Cuerrier, M., Humphries, M., 2020. Culture and the social-ecology of
1345 local food use by Indigenous communities in northern North America. Ecol. Soc. 25.
1346 Tribe, K., 2019. Karuk climate adaptation plan. In: Norgaard, K.M., Tripp, W. (Eds.). Karuk
1347 Tribe, Happy Camp, CA, p. 232 p.
1348 Trudeau, M., 1996. The short-term effect of fire on Lupinus perennis (L.). Nat. Areas J. 16, 41-
1349 48.
1350 Turner, N.J., 1999. “Time to burn”: traditional use of fire to enhance resource production by
1351 aboriginal peoples in British Columbia. In: Boyd, R. (Ed.), Indians, fire and the land in the
1352 Pacific Northwest. Oregon State University Press, Corvallis.
1353 Tushingham, S., Ardura, D., Eerkens, J.W., Palazoglu, M., Shahbaz, S., Fiehn, O., 2013. Hunter-
1354 gatherer tobacco smoking: earliest evidence from the Pacific Northwest Coast of North America.
1355 J. Archaeol. Sci. 40, 1397-1407.

1356 Tveten, R.K., Fonda, R., 1999. Fire effects on prairies and oak woodlands on Fort Lewis,
1357 Washington. Northwest Sci. 73, 145-158.
1358 Underwood, E., 2020. Sacred pollinators: An interview with Frank K. Lake. In, Flora. California
1359 Native Plant Society.
1360 Vale, T., 2002. Reflections. In: Vale, T. (Ed.), Fire, native peoples, and the natural landscape.
1361 Island Press, Washington DC, pp. 295-302.
1362 Varner, J., Jules, E., Engber, E., Sahara, A., Sullivan, C., Sarr, D., 2012. Ecology of the Bald
1363 Hills and Little Bald Hills of Redwood National Park: An assessment of vegetation change.
1364 Varner, J.M., Jules, E.S., 2017. The enigmatic fire regime of coast redwood forests and why it
1365 matters. In, US Department of Agriculture, Forest Service, Pacific Southwest Research Station,
1366 Albany, CA:, pp. 15-18.
1367 Wei, Y., Thompson, M.P., Scott, J.H., O'Connor, C.D., Dunn, C.J., 2019. Designing
1368 operationally relevant daily large fire containment strategies using risk assessment results.
1369 Forests 10.
1370 Welch, J.R., 2012. Effects of fire on intangible cultural resources: Moving toward a landscape
1371 approach. In: Ryan, K.C., Jones, A.T., Koerner, C.L., Lee, K.M. (Eds.), Wildland fire in
1372 ecosystems: Effects of fire on cultural resources and archaeology. U.S. Department of
1373 Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, pp. 157-170.
1374 Whitlock, C., Knox, M.A., 2002. Prehistoric burning in the Pacific Northwest: human versus
1375 climatic influences. Fire, Native peoples, and the natural landscape, 195-231.
1376 Whitlock, C., Skinner, C.N., Bartlein, P.J., Minckley, T., Mohr, J.A., 2004. Comparison of
1377 charcoal and tree-ring records of recent fires in the eastern Klamath Mountains, California, USA.
1378 Can. J. For. Res. 34, 2110-2121.

1379 Whyte, K., 2018. Critical investigations of resilience: a brief introduction to Indigenous
1380 environmental studies & sciences. Daedalus 147, 136-147.
1381 Wildland Fire Leadership Council, 2014. The National Strategy: the final phase in the
1382 development of the National Cohesive Wildland Fire Management Strategy. In. US Departments
1383 of Agriculture and Interior, Washington, DC, USA, p. 93 p.
1384 Willette, M., Norgaard, K., Reed, R., Tribe, K., 2016. You got to have fish: families,
1385 environmental decline and cultural reproduction. Families, Relationships and Societies 5, 375-
1386 392.
1387 Williams, G.W., 1994. References on the American Indian use of fire in ecosystems. In, Natural
1388 Resources Conservation Service.
1389 Willot, P.-A., Aubin, J., Salles, J.-M., Wilfart, A., 2019. Ecosystem service framework and
1390 typology for an ecosystem approach to aquaculture. Aquaculture 512, 734260.
1391 Wray, J., Elle, E., 2017. Pollen preference of two Andrenid bees in British Columbia's oak-
1392 savannah ecosystem. J. Entomol. Soc. B. C. 113, 39-48.
1393 Wynecoop, M.D., Morgan, P., Strand, E.K., Sanchez Trigueros, F., 2019. Getting back to fire
1394 sumés: exploring a multi-disciplinary approach to incorporating traditional knowledge into fuels
1395 treatments. Fire Ecol. 15, 17.
1396 Zevit, P., Fairbarns, M., 2010. Snake-root sanicle (Sanicula arctopoides. In, BC's Coast Region:
1397 Species & Ecosystems of Conservation Concern. South Coast Conservation Program (SCCP).
1398 Zimmerman, G.T., Laven, R.D., 1987. Effects of forest fuel smoke on dwarf mistletoe seed-
1399 germination. Great Basin Nat. 47, 652-659.

Table 1: Services associated with Indigenous cultural burning in this study and others with different spatial scopes.

		Source and region		
Service category	Pacific West USA (this paper)	USA (Williams, 1994)	Global (Trauernicht et al., 2015), with numbers ranked from most frequent (1) to least frequent	California (Anderson, 2018; Anderson and Keeley, 2018)
Services for ecosystems	Duties to places and non-human relatives		15. Ownership/ responsibility	
Non-material cultural services	Maintenance of lifeways	Clearing areas for travel Clearing riparian areas	1. Clean/clear landscape	Keeping the country open
		Economic extortion Warfare & signaling	13. Communication 17. Warfare/conflict	
	Transmission of knowledge			Retaining traditional knowledge
	Ceremonies and spiritual well-being		14. Ceremonial/medicinal	Ceremonial and medicinal purposes, including tobacco and *Lomatium*
	Sense of place			
Material cultural-provisioning services	Foods, medicines, and materials from plants, fungi, and animals	Improve growth and yields Crop management	2. Manipulate plant traits 4. NTFP harvest 6. Cultivation	Creating plant material for the manufacture of baskets and other cultural items Enhancing food production (plants and fungi)
		Felling trees	10. Forest management 16. Firewood collection	Firewood and structures
		Hunting Insect gathering	3. Drive game animals 5. Attract game 18. Fishing	Managing and hunting wildlife
			7. Pasture management 11. Animal safety 12. Animal gathering	
Regulating and supporting services	Species biodiversity			Increased patchiness of plant populations Higher species diversity

	Ecosystem biodiversity			Increase landscape heterogeneity Expand special plant community types (e.g., ponds, marshes, meadows, and prairies)
	Pollination			Promote butterflies
	Regulating pests and diseases	Pest management	9. Pest management	Combat insects and diseases
	Soil health			Increase nutrient cycling and soil moisture
	Hydrology			Increase water resources, including spring flows
	Regulating wildfire	Fireproof areas	8. Prevent destructive fires	Reduce the chance of catastrophic fires

Forest Ecology and Management 450 (2019) 117517

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Effects of understory fire management treatments on California Hazelnut, an ecocultural resource of the Karuk and Yurok Indians in the Pacific Northwest

Tony Marks-Block[a,*], Frank K. Lake[b], Lisa M. Curran[a,c]

[a] Department of Anthropology, Stanford University, Main Quad, Building 50, 450 Serra Mall, Stanford, CA 94305, United States
[b] Pacific Southwest Research Station, Fire and Fuels Program, USDA Forest Service, 1700 Bayview Drive, Arcata, CA 95521, United States
[c] Woods Institute for the Environment, Jerry Yang & Akikio Yamazaki Environment & Energy Building, 473 Via Ortega, Stanford University, Stanford, CA 94305, United States

ARTICLE INFO

Keywords:
Indigenous resource use
Traditional ecological knowledge
Basketry
Prescribed fire
Fuel reduction
American Indians
Nontimber forest products
Corylus cornuta var. *californica*

ABSTRACT

Before widespread fire exclusion policies, American Indians used broadcast understory fires or cultural burns to enhance resources integral for their livelihood and cultural practices. To restore ecocultural resources depleted from decades of fire exclusion and to reduce wildfire risks, the Karuk and the Yurok Tribes of Northwest California are leading regional collaborative efforts to expand broadcast fires and fuel reduction treatments on public, private, and Tribal lands in their ancestral territories. Through collaboration with Karuk and Yurok Tribal members and basketweavers, we evaluated the effects of broadcast fires and three fire proxy treatments on California hazelnut shrubs (*Corylus cornuta* var. *californica*) that produce highly valued ecocultural resources for basketry materials. Across a 10 ha Douglas-fir and mixed hardwood forest (500 m a.s.l.) in the Klamath mountains, we established 27 stratified blocks (16 m^2) and within each block applied three fire proxy treatments designed and used by Tribal members with an untreated control. These treatments involved manual hazelnut stem cutting, directly blistering hazelnut stems via propane torch, and igniting surface fuels piled within hazelnut shrubs to top-kill stems. Broadcast fire was applied to 12 separate blocks. After a full growing season (12–18 months post-treatment/burn), shrubs were re-measured. We then harvested these stems (n = 604; 50 shrubs) across treatments and compared results with stems gathered independently by two experienced Karuk/Yurok basketweavers (n = 396 and n = 73) from an adjacent broadcast burned site. Compared to the untreated shrubs, pile burning, propane torching, and broadcast burning increased basketry stem production by 7–10 fold ($p < 0.001$), while the cutting treatment increased production by 4-fold ($p = 0.006$). Shrubs with relatively greater access to sunlight (southern aspect, ≥51% and < 70% canopy cover) produced fewer quality stems when compared to shrubs with an eastern aspect ($p < 0.01$) and ≥70% canopy cover ($p < 0.05$). Harvested stems across all treatments displayed similar stem length distributions to those gathered by one of the two basketweavers ($p > 0.05$). Our results demonstrate that these fire-proxy methods are an effective means to increase the production and quality of basketry materials. Expanding the area and frequency of targeted understory fire-based forest treatments on private, public and Tribal lands in California and the Pacific Northwest would substantially increase the availability of these fire-enhanced ecocultural resources that are currently limited in supply and in high demand.

1. Introduction

As a result of historic fire exclusion policies in the American West, American Indian communities have sought to re-integrate prescribed fire and other fuel reduction treatments to decrease wildfire risks on Tribal lands and across other jurisdictions within their ancestral territories (Carroll et al., 2010; Kolden, 2019; Long and Lake, 2018). Tribes have expressed strong interest to use prescribed fire to improve the density and availability of culturally and economically important plants, fungi, and animals, referred to as 'ecocultural resources' (Anderson, 2018; Carroll et al., 2004; Lake et al., 2017; Long and Lake, 2018). Although ecocultural resources are similar to nontimber forest products (Chamberlain et al., 2018; Charnley et al., 2007; Jones and Lynch, 2007), ecocultural resources are also integral to Indigenous identity (Kimmerer, 2011; Long et al., 2018).

Co-management agreements between Tribes and public land

* Corresponding author.
E-mail addresses: tonymb@stanford.edu (T. Marks-Block), frank.lake@usda.gov (F.K. Lake), lmcurran@stanford.edu (L.M. Curran).

https://doi.org/10.1016/j.foreco.2019.117517
Received 10 April 2019; Received in revised form 29 July 2019; Accepted 30 July 2019
0378-1127/ © 2019 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/BY-NC-ND/4.0/).

agencies, such as the United States Department of Agriculture (USDA) Forest Service, reflect recent efforts to integrate Tribal ecocultural resource objectives into management plans (Bussey et al., 2015; Carroll et al., 2010; Catton, 2016; Diver, 2016; Dockry et al., 2017; Donoghue et al., 2010; Jurney et al., 2017; Long and Lake, 2018). Although numerous studies exist on the effects of prescribed fire, along with manual, mechanical, and pile burning fuel reduction treatments on fire severity (Kalies and Kent, 2016), only a few studies in North America examine the effects of such treatments on ecocultural resources (Halpern, 2016; Hankins, 2013; Lake, 2007; Lathrop and Martin, 1982; Peter et al., 2017; Shebitz et al., 2009; Wynecoop et al., 2019). Given that pre-colonial Indigenous burning, coppicing, transplanting, and harvesting sought to enhance ecocultural resources, specifically examining how such treatments affect these resources may provide useful information to support the objectives of Tribes and land management agencies involved in ecological restoration, socio-economic development, and wildfire risk reduction (Anderson, 2018; Charnley et al., 2018; Kalies and Kent, 2016; Senos et al., 2006).

After several decades of limited fuel treatments, the Karuk and the Yurok Tribes in Northwest California are leading regional efforts to expand fuel reduction treatments and prescribed fires on public, private, and tribal reservation lands in their ancestral territories to protect structures and to restore ecocultural resources (Fig. 1A; Diver, 2016; Harling, 2015; Long et al., 2018; Robbins et al., 2016). Fire-enhanced ecocultural resources (e.g., acorns, berries, basketry materials, and wildlife) are integral to the Karuk and Yurok Tribes (Baldy, 2013; Harrington, 1932; Heffner, 1984; Huntsinger and McCaffrey, 1995; Norgaard, 2014). In Karuk and Yurok territory, and elsewhere in California, American Indians refer to their prescribed fires as 'cultural burns', because the burns aim to improve the qualities and densities of ecocultural resources central to subsistence and ceremonial practices (Aldern and Goode, 2014; Long et al., 2018). Cultural burning is a critical component of 'ecocultural revitalization' efforts in Northwest California given the centrality of fire-enhanced resources to cultural practices. Cultural burning distinguishes these fires from the fuel reduction-focused prescribed burns of public land agencies whose primary objective is to reduce fuel loads, and thus, moderate wildfire intensity (Collins et al., 2010; Schwilk et al., 2009).

Since the early 1990s, forest management in the Pacific Northwest and Tribal consultation policies have undergone several major conceptual and programmatic changes coupled with legislation (Thomas et al., 2006; Vinyeta and Lynn, 2015). American Indian political organizing resulted in the passage of legislation to reform the National Historic Preservation Act in 1992 that required US governmental consultation with Tribes surrounding cultural resources in their ancestral territories (Stapp and Burney, 2002). In 1994 and 2000, US President Clinton issued executive orders that expanded consultation requirements to all decisions that had implications for Tribes (Clinton, 2000, 1994). These executive orders along with other internal actions of USDA Forest Service staff catalyzed the hiring of Tribal liaisons and the formation of the Office of Tribal Relations (Catton, 2016). Consequently, to meet these treaty and federal Indian trust obligations, collaborations among Tribes and public land agencies became increasingly formalized (Lake et al., 2018; Long et al., 2018).

With the implementation of the Northwest Forest Plan (NWFP) in the 1990s (Fig. 1B), forest management on public lands in Karuk and Yurok ancestral territories shifted from timber extraction toward ecological restoration and endangered species conservation (e.g., Northern Spotted Owl, *Strix occidentalis*) dependent upon old-growth forests (Thomas et al., 2006). The NWFP also precipitated the development of

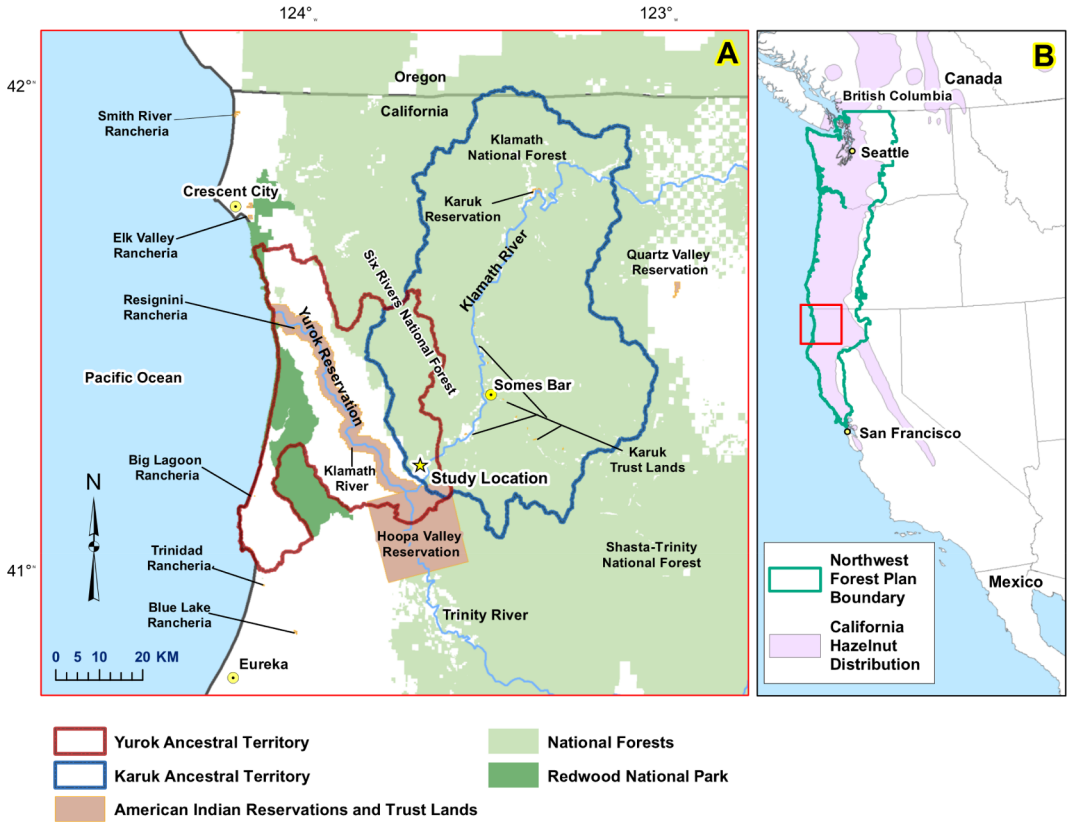


Fig. 1. (A) Study region with federal jurisdictional boundaries and Karuk and Yurok territories. Ancestral territory boundaries, provided by the Karuk and Yurok Tribes, represent reconstructions, but currently are not fixed or rigid boundaries. Ancestral lands of other Northwest California Tribes (e.g., Tolowa, Wiyot, Hupa, Shasta) are not included here, but note that their ancestral lands may partially overlap with the boundaries rendered here (Baumhoff, 1963). (B) Western region of the United States of America, including California hazelnut (*Corylus cornuta* var. *californica*) distribution derived from the *Atlas of US Trees* (Little Jr, 1971) as well as the area encompassed under the Northwest Forest Plan (2002). The study region is depicted by the red square.



Fig. 2. Hopper basket (center) used to pound acorns with unpeeled (left) and peeled (right) hazelnut basketry stems. This basket is composed of peeled hazelnut stems similar to those shown along with other materials. [Photo: Frank K. Lake, USDA Forest Service and Karuk Tribe]

new National Forest plans and established regular federal monitoring of Tribal consultation processes that created opportunities for the Karuk Tribe to influence forest policy and resource management within their ancestral territory (Diver, 2016; Long et al., 2018; Senos et al., 2006; Vinyeta and Lynn, 2015). These policy changes as well as the 2001 National Fire Plan and the 2003 Healthy Forests Restoration Act (PL 108-148) established benchmarks and best practices coupled with earmarked funds for fuel reduction treatments, and supported collaborative projects to manage fire in Karuk and Yurok ancestral lands (Lake, 2011). In California and the Pacific Northwest, the USDA Forest Service annually treats more area with understory mechanical thinning than prescribed fire to reduce forest surface fuels (Vaillant and Reinhardt, 2017). Impediments to prescribed fire and fuel reduction include seasonal restrictions on fuel reduction activities for threatened and endangered wildlife, staff reductions associated with the decrease in timber receipts from NWFP mandates, burn restrictions during major wildfire events, and air quality regulations that constrain available burn days (Calkin et al., 2015; Quinn-Davidson and Varner, 2012; Schultz et al., 2018; Stephens et al., 2016; Williams, 2009). However, recent efforts within the USDA Forest Service to increase cross-jurisdictional landscape-scale treatments, known as the 'Shared Stewardship' initiative seek to address several of these constraints (USDA Forest Service, 2018).

Despite these challenges, the Karuk and Yurok Tribes collaborate with the Fire Learning Network (FLN) and other agencies to host annual prescribed fire training exchanges (TREX: Butler and Goldstein, 2010; Harling, 2015; Long et al., 2018; Robbins et al., 2016; Spencer et al., 2015). The FLN is an effort by the USDA Forest Service, US Department of the Interior, and The Nature Conservancy to restore fire-dependent landscapes by engaging in collaborative, community-based planning. On the Yurok reservation, the Cultural Fire Management Council (CFMC) leads efforts to expand cultural burning in partnership with the Yurok Tribe and the California Department of Forestry and Fire Protection (Yurok Tribe, 2015). CFMC is a community-based organization led by Yurok Tribal members that support private and Tribal landowners who seek to conduct cultural burns on their properties by sharing equipment, providing necessary personnel, and submitting permits. The Karuk Tribe is collaborating with the USDA Forest Service, the Orleans-Somes Bar Fire Safe Council, and other community organizations to initiate fuel reduction and cultural burn treatments in their territory through the Western Klamath Restoration Partnership (WKRP; Lake et al., 2018; Long et al., 2018; USDA Forest Service PSW Region, 2018; Vinyeta and Lynn, 2015). The WKRP is composed of NGOs, Tribes, and government agencies that have initiated a pilot project near Somes Bar, CA to apply mechanical and prescribed fire treatments in fire excluded forests. Upon completion, they have proposed to expand these fire treatments across 480,000 ha. (Lake et al., 2018; Long et al., 2018; USDA Forest Service PSW Region, 2018).

Substantial ethnohistorical information exists on the effects of fire on ecocultural resources worldwide (Scherjon et al., 2015; Trauernicht et al., 2015) and in the Pacific Northwest, and California, in particular (Anderson, 2005; Blackburn and Anderson, 1993; Boyd, 1999; Lewis, 1993). However, empirical ecological effects of contemporary fuel reduction treatments on ecocultural resources are not well known, and such studies may serve to inform adaptive and collaborative management projects in American Indian territories (Anderson, 2002; Berkes et al., 2000; Long et al., 2018; Wynecoop et al., 2019). Species-specific studies have demonstrated that prescribed burning improves the densities of blueberries (*Vaccinium* spp., Duchesne and Wetzel, 2004) and reduces insect infestation in tanoak acorns (*Notholithocarpus densiflorus*, Halpern, 2016). Fire has been shown to increase the density and enhance the quality of several plant species (e.g., *Xerophyllum tenax* beargrass, *Muhlenbergia rignes* deergrass, *Anthoxanthum nitens* sweetgrass) used for American Indian basketry resources (Anderson, 1999; Gagnon and Platt, 2008; Griffith et al., 2007; Hart-Fredeluces and Ticktin, 2019; Lathrop and Martin, 1982; Peter et al., 2017; Shebitz et al., 2009; Shebitz and Kimmerer, 2005).

California hazelnut (*Corylus cornuta* Marsh. var. *californica*) is a critically important ecocultural resource for Karuk and Yurok Tribal members. California hazelnut ranges from British Columbia to the southern Sierra Nevada and central coastal mountains of California and extends over ~76% (180,471 km^2) of the NWFP area (Fig. 1B; Little Jr, 1971; Thompson et al., 2015). California hazelnut is a deciduous, multi-stemmed shrub that resprouts vegetatively after disturbance, similar to *Corylus americana* and *Corylus cornuta* var. *cornuta* in central and eastern North America (Buckman, 1964; Pelc et al., 2011). Throughout California hazelnut's range, the nuts are consumed by American Indians (Armstrong et al., 2018; Cuthrell, 2013; Fine et al., 2013; LaLande and Pullen, 1999; Thompson, 1991). Across the Pacific Northwest, California hazelnut stems continue to be used by American Indians for basketry and material culture (Mason and Coville, 1904; Moerman, 1998; Turner, 1998; Zobel, 2002) with similar uses of *Corylus* spp. persisting throughout Europe (Batsatsashvili et al., 2017; Bichard, 2008). The straight and unbranched stems of recently burned hazelnut shrubs are in high demand by California Indians to produce baskets for diverse uses (Fig. 2, Anderson, 1999; Bibby, 2004; Harrington, 1932; Heffner, 1984; Hunter, 1988; Johnson and Marks, 1997; Kallenbach, 2009; Levy, 2005; Mathewson, 2007; O'Neale, 1932; Ortiz, 1998, 1993; Salberg, 2005; Shanks, 2006; Thompson, 1991; Underwood et al., 2003). In 2017, basketweavers reported hazelnut stems selling for $1 per stem, indicating their socio-economic value (T. Marks-Block, *pers. obs.*, 2018). Moreover, the diverse products constructed from these materials reflect their artistry skills, cultural significance, and ancestral history and identity as well as bestow respect for these talented basketweavers (Bibby, 2012; Johnson and Marks, 1997; Mathewson, 1998). One type of basket in high demand is the baby cradle as these cradles remain a central component of child rearing in Northwest California Indian culture (Bibby, 2004). These baskets often require ~300 hazelnut stems to produce and then may be sold for ~$800 dollars (T. Marks-Block *pers. obs.*, 2018).

Based on ethnographic studies, Northwest California Indians such as the Karuk and Yurok reportedly initiated relatively small (< 4 ha)

understory broadcast fires in the summer and fall months every 2–5 years in hazelnut groves to increase concentrations and quality of basketry stems (Anderson, 2005; Busam, 2006; Harrington, 1932; Huntsinger and McCaffrey, 1995; LaLande and Pullen, 1999; Stewart, 2002; Thompson, 1991). As cultural burning diminished due to the enforcement of fire exclusion policies, basketry stems reportedly became scarce because only poor quality gathering areas remained that, in turn, highly constrained basketry production (Bright, 1957; Heffner, 1984; Huntsinger and McCaffrey, 1995; Levy, 2005; Norgaard, 2014; O'Neale, 1932). For example, based upon 43 interviews with basket-weavers in 1929, anthropologist Lila O'Neale reported that:

> "Hazel sticks are conceded by the women of both tribes [Yurok and Karok] to be the best, but the most difficult to procure nowadays. New little shoots from a ground recently burned over are ideal. This statement is followed, however, by the lament that fires cannot be set as they used to be by the old-time weavers, and by the regret that accidental burnings occur seldom in places where they do basket makers any good" (O'Neale 1932:15).

Because of these resource availability challenges, basketweavers and stem gatherers have used permitted techniques to generate hazelnut re-sprouting that serve as substitutes or proxies for cultural burns (F. Lake, *pers obs*; Hunter, 1988).

To evaluate these techniques for potential inclusion into larger-scale fuel reduction management areas, we collaboratively designed a field experiment to compare the efficacy of four practices (Fig. 3) used by Yurok and Karuk Tribal members to increase hazelnut stems for basketry: (1) cutting or the manual coppicing of hazelnut shrubs (Hunter, 1988); (2) pile burning of surface fuels including needle/leaf litter and 1-hour (0.00–0.64 cm diameter) and 10-hour (0.64–2.54 cm diameter) fuels within individual hazelnut shrubs; (3) propane torch burning of individual hazelnut shrubs (Ortiz, 1998); and, (4) prescribed cultural burns set to broadcast, or move through the understory, to top-kill multiple hazelnut shrubs. Among these treatments, we compare and contrast the production of suitable shoots: straight, unbranched basal re-sprouts of hazelnut shrubs (Fig. 2). Then we evaluate if canopy cover, aspect, and the presence of deer browse influence the productivity of basketry stems. Basketry stems were harvested post-treatment and compared and then contrasted by length and diameter with stems harvested independently by two experienced Karuk/Yurok basketweavers from an adjacent broadcast burned site.



Fig. 3. Four hazelnut shrub treatments. (A) Pre- and post-cut treatment. All stems in each shrub were cut to ground level (< 5 cm) to stimulate coppicing, and to mimic mechanical understory clearing and piling for fuel reduction. (B) Pile burn treatment during combustion. Surface fuels (primarily 1-h, 10-h fuels, and surface litter comprised of conifer needles and hardwood/shrub leaves) were placed between hazelnut stems within a shrub to form a burn pile (< 25 cm height). (C) Propane torch burn treatment. Hazelnut shrub stems were burned at ground level to cause bark blistering and stem mortality. (D) Broadcast burn treatment. A fire was set with drip torches to back down-hill and allowed to spread to kill above-ground hazelnut stems.

These treatments and measures were conducted in direct collaboration with Karuk and Yurok basketweavers whose ecological knowledge and harvesting practices informed this study and sampling design (Lake, 2013; McLaughlin and Glaze, 2008). Basketweavers have observed that hazelnut shrubs that grow in areas with relatively greater sun exposure produce extensive lateral branching, thus reducing viable basketry stems post-treatment (Johnson and Marks, 1997; Mathewson, 1998; Ortiz, 1998), but may increase nut production. Basketweavers also report that stem sprouts from coppiced hazelnut are not as pliable as stem sprouts that emerge from burned hazelnut (F. Lake and T. Marks-Block, *pers obs*). While we did not evaluate this stem characteristic, Rentz (2003) demonstrated that burned hazelnut stems contained a greater wood-to-pith ratio than unburned, coppiced hazelnut stems, lending empirical support to basketweavers' observations. Because basketweavers and managers have also reported that deer and elk browse may negatively affect basketry production (Underwood et al., 2003), we also included the presence of this activity in our observations.

Our study combines Indigenous ecocultural and 'western' scientific epistemologies to monitor and manage forests as advocated by American Indian fire and forest managers (Lake et al., 2017; Mason et al., 2012; Mazzocchi, 2006). This integrated participatory approach seeks to identify effective practices for improved ecocultural resource management, such as enhancing both the density and quality of basketry materials (Bussey et al., 2015; Emery et al., 2014; Hummel and Lake, 2015; Mockta et al., 2018).

2. Methods

2.1. Social science methods

To develop an ecological research project focused upon an Indigenous ecocultural resource, we initially drew from Indigenous and anthropological research methods such as participatory and reciprocal study design and observations that serve to foster relationships of trust among academics, Indigenous scientists, and cultural practitioners (Bernard, 2011; Lake et al., 2017; Smith, 1999; Wilson, 2008). We worked with Tribal cultural practitioners and Tribal government staff over several years to integrate ecocultural resource objectives into land management plans. This investment and participation in the community generated trust and led to accountability, reciprocity, and collaboration among researchers and Tribal members (Lake, 2013). The collection of qualitative and quantitative social science data was developed and reviewed iteratively by as the Karuk and Yurok Tribes, who have their own independent research review processes to generate accountability and collaboration with researchers (Karuk Tribe et al., 2017; Sarna-Wojcicki, 2014). These proposals then received approval by our institutional human subject review boards at the Oregon State University and Stanford University.

Sampling design and implementation initially was informed by semi-structured interviews, participant observations and collaborative field work with Karuk and Yurok basketweavers and cultural

practitioners conducted by Lake (2002–2008; Lake, 2007; McLaughlin and Glaze, 2008). Initially, Lake worked closely with key basketweavers to develop research objectives and accountability. Building on collaborations established by Lake, Marks-Block conducted ecological field measurements from 2014 to 2019 of cultural burns (n = 15) for hazelnut stem production supplemented by additional interviews and direct observation of basketry stem gathering with basketweavers (n = 44) that informed the analyses and interpretation of the treatment data.

Our interviews and interactions with basketweavers corroborated that suitable basketry stems were scarce due to fire exclusion (Heffner, 1984; Hunter, 1988; Ortiz, 1998). Interviews also confirmed that in the absence of broadcast burning, basketweavers and friends gathered hazelnut stems from shrubs treated using the three fire treatment proxies (Fig. 3), although the relative efficacy of these treatments remained unclear. Basketweavers also consistently recalled that the departure of supportive USDA Forest Service managers created major set-backs, because they had to re-establish lines of communication with new staff and inform them about their basketry materials and fire treatment needs. Hence, as the National Fire Plan (2001) and the Healthy Forests Restoration Act of 2003 (P.L. 108-148) initiated increased fuel reduction treatments throughout this region (Schoennagel et al., 2009), basketweavers and Tribal members often were not informed about the schedules or locations of understory mechanical treatments and broadcast burns, and thus they missed opportunities to gather hazelnut stems. As a result, basketweavers and collaborators believed that an empirical study on the effects of several fire treatments on hazelnut shrubs could assist managers in incorporating Indigenous resource objectives into their plans.

To evaluate what basketweavers consider to be stems of basketry quality, we attended over 50 basketry classes and workshops supported by the Karuk and Yurok Tribes where we received direct instruction from basketweavers. We also observed over 50 independent hazelnut stem gathering trips to describe stem gathering practices. In these settings, all basketweavers stated that stems must be straight, unbranched, and free of insect intrusions or bark blemishes. Moreover, a wide range of both stem lengths and diameters are used depending on the type and size of basket they are weaving. Stems having lengths (e.g., 10–50 cm) can be used to weave earrings, tobacco pouches, or baby rattles, whereas longer stems (e.g., 50–100 cm) are suitable for producing storage baskets or baby cradles. Small diameter stems (1–3 mm) are preferred by basketweavers conducting fine weaving, although the tapered tips of long stems with 4–12 mm diameters may be used for similar purposes. Other basketweavers may select wide stems (5–12 mm diameter) for fish traps, storage baskets, or baby cradles.

As participant observers in both material gathering and production, we documented basketweaver gathering site preferences and also constraints such as gathering in marginal locations (e.g., clear cuts and mechanically thinned roadsides). Basketweaver Mrs. Verna Reece stated: “it’s kind of hard to get burn[ing done]…When logging…they just burn [slash]…so it wasn’t that good of material…Out in the open…[hazel stems are] kinda stalky, fat. It’s different when you have…a canopy over it. It kind of reaches for the sun and kinda grows long, slender” (Lake, 2007: 600).

From these basketweaver observations, we then broadly defined suitable quality basketry stems, and focused our efforts on measuring the length and diameters of stems produced from multiple treatments under a suite of biophysical conditions. Hazelnut morphology, structural integrity, autecology, and basketry use criteria garnered from basketweavers informed the sampling design, treatments, and measurements used here (Fig. 4).



Fig. 4. Karuk basketweavers Ms. Janet Morehead (left) and Ms. Lillian Rentz (right), peeling and evaluating the quality of hazelnut stems gathered from the treatment area.

2.2. Experimental methods

2.2.1. Study area

Treatments were conducted on a 10 ha forest with abundant hazelnut shrubs on a privately owned parcel that adjoins the Orleans Ranger District of the Six Rivers National Forest in the Klamath River watershed. The study location is within the 1919 km^2 ancestral territory of the Yurok Tribe and the 2728 km^2 ancestral lands of the Karuk Tribe (Fig. 1A; Waterman 1920, Baumhoff 1963). In Karuk territory, the federal government did not establish a reservation, leaving merely 3.83 km^2 of Karuk trust lands in their ancestral territory, with the remainder largely under the jurisdiction of the Klamath and Six Rivers National Forests and scattered private homesteads (Fig. 1A; Davies and Frank, 1992; Norgaard, 2014; US Census Bureau, 2017). As a result, Karuk Tribal members and management agencies must navigate the USDA Forest Service claims on their ancestral territory and have limited options to expand their land base through the acquisition of private land holdings. In Yurok territory, multiple overlapping jurisdictions occur including Redwood National Park (192 km^2, Underwood et al., 2003) and Six Rivers National Forest (577 km^2) outside of the reservation established by the federal government. The reservation is located along a one mile buffer from the Klamath River’s estuary to ~80 km upriver (~225 km^2; Huntsinger and Diekmann, 2010). However, 106 km^2 (47%) of the reservation is under private timber company ownership (Yurok GIS Program, 2015). Consequently, the Yurok Tribe must either coordinate or interact with multiple actors within their ancestral territory, but they presently have greater options for acquiring private properties than the Karuk Tribe.

Douglas-fir (*Pseudotsuga menziesii*) and mixed hardwoods (e.g., *Arbutus menziesii*, *Quercus kelloggii*, *Notholithocarpus densiflorus*, *Acer macrophyllum* and *Umbellularia californica*) comprise the forest overstory at the study site. In California, hazelnut is an understory, multi-stemmed shrub (< 6 m ht in this study region) that typically occurs below 2,100 m above sea level on mesic sites with well-drained soils (Fryer, 2007). Relatively low-intensity fires that historically scarred canopy trees every 10–17 years (Crawford et al., 2015; Skinner et al., 2018; Taylor and Skinner, 1998; Wills and Stuart, 1994) often ‘top-kill’ understory hazelnut stems, which is when above-ground plant tissues are killed, while below-ground plant tissues remain alive (Anderson, 1999).

2.2.2. Fire proxy treatments and prescribed burning of hazelnut shrubs

We replicated fire proxy treatments used by Karuk and Yurok Tribal members to mimic prescribed fires that could be implemented by forest managers at fuel reduction sites with hazelnut shrubs. These fire proxy treatments were: (A) cutting all stems in each shrub to ground level (< 5 cm) as a means to stimulate coppicing, and to mimic mechanical understory clearing and piling for fuel reduction; (B) piling surface fuels

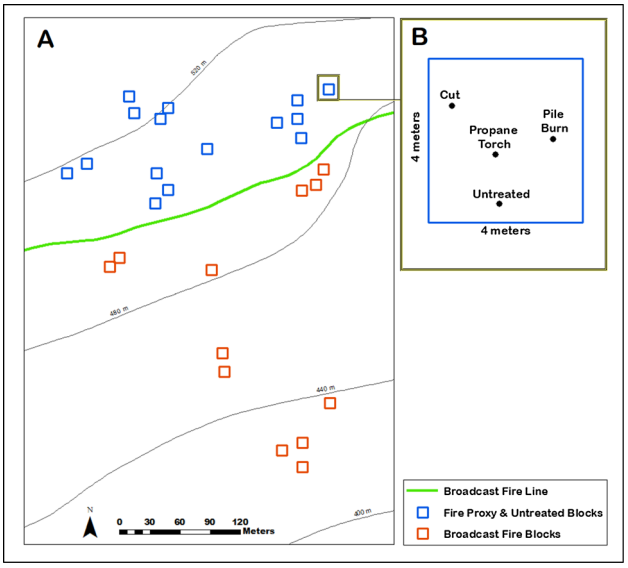


Fig. 5. Study site with treatment block design. (A) Spatial distribution of treatment blocks. The broadcast fire line divides the 15 fire proxy and untreated blocks from the 12 broadcast fire treated blocks. Contour lines depict the elevation and aspect at the site. (B) Schematic block (16 m^2) with four hazelnut shrubs (filled circles) that received fire proxy treatments.

(primarily 1-h, some 10-h fuels, and adjacent surface litter consisting of needles/leaves) between hazelnut stems to form a small pile (< 25 cm height) that was subsequently burned; and, (C) applying a propane torch flame near ground level to hazelnut shrub stems until stems blistered indicating stem mortality (Fig. 3). The prescribed fire treatment, referred to here as a 'broadcast' fire treatment, was allowed to spread across multiple hazelnut shrubs (Fig. 3D), while all other fire treatments were constrained to individually targeted shrubs.

We employed a randomized block design to establish 27 stratified blocks (block = 16 m^2) that included each treatment, except for the broadcast fire treatment (Fig. 5A). Blocks were selected if they contained at least four hazelnut shrubs spaced > 1–2 m apart with similar dimensions (e.g., shrub height, total stems, and stem diameter; Fig. 5B). Subsequently, total stems and the potential 'usable' basketry stems were counted within each hazelnut shrub and shrub height was measured over a 15 day period preceding the implementation of treatments on May 14, 2008. Based on basketweaver selection criteria, basketry stems were defined as straight stems > 10 cm long without branching. Shrub height as well as the slope, aspect, and canopy cover were recorded within each block. Slope was measured using a Suunto PM-5/360 PC Clinometer, aspect was recorded using a compass, and canopy cover was measured four times with a spherical concave densiometer at each cardinal direction above each shrub, to obtain a mean value (%) for each individual (Fiala et al., 2006; Lemmon, 1956). Aspects between 135° and 225° were classed as southern (n = 56) and aspects between 45° and 134° were classed as eastern (n = 49). Canopy cover ≤50% (n = 12) was categorized as 'low', cover ≥51% and < 70% as 'medium' (n = 63), and ≥70% as 'high' (n = 30). After our pre-treatment surveys, we randomly treated three of the shrubs within each block with a fire proxy and one shrub was designated as an untreated control (Fig. 5B).

Historically in Karuk and Yurok territory, cultural burns primarily were applied in the fall months (Harrington, 1932; O'Neale, 1932; Stewart, 2002; Thompson, 1991) with some occurring in spring months (Halpern, 2016; Lake, 2007). Given the unpredictable availability of broadcast burn conditions, the experimental and sampling design was conservative with all three fire proxy treatments and controls replicated as we were unsure whether broadcast burns could be included in this study. Fortunately, suitable prescribed fire conditions occurred on October 28, 2008 and a broadcast burn was applied to ~5 ha affecting 12 of the 27 treatment blocks (Fig. 5A). Fire lines were established to preserve ~50% of the previously treated blocks in order to compare the intact fire proxy treatments to the broadcast burn treatment (Fig. 5A). A backing fire with strip ignitions (3–5 m apart) was set with drip torches, and the fire burned from 14:20 to 16:30 h (Fig. 3D). Temperature ranged from 69.5° F to 75.0° F, relative humidity spanned 39.5–48.0% and the Yurok RAWS station (9 km from site) recorded fuel moistures between 7.4% and 12.3%. The fifteen blocks with three fire proxy treatments and a control that were not affected by the prescribed broadcast fire were then re-surveyed the following year (May 2009) when stems were suitable for harvest (n = 60 shrubs). Only one of the fifteen pile burned shrubs died. After a full growing season (18 months post-burn; April 2010), we re-surveyed 45 out of 48 shrubs in the 12 broadcast burned blocks as three tagged shrubs could not be re-located. Post-treatment measurements included the density of basketry stems, total live stems, and the presence of deer browse within each shrub.

2.2.3. Hazelnut stem measurements

On May 8, 2009, we harvested basketry stems (n = 604) produced from 50 shrubs in the cut (n = 233), propane (n = 205), pile burn (n = 148), and control (n = 18) treatments. Stems were cut < 5 cm from the ground, labeled, and then bark was removed to prepare the stem for weaving. Stem diameter was measured with a digital caliper and stem length with a meter tape. These stems harvested from the fire proxy treatments were then compared to hazelnut stem collections gathered on May 3, 2008 by two experienced Karuk/Yurok basketweavers (n = 396 and n = 73) from an earlier prescribed broadcast burn (October 2006) adjacent to the experimental study site.

2.2.4. Data analyses

To evaluate the production of post-treatment basketry stems in each shrub among the different treatments, we developed a negative-binomial generalized linear mixed model (GLMM) using the glmmTMB package in R (Magnusson et al., 2017; R Core Team, 2014). Block was set as a random effect, and treatment, aspect class, slope, the presence of deer browse, pre-treatment total stems, and canopy cover classes were included as covariate fixed effects. Pre-treatment total stems were also included as a fixed effect to evaluate if shrub size affected the quantity of post-treatment basketry stems. We used Type III Wald Chi Square tests to perform backwards selection to find the model of best fit. To analyze the differences within categorical variables that showed significance in the GLMM, we generated Estimated Marginal Means (EMMs) to address imbalances in the study design (e.g., 45 broadcast shrubs versus 15 pile burned shrubs) using the emmeans package and compared 95% confidence intervals using the Tukey and Dunnett methods (Lenth, 2018).

To analyze the length and diameter of stems gathered from the fire proxy treated and control shrubs, we developed two gamma distributed GLMMs using the glmmTMB package. Each shrub was set as a random effect in the model, and treatment, pre-treatment shrub height, aspect class, and canopy cover class were treated as covariate fixed effects. We generated models of best fit using backwards selection with Type III Wald Chi Square tests, and produced EMMs to analyze differences in stem lengths and diameters within categorical variables using the Tukey method. Stem length and diameter distributions from our treatment samples were compared with the collections of two basketweavers using a multiple comparison Wilcoxon Rank Sum test (Kabacoff, 2015).

3. Results

The 86 treated hazelnut shrubs produced a total of 923 basketry stems (10.73 per shrub ± 1.02), whereas the 19 control shrubs produced only 20 basketry quality stems (1.05 per shrub ± 0.45). Within the broadcast burned blocks, six shrubs had died while four shrubs were

Table 1
Effects of the fire proxy and broadcast burn treatments (e.g., cut, pile burn, propane, broadcast) on hazelnut basketry stem production compared with the untreated control. Estimated Marginal Mean (EMM) is back-transformed from the log scale and averaged over the values of aspect and canopy classes. The contrast to control ratio is the treatment EMM to untreated control EMM (1.54, SE = 0.60). The confidence intervals, *t*-statistic and *p*-values were generated using the Dunnett method.

Treatment	n	EMM	Contrast to control ratio	Contrast SE	CI	*t* ratio	*p* value
Cut	15	6.45	4.19	1.87	1.38–12.7	3.22	0.0066
Pile Burn	15	10.98	7.13	3.05	2.46–20.7	4.59	0.0001
Propane	15	15.45	10.05	4.16	3.57–28.2	5.57	< 0.0001
Broadcast	41	11.54	7.50	3.07	2.70–20.9	4.92	< 0.0001

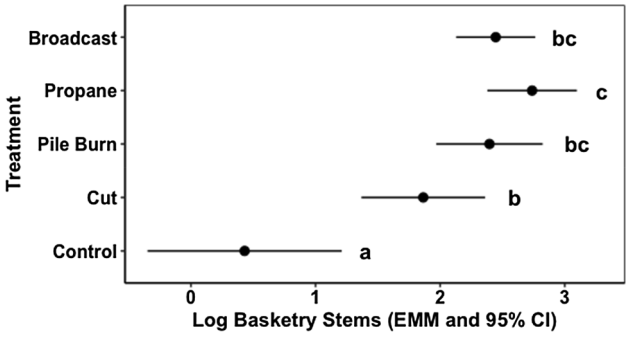


Fig. 6. Fire proxy treatment, broadcast burn, and untreated control effects on hazelnut basketry stem production. Estimated marginal means (EMM) of basketry stems with 95% confidence intervals (log scale) within the control and four fire proxy treatments. Letters indicate significant differences between treatments ($p < 0.05$).

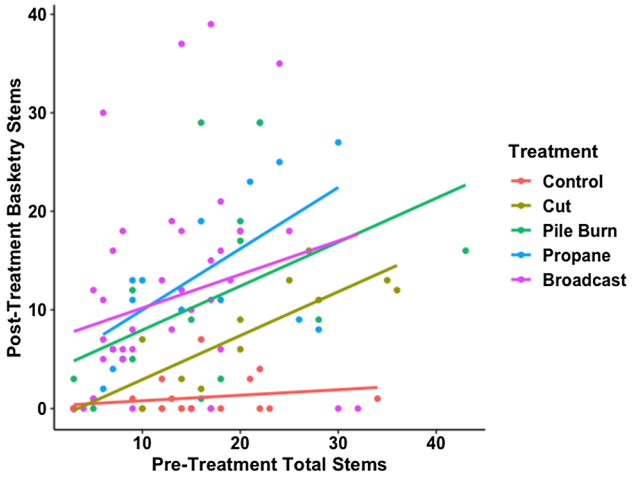


Fig. 7. Pre-treatment total stems (shrub size) positively affect post-treatment basketry stem production. Pre-treatment total stems and post-treatment basketry stems are plotted by treatment with lines of best fit determined by ordinary least squares regression.

unburned and were then included in the untreated (control). All hazelnut shrubs that were treated with either pile burning, propane torching, and, or a prescribed broadcast burn increased the production of basketry stems from 7 to 10-fold in comparison with the shrubs in the untreated controls ($p < 0.001$, Table 1, Fig. 6). However, the quantity of basketry stems per shrub produced by the cut treatment (EMM = 6.5, SE = 1.61) was only 4-fold greater than the untreated controls (EMM = 1.54, SE = 0.60, $p = 0.006$, Table 1). The EMM of the cut treatment was reduced significantly when compared with the EMM of the propane treatment (EMM = 15.45, SE = 2.79, $p = 0.025$, Fig. 6). Basketry stems among the propane, pile burn (EMM = 10.98, SE = 2.36), and broadcast (EMM = 11.54, SE = 1.84) treatments did not exhibit significant differences (all = $p > 0.25$, Fig. 6).

Pre-treatment total stems ($p < 0.001$), aspect class ($p < 0.01$), and canopy cover class ($p < 0.05$) imparted significant effects on basketry stem production in hazelnut shrubs (Wald Type III Chi Square test; Table 2). Shrub size (pre-treatment total stems) and basketry stem production exhibited a strong positive relationship ($p < 0.001$, Fig. 7).

Table 2
Variables affecting basketry stems within study blocks. Results of a Wald Type III Chi Square test on the significance of the treatments (control, cut, pile burn, propane, broadcast), pre-treatment total stems, aspect class, and canopy class on basketry stems generated from a negative-binomial generalized linear mixed model (GLMM). Aspects between 135° and 225° were classed as southern ($n = 56$) and aspects between 45° and 134° were classed as eastern ($n = 49$). Canopy cover ≤50% ($n = 12$) was categorized as 'low', cover ≥51% and < 70% as 'medium' ($n = 63$), and ≥70% as 'high' ($n = 30$). Two additional biophysical variables (deer browse, slope) did not exhibit strong effects on basketry stems ($p > 0.05$) and were removed from the model. Hazelnut shrub blocks ($n = 27$; 16 m^2) are set as random effects.

Fixed effect	χ^2	Df	$p(>\|\chi^2\|)$
Treatment	35.38	4	< 0.001
Pre-treatment total stems	23.11	1	< 0.001
Aspect class	6.99	1	0.008
Canopy class	7.14	2	0.028

Shrubs within eastern aspect classes produced 1.73-fold more basketry stems ($n = 49$, EMM = 9.48, SE = 1.18) than those in southern aspect classes ($n = 56$, EMM = 5.47, SE = 1.19, $p < 0.01$). Within the canopy cover classes, the shrubs within the medium canopy cover class ($n = 63$) produced a 5.08 EMM (SE = 0.86) of basketry stems, whereas shrubs within the high canopy cover class ($n = 30$) produced 1.84-fold greater basketry stems (9.36 EMM, SE = 1.75, $p = 0.03$) than the medium canopy cover class. Shrubs within the low canopy class ($n = 12$) had a 7.87 EMM (SE = 2.00) and did not differ significantly from shrubs in the high ($p = 0.83$) or medium canopy cover classes ($p = 0.27$). Within the initial negative-binomial GLMM, deer browse and slope did not impart significant effects on basketry stem production ($p > 0.05$).

Basketry stem lengths gathered from the treated and control shrubs ranged from 11.00 to 118.60 cm (μ = 43.24, SE = 0.83) and stem diameters ranged from 0.53 to 5.76 mm (μ = 2.30, SE = 0.04, Fig. 8). Basketweaver1 gathered stem lengths ranging 14.10–81.20 cm (μ = 38.97, SE = 0.58), and Basketweaver2 gathered stem lengths ranging 27.80–73.40 cm (μ = 47.76, SE = 1.29, Fig. 8B). From basketweavers' sourced materials, stem diameter ranged from 0.96 to 4.11 mm (μ = 2.13, SE = 0.03) and 1.64–4.45 cm (μ = 2.89, SE = 0.07), respectively (Fig. 8A). The distribution of basketry stem lengths and stem diameters gathered by Basketweaver2 were greater than those gathered by Basketweaver1 as well as those stems harvested from the fire proxy treatment blocks and broadcast burn (Wilcoxon rank sum; $p < 0.001$, Fig. 8). However, similar stem length and diameter distributions were recorded from stems harvested in the fire proxy treatment blocks and broadcast burn as well as those gathered by Basketweaver1 ($p > 0.05$).

Results from the gamma GLMMs showed that pre-treatment shrub heights and aspect classes had a significant affect on basketry stem lengths and diameters from treated and control shrubs. A strong positive relationship was detected between pre-treatment shrub height and

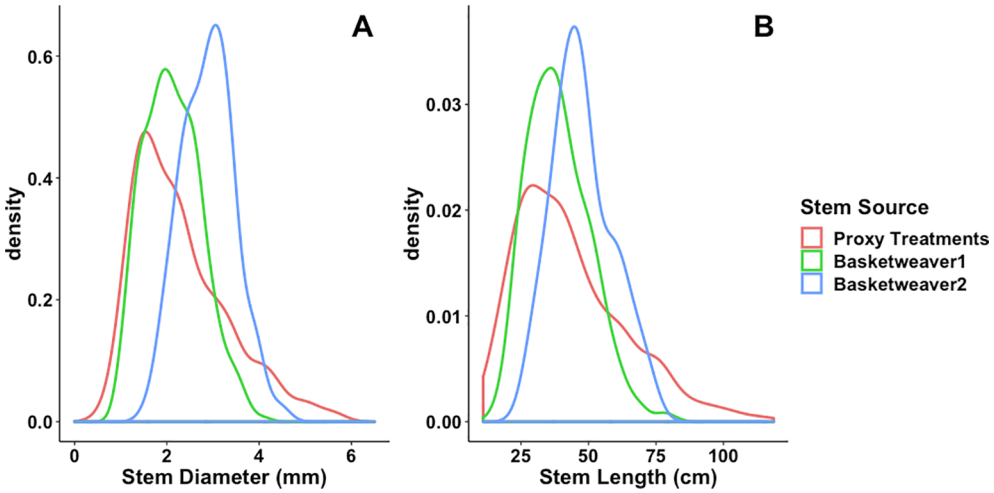


Fig. 8. Treatment effects on hazelnut basketry stem size distributions compared with basketweavers' harvests. Samples were gathered from 46 treated and 4 untreated shrubs (n = 604), and collected by Basketweaver1 (n = 396) and Basketweaver2 (n = 73). Fire proxy treatment and control stem size distributions did not differ significantly from the distributions gathered by Basketweaver1 (Wilcoxon Rank Sum; p = 0.5). However, the stem size distributions from Basketweaver2 differed significantly from all treatments and Basketweaver1, but based on a relatively small sample size (Wilcoxon Rank Sum; p < 0.001). (A) Stem diameter (mm) and (B) stem length (cm). Distributions shown as kernel density plots.

post-treatment stem lengths and diameters (p < 0.001). Shrubs within the southern aspect class produced both shorter length (EMM = 34.4 cm, SE = 1.62) and smaller diameter (EMM = 1.87 mm, SE = 0.08) stems post-treatment than eastern aspects (diameter EMM = 2.52 mm, SE = 0.15; length EMM = 47.6 cm, SE = 2.79, p < 0.001). Between the treated and control shrubs, basketry stem length did not differ significantly. However, the stem diameters harvested from the pile burn (EMM = 2.00 mm, SE = 0.12) and cut (EMM = 2.49 mm, SE = 0.127) treatments were significantly different (p = 0.02). Propane treated stem diameters (EMM = 2.14, SE = 0.11) were nonsignificant in the model (p = 0.15). No discernable effects of canopy cover classes on stem diameter or length were detected.

4. Discussion

The application of three fire proxy treatments and a prescribed broadcast fire treatment indicate that all treatments generated 4–10-fold increases in basketry quality hazelnut stems when compared with the untreated hazelnut shrubs. Untreated (control) hazelnut shrubs contained only 1.54 ± 0.60 basketry stems per shrub, and thus, are deemed marginal, or too limited in value for California Indian basketweavers (Anderson, 1999). Thus, broadcast fires or substitute treatments are required to generate basketry quality stems.

Basketweavers prefer cultural burns to treat hazelnut shrubs for basketry because they efficiently top-kill many hazelnut shrubs relatively rapidly, and thus, create improved gathering rates for basketweavers. Cultural burns also may have positive effects upon additional ecocultural species and may reduce understory fuels. Although our broadcast burn treatment was effective at producing basketry stems, ~15% of broadcast burned hazelnut shrubs died, and thus reduced the basketry stems expected from this treatment. While we did not assess pre-burn surface fuel loads before ignition, the landowner had not previously conducted fire treatments in the broadcast burn area, suggesting that surface fuel loads may have been relatively higher than in a historically, and thus, more frequently burned forest. Decades of fire exclusion increase surface fuel loadings that generate increased fire intensities and shrub mortality during prescribed burns (Kauffman and Martin, 1990; Thaxton and Platt, 2006). In the absence of broadcast burns, pile burning and propane torch burning treatments also are effective methods to top-kill hazelnut shrubs. When creating piles within hazelnut shrubs practitioners may avoid piles with high fuel loads and inordinate fire residence time to prevent shrub mortality resulting from excessive direct heat (Siefkin et al., 2002). Only ~7% of monitored shrubs died from our surface fuel piles when they were composed of 1-h, 10-h, and surface litter fuels with height limited to < 25 cm, but establishing fuel load and fire residence time limits or guidelines through additional research would be useful especially when expanding these applications over large areas.

In contrast to our cutting treatment that focused solely of hazelnut stems, mechanical cutting is widely used by agencies and landowners to create shaded fuel breaks (65–400 m wide) and is typically paired with the pile burning of cut woody debris (Agee et al., 2000; Rhoades and Fornwalt, 2015; Vaillant and Reinhardt, 2017). When burned hazelnut shrubs are unavailable or insufficient basketweavers will gather basketry stems opportunistically within these mechanically created fuel breaks if suitable coppiced hazelnut shrubs occur. However, basketweavers report reduced stem strength or pliability from mechanical treatments compared to burn treatments, which is supported by lower wood-to-pith ratios in these stems (Rentz, 2003). The lower stem quality and reduced expected stem density from cut treatments considerably reduces basketweavers' preference for this treatment.

The four environmental variables we measured (e.g., slope, deer browse, canopy cover, and aspect) appear to explain some of the variation observed in hazelnut basketry stems production. Deer browse occurred on only five of the 105 hazelnut shrubs measured, and thus, in this particular case deer browse was inconsequential. Yet, deer herbivory typically occurs at the axil tip of new basal shoots. Subsequently, the hazelnut shrub typically produces two or more lateral branches below where the apical bud and leaves were eaten, producing an unsuitable basketry stem. Thus, if deer or other ungulate browsers are abundant (e.g., at sites further from private residences), browse could become a major factor in the reduction of basketry stems.

Hazelnut shrubs in the 'high' canopy cover class produced 1.84-fold more basketry stems than those in the 'medium' canopy cover class. These results support Karuk and Yurok basketweavers' experience and observations. Areas with relatively low canopy cover (i.e., 0–20%) and increased light conditions stimulate lateral branching within hazelnut basal resprouts, reducing the potential density of basketry quality stems (Johnson and Marks, 1997; Lake, 2007; Ortiz, 1998). However, the shrubs within the 'low' canopy cover class produced highly variable basketry stems whose EMM was 1.55-fold greater than shrubs in the 'medium' canopy cover class although the EMM did not differ significantly. Only four shrubs in the low canopy cover class had 30% cover, and the remaining eight shrubs in that class were 50% cover, which reflects limitations in both our sampling effort and truncated range of measured canopy cover (30–85%) within a 10 ha sampled area. Given that southern aspects in the northern hemisphere are exposed to additional solar radiation than eastern aspects, shrubs with southern exposures (EMM = 5.48) produced significantly fewer basketry stems than those in eastern aspects (EMM = 9.48, Barbour et al., 1987: 341). Overall, additional sampling of shrub responses to treatments across the full aspect range would improve these analyses and

our understanding.

Plant branching and architectural responses to sunlight are exceptionally diverse and show phenotypic plasticity (Valladares and Niinemets, 2007). In unburned and non-coppiced temperate deciduous understory trees and shrubs, lateral branching can be stimulated by increased light conditions (Bonser and Aarssen, 1994; Canham, 1988; Charles-Dominique et al., 2012; Hamelin et al., 2015; Pickett and Kempf, 1980). California hazelnut appears to change its plant architecture from a sympodial form in full sun to a monopodial form under forest canopies much like the multi-stemmed shrub, *Rhamnus cathartica* (Charles-Dominique et al., 2012). However, more detailed morphological measurements are required to confirm these hazelnut architecture forms.

Aspect class also affected stem length and diameter in the GLMMs analyses. Stems measured from eastern aspects were 1.38-fold longer and 1.35-fold wider compared with those in southern aspects. These results align with basketweaver knowledge that shrubs with full sun exposure produce shorter stems than those under canopy cover. Similarly, the Mediterranean shrub *Arbutus unedo* has been shown to produce taller resprouts post-fire when growing in northern and eastern aspects compared to southern and western aspects (Konstantinidis et al., 2006). However, our observed decrease in viable basketry stems in southern aspects and medium canopy cover should not be misconstrued to suggest that burning should be limited under these site conditions because shrubs under these conditions still produce at least a 5-fold increase in basketry stems as untreated shrubs.

Treatments did not have a detected effect on stem length. However, the cut treatment produced 1.25-fold greater stem diameters than the pile burn treatment. Cut treatments may not induce as much physiological stress or loss of stored energy as compared with burning treatments, and thus, the shrub may have sufficient resources to produce more robust stems with greater diameter. Several studies have found that high severity fires reduce shrub resprouting vigor and biomass compared with low severity fires and cutting treatments (Clarke et al., 2013; Fernández et al., 2013a; Keeley, 2006; Lloret and López-Soria, 1993), however other studies have found that severity does not correlate with resprout vigor in other shrub species (Drewa et al., 2002; Fernández et al., 2013b; Keeley et al., 2008).

Stem diameter and stem length distributions harvested from the treated and control shrubs ($n = 604$), were similar to those harvested from a broadcast burn by Basketweaver1 ($n = 396$). Thus, our fire proxy and broadcast burn treatments appeared to produce stem qualities that are preferred by basketweavers. However, Basketweaver2 harvested a distinctive set of stems. Admittedly, this stem sample from Basketweaver2 is relatively limited ($n = 73$) when contrasted with our treatments and Basketweaver1. Most importantly, basketweavers reported that some basketry projects may require different sets of stem diameters and lengths. Therefore, basketweavers' aims must be considered when comparing hazelnut stem harvesting activities.

Our results demonstrate that expanding the area and frequency of targeted understory fire-based forest treatments on private, public and Tribal lands in the Pacific Northwest and California would generate greater availability and distribution of basketry hazelnut stems that are currently limited in supply and in high demand (Baldy, 2013; Long and Lake, 2018; Ortiz, 1993). Small-scale (≤ 10 ha) application of these fire proxy treatments appears quite feasible both for private landholders or on public lands that would require minimal permitting as well as limited labor and low material costs. The constraints associated with prescribed and cultural burns, such as the limited burning season and increased liability concerns in close proximity to residences within the Wildland Urban Interface, do not necessarily apply to these fire proxy treatments because they can be conducted when prescribed burning conditions are risky or biophysically not possible (e.g., either elevated or low dead surface fuel moisture). Due to these and other constraints, the USDA Forest Service currently is able to implement understory mechanical fuel reduction treatments across a greater area than broadcast burning to reduce fuels in California and the Pacific Northwest (Vaillant and Reinhardt, 2017). Yet, the three fire proxy practices examined here appear to be highly compatible for integration into larger-scale USDA Forest Service, or other fuel treatment programs (≥ 10 ha), and likely would require only minor adjustments to current understory mechanical fuel reduction practices to meet these additional Tribal ecocultural objectives. For example, if the woody debris from these understory mechanical treatments are pile burned, hazelnut burn piles (< 25 cm) or propane torching could be incorporated into this fuel reduction activity, increasing hazelnut stem productivity. Further, hazelnut stems could be included for removal in mechanical understory thinning treatments, if they were initially excluded from the prescription. While Tribal members prefer broadcast burning for ecocultural resource production, they recognize that mechanical understory treatments are necessary to address decades of fire exclusion, and prepare sites for broadcast burning in the near future (USDA Forest Service PSW Region, 2018). If areas of high hazelnut shrub densities are either known or identified in consultation with Tribes and basketweavers, and align with fuel reduction objectives, the subsequent production of basketry stems from mechanical treatments would provide additional benefits to the fuel reduction value of this treatment. Given that hazelnut is distributed across 75% of the NWFP area, limited efforts are required to identify these suitable areas (Long et al., 2018).

Policies that support Tribal consultation within public land agencies offer effective opportunities for increased and effective collaborations and communication in forest management (Bussey et al., 2015; Dockry et al., 2017; Donoghue et al., 2010; Lake et al., 2017). Since this initial experimental study was conducted, prescribed burning and fuel treatments have expanded throughout northwest California, largely as a result of inter-governmental and community partnerships that aim to manage public, Tribal, and private lands (Harling, 2015; Long et al., 2018; USDA Forest Service PSW Region, 2018; Yurok Tribe, 2015).

Throughout this study, we sought to incorporate Indigenous knowledge and participation with 'western' scientific approaches to support these expanding collaborative efforts among Tribal governments and public land agencies. Fire exclusion policies forced California Indian communities and forest managers to curtail their routine cultural and prescribed burning practices. Despite these policies, Karuk and Yurok basketweavers retained their knowledge, maintained their practices and, most importantly, developed several innovative techniques to replicate fire's effects on hazelnut to produce essential basketry materials. To support their efforts, we quantified their hazelnut fire treatment outcomes with the aim to inform managers of their efficacy and material importance, to facilitate increased forest access, and to reduce bureaucratic processes required for Tribal members who seek to employ these fire proxy treatment methods and broadcast burns. Moreover, we encourage efforts to explore creative applications that aim to incorporate these hazelnut fire proxy practices within government-led understory mechanical fuel thinning and large-pile burning treatments. Through such collaborative processes, basketweavers and Tribes may be able to receive financial and logistical support, and, most importantly, recognition and respect for their priorities and experience in managing hazelnut as well as other critical ecocultural resources.

Declaration of Competing Interest

The authors declare no competing interests.

Acknowledgements

We truly appreciate the Karuk and Yurok Tribal Councils for their permission and continuing support to conduct this work on their lands and within their communities. Tribal GIS programs provided mapping data resources. The Orleans-Somes Bar Fire Safe Council, Ben Riggan, and the Karuk Indigenous Basketweavers graciously offered field assistance with burning activities. Our research design benefited

immeasurably from the critical input and generous involvement of Karuk and Yurok basketweavers and gatherers: Elizabeth Azzuz, Laverne Glaze, Chook-Chook Hillman, Lisa Hillman, Robert McConnell, Robert McConnell Jr., Kathy McCovey, Janet Morehead, Bertha Peters, Maggie Peters, Verna Reece, Lillian Rentz, Margo Robbins, Brittany Souza, and Bill Tripp. For their efforts in developing collaborations that facilitated this project, we thank Rebecca Bliege Bird and Douglas Bird. Theresa Alves and Rose Leonard (USDA Forest Service PSW research station Redding lab) assisted with preliminary data analyses. We thank Nels Johnson (USDA Forest Service PSW research station) for providing invaluable statistical contributions. Stanford IRB supported with human subjects approvals (#33064). Two anonymous reviewers provided constructive feedback and suggestions that greatly improved this manuscript.

Financial funds instrumental in the initial development of this project were received from the United States National Science Foundation (NSF)'s Coupled Natural and Human Systems grant (DEB-1232319) to Rebecca Bliege Bird and Curran at Stanford University. For this project and ongoing collaborative programs with the Tribes, Curran and Marks-Block appreciate the financial support from the United States Joint Fire Science Program (#L17AC00214) and NSF Doctoral Dissertation Improvement Grant (1657569). Marks-Block received additional support from a NSF Graduate Research Fellowship (DGE-114747), Stanford's Department of Anthropology, VPGE Diversity Dissertation Research Opportunity, and School of Humanities and Sciences Community Engagement grant.

All opinion, findings, and conclusions or recommendations expressed here are those of the authors and do not necessarily reflect the views of the NSF, USDA Forest Service, or Tribes.

References

Agee, J.K., Bahro, B., Finney, M.A., Omi, P.N., Sapsis, D.B., Skinner, C.N., Van Wagtendonk, J.W., Weatherspoon, C.P., 2000. The use of shaded fuelbreaks in landscape fire management. For. Ecol. Manage. 127, 55–66.

Aldern, J.D., Goode, R.W., 2014. The stories hold water: Learning and burning in North Fork Mono homelands. Decolonization Indig. Educ. Soc. 3, 26–51.

Anderson, M.K., 2018. The use of fire by Native Americans in California. In: van Wagtendonk, J., Sugihara, N.G., Stephens, S.L., Thode, A.E., Shaffer, K.E., Fites-Kaufman, J. (Eds.), Fire in California's Ecosystems. University of California Press, Berkeley, pp. 381–397.

Anderson, M.K., 2005. Tending the wild: Native American Knowledge and the Management of California's Natural Resources. University of California Press, Berkeley, California.

Anderson, M.K., 2002. An ecological critique. In: Stewart, O. (Ed.), Forgotten Fires: Native Americans and the Transient Wilderness. University of Oklahoma Press, Norman, OK, pp. 37–64.

Anderson, M.K., 1999. The fire, pruning, and coppice management of temperate ecosystems for basketry material by California Indian tribes. Hum. Ecol. 27, 79–113.

Armstrong, C., Dixon, W., Turner, N., 2018. Management and traditional production of Beaked Hazelnut (k'áp'xw-az', Corylus cornuta; Betulaceae) in British Columbia. Hum. Ecol. 46, 547–559.

Baldy, C., 2013. Why we gather: traditional gathering in native Northwest California and the future of bio-cultural sovereignty. Ecol. Process. 2, 1–10.

Barbour, M.G., Burk, J.H., Pitts, W.D., 1987. Terrestrial Plant Ecology, 2nd ed. Benjamin/Cummings, San Francisco, California.

Batsatsashvili, K., Mehdiyeva, N., Fayvush, G., Kikvidze, Z., Khutsishvili, M., Maisaia, I., Sikharulidze, S., Tchelidze, D., Aleksanyan, A., Alizade, V., 2017. In: Corylus avellana, L., Corylus Colurna, L., Bussman, R.W. (Eds.), Ethnobotany of the Caucasus. Springer, New York, pp. 225–232.

Baumhoff, M., 1963. Ecological determinants of aboriginal California populations. Am. Archaeol. Ethnol. 49, 155–236.

Berkes, F., Colding, J., Folke, C., 2000. Rediscovery of traditional ecological knowledge as adaptive management. Ecol. Appl. 10, 1251–1262.

Bernard, H.R., 2011. Research Methods in Anthropology: Qualitative and Quantitative Approaches. Rowman Altamira, Lanham, MD.

Bibby, B., 2012. Essential Art: Native Basketry from the California Indian Heritage Center. Heyday Press, Berkeley, California.

Bibby, B., 2004. Precious Cargo: California Indian Cradle Baskets and Childbirth Traditions. Heyday Press, Berkeley, California.

Bichard, M., 2008. Baskets in Europe. Fyfield Wick Editions, Abingdon, UK.

Blackburn, T.C., Anderson, M.K., 1993. Before the Wilderness: Environmental Management by Native Californians. Ballena Press, Menlo Park, CA.

Bonser, S.P., Aarssen, L.W., 1994. Plastic allometry in young sugar maple (Acer saccharum): adaptive responses to light availability. Am. J. Bot. 81, 400–406.

Boyd, R., 1999. Indians, Fire, and the Land in the Pacific Northwest. Oregon State University Press, Corvallis, OR.

Bright, W., 1957. The Karok Language. University of California Press, Berkeley, California.

Buckman, R.E., 1964. Effects of prescribed burning on hazel in Minnesota. Ecology 45, 626–629.

Busam, H., 2006. Characteristics and Implications of Traditional Native American Fire Management on the Orleans Ranger District, Six Rivers National Forest. M.A. Thesis. California State University, Sacramento.

Bussey, J., Davenport, M.A., Emery, M.R., Carroll, C., 2015. "A lot of it comes from the heart": The nature and integration of ecological knowledge in tribal and nontribal forest management. J. For. 114, 97–107.

Butler, W.H., Goldstein, B.E., 2010. The US fire learning network: springing a rigidity trap through multi-scalar collaborative networks. Ecol. Soc. 15, 21.

Calkin, D.E., Thompson, M.P., Finney, M.A., 2015. Negative consequences of positive feedbacks in US wildfire management. For. Ecosyst. 2, 9.

Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69, 786–795.

Carroll, M.S., Cohn, P.J., Blatner, K.A., 2004. Private and tribal forest landowners and fire risk: a two-county case study in Washington State. Can. J. For. Res. 34, 2148–2158.

Carroll, M.S., Cohn, P.J., Paveglio, T.B., Drader, D.R., Jakes, P.J., 2010. Fire burners to firefighters: the Nez Perce and fire. J. For. 108, 71–76.

Catton, T., 2016. American Indians and National Forests. University of Arizona Press, Tuscon, Arizona.

Chamberlain, J.L., Emery, M.R., Patel-Weynand, T., 2018. Assessment of nontimber forest products in the United States under changing conditions, General Technical Report SRS-232, US Forest Service, Southern Research Station.

Charles-Dominique, T., Edelin, C., Brisson, J., Bouchard, A., 2012. Architectural strategies of Rhamnus cathartica (Rhamnaceae) in relation to canopy openness. Botany 90, 976–989.

Charnley, S., Fischer, A., Jones, E., 2007. Integrating traditional and local ecological knowledge into forest biodiversity conservation in the Pacific Northwest. For. Ecol. Manage. 246, 14–28.

Charnley, S., Kline, J.D., White, E.M., Abrams, J., McLain, R.J., Moseley, C., Huber-Stearns, H., 2018. Socioeconomic well-being and forest management in northwest forest plan-area communities. In: Spies, T.A., Stine, P.A., Gravenmier, R., Long, J.W., Reilly, M.J., tech. cords, (Eds.). 2018. Synth. Sci. to Inf. L. Manag. within Northwest For. Plan area. Gen. Tech. Rep. PNW-GTR-966. Portland, OR US Dep. Agric. For. Servi 966, pp. 625–715.

Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J., Knox, K.J.E., 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytol. 197, 19–35.

Clinton, W., 2000. Consultation and Coordination with Indian Tribal Governments. Fed. Regist. 65, Doc No: 00-29003.

Clinton, W., 1994. Government-to-government relations with Native American tribal governments. Fed. Regist. 59, Doc No: 94-10877.

Collins, B.M., Stephens, S.L., Moghaddas, J.J., Battles, J.J., 2010. Challenges and approaches in planning fuel treatments across fire-excluded forested landscapes. J. For. 108, 24–31.

Crawford, J.N., Mensing, S.A., Lake, F.K., Zimmerman, S.R., 2015. Late Holocene fire and vegetation reconstruction from the western Klamath Mountains, California, USA: a multi-disciplinary approach for examining potential human land-use impacts. The Holocene 25, 1341–1357.

Cuthrell, R.Q., 2013. Archaeobotanical evidence for indigenous burning practices and foodways at CA-SMA-113. Calif. Archaeol. 5, 265–290.

Davies, G., Frank, F., 1992. Stories of the Klamath National Forest: The First 50 years: 1905–1955. HiStory ink Books, Hat Creek, California.

Diver, S., 2016. Co-management as a catalyst: pathways to post-colonial forestry in the Klamath Basin, California. Hum. Ecol. 44, 533–546.

Dockry, M.J., Gutterman, S.A., Davenport, M.A., 2017. Building Bridges: perspectives on partnership and collaboration from the US Forest Service Tribal Relations Program. J. For. 116, 123–132.

Donoghue, E.M., Thompson, S.A., Bliss, J.C., 2010. Tribal-federal collaboration in resource management. J. Ecol. Anthropol. 14, 22–38.

Drewa, P.B., Platt, W.J., Moser, E.B., 2002. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. Ecology 83, 755–767.

Duchesne, L.C., Wetzel, S., 2004. Effect of fire intensity and depth of burn on Lowbush Blueberry, Vaccinium angustifolium, and Velvet Leaf Blueberry, Vaccinium myrtilloides, production in eastern Ontario. Can. Field-Naturalist 118, 195–200.

Emery, M.R., Wrobel, A., Hansen, M.H., Dockry, M., Moser, W.K., Stark, K.J., Gilbert, J.H., 2014. Using traditional ecological knowledge as a basis for targeted forest inventories: Paper birch (Betula papyrifera) in the US Great Lakes region. J. For. 112, 207–214.

Fernández, C., Vega, J.A., Fonturbel, T., 2013a. Shrub resprouting response after fuel reduction treatments: comparison of prescribed burning, clearing and mastication. J. Environ. Manage. 117, 235–241.

Fernández, C., Vega, J.A., Fonturbel, T., 2013b. Does fire severity influence shrub resprouting after spring prescribed burning? Acta oecologica 48, 30–36.

Fiala, A.C.S., Garman, S.L., Gray, A.N., 2006. Comparison of five canopy cover estimation techniques in the western Oregon Cascades. For. Ecol. Manage. 232, 188–197.

Fine, P.V.A., Misiewicz, T.M., Chavez, A.S., Cuthrell, R.Q., 2013. Population genetic structure of California hazelnut, an important food source for people in Quiroste Valley in the Late Holocene. Calif. Archaeol. 5, 353–370.

Fryer, J., 2007. Corylus cornuta [WWW Document]. Fire Eff. Inf. Syst. [Online]. URL https://www.fs.fed.us/database/feis/plants/shrub/corcor/all.html (accessed 7.9.18).

Gagnon, P.R., Platt, W.J., 2008. Multiple disturbances accelerate clonal growth in a

potentially monodominant bamboo. Ecology 89, 612–618.
Griffith, A., McDowell, K., Young, R.S., 2007. Rivercane restoration project: recovering an ecologically and culturally significant species (North Carolina). Ecol. Restor. 25, 144–145.
Halpern, A., 2016. Prescribed Fire and Tanoak (Notholithocarpus densiflorus) Associated Cultural Plant Resources of the Karuk and Yurok Peoples of California. PhD Dissertation. UC Berkeley, Berkeley, California.
Hamelin, C., Gagnon, D., Truax, B., 2015. Aboveground biomass of glossy buckthorn is similar in open and understory environments but architectural strategy differs. Forests 6, 1083–1093.
Hankins, D., 2013. The effects of indigenous prescribed fire on riparian vegetation in central California. Ecol. Process. 2, 1–9.
Harling, W., 2015. Learning together, burning together. Wildfire Mag. 24, 26–30.
Harrington, J., 1932. Tobacco among the Karuk Indians of California, Smithsonian Institution, Bureau of American Ethnology Bulletin 94. United States Government Printing Office, Washington DC.
Hart-Fredeluces, G., Ticktin, T., 2019. Fire, leaf harvest, and abiotic factors drive demography of an ecologically and culturally important understory plant. Ecosphere 10, e02813.
Heffner, K., 1984. "Following the Smoke": Contemporary plant procurement by the Indians of Northwest California. Manuscript on file, Heritage Resource Program, Six Rivers National Forest, Eureka, California.
Hummel, S., Lake, F.K., 2015. Forest site classification for cultural plant harvest by tribal weavers can inform management. J. For. 113, 30–39.
Hunter, J.E., 1988. Prescribed burning for cultural resources. Fire Manag. Notes 49, 8–9.
Huntsinger, L., Diekmann, L., 2010. Virtual reservation: Land distribution, natural resource access, and equity on the Yurok forest. Nat. Resour. J. 50, 341–370.
Huntsinger, L., McCaffrey, S., 1995. A forest for the trees: forest management and the Yurok environment, 1850 to 1994. Am. Indian Cult. Res. J. 19, 155–192.
Johnson, R., Marks, C.K., 1997. Her Mind Made Up: Weaving caps the Indian way. Ron Johnson, Humboldt State University, Arcata, California.
Jones, E.T., Lynch, K.A., 2007. Nontimber forest products and biodiversity management in the Pacific Northwest. For. Ecol. Manage. 246, 29–37.
Jurney, D.H., Bragg, D.C., Coleman, R.E., Gonzalez, B., 2017. Lessons from a programmatic agreement and heritage-based consultations between Tribes and the National Forests of Arkansas and Oklahoma. J. For. 115, 458–467.
Kabacoff, R., 2015. R in Action: Data Analysis and Graphics with R. Manning Publications, Shelter Island, New York.
Kalies, E.L., Kent, L.L.Y., 2016. Tamm Review: Are fuel treatments effective at achieving ecological and social objectives? A systematic review. For. Ecol. Manage. 375, 84–95.
Kallenbach, E., 2009. The California Indian Basketweavers Association: advocates for the use of museum collections by contemporary weavers. Museum Anthropol. Rev. 3, 1–13.
Tribe, Karuk, Hillman, Lisa, Hillman, Leaf, Harling, A.R.S., Talley, B., McLaughlin, A., 2017. Building Sípnuuk: a digital library, archives, and museum for indigenous peoples. Collect. Manag. 42, 294–316.
Kauffman, J.B., Martin, R.E., 1990. Sprouting shrub response to different seasons and fuel consumption levels of prescribed fire in Sierra Nevada mixed conifer ecosystems. For. Sci. 36, 748–764.
Keeley, J.E., 2006. Fire severity and plant age in postfire resprouting of woody plants in sage scrub and chaparral. Madrono 53, 373–380.
Keeley, J.E., Brennan, T., Pfaff, A.H., 2008. Fire severity and ecosytem responses following crown fires in California shrublands. Ecol. Appl. 18, 1530–1546.
Kimmerer, R.W., 2011. Restoration and reciprocity: the contributions of traditional ecological knowledge. In: Egan, D., Hjerpe, E., Abrams, J. (Eds.), Human Dimensions of Ecological Restoration. Springer, New York, pp. 257–276.
Kolden, C.A., 2019. We're not doing enough prescribed fire in the Western United States to mitigate wildfire risk. Fire 2, 30.
Konstantinidis, P., Tsiourlis, G., Xofis, P., 2006. Effect of fire season, aspect and pre-fire plant size on the growth of Arbutus unedo L. (strawberry tree) resprouts. For. Ecol. Manage. 225, 359–367.
Lake, F.K., 2013. Trails, trials and tribulations: tribal resource management and research issues in northern California. Occasion 5, 1–22.
Lake, F.K., 2011. Working with American Indian tribes on wildland fires: protecting cultural heritage sites in northwestern California. Fire Manag. Today 71, 14–21.
Lake, F.K., 2007. Traditional Ecological Knowledge to Develop and Maintain Fire Regimes in Northwestern California, Klamath-Siskiyou Bioregion: Management and Restoration of Culturally Significant Habitats. PhD Dissertation. Oregon State University, Corvallis, Oregon.
Lake, F.K., Parrotta, J., Giardina, C.P., Davidson-Hunt, I., Uprety, Y., 2018. Integration of traditional and Western knowledge in forest landscape restoration. In: Mansourian, S., Parrotta, J. (Eds.), Forest Landscape Restoration: Integrated Approaches to Support Effective Implementation. Routledge, Abingdon-on-Thames, UK, pp. 214–242.
Lake, F.K., Wright, V., Morgan, P., McFadzen, M., McWethy, D., Stevens-Rumann, C., 2017. Returning fire to the land—celebrating traditional knowledge and fire. J. For. 115, 343–353.
LaLande, J., Pullen, R., 1999. Burning for a "Fine and Beautiful Open Country": Native uses of fire in southwestern Oregon. In: Boyd, R. (Ed.), Indians, Fire and the Land in the Pacific Northwest. Oregon State University Press, Corvallis, Oregon, pp. 255–276.
Lathrop, E.W., Martin, B.D., 1982. Fire ecology of deergrass (Muhlenbergia rigens) in Cuyamaca Rancho State Park, California. Crossosoma 5, 1–10.
Lemmon, P.E., 1956. A spherical densiometer for estimating forest overstory density. For. Sci. 2, 314–320.
Lenth, R., 2018. Emmeans: Estimated marginal means, aka least-squares means. R Packag. version 1.
Levy, S., 2005. Rekindling native fires. Bioscience 55, 303–308.
Lewis, H., 1993. Patterns of Indian burning in California: ecology and ethnohistory. In: Blackburn, T.C., Anderson, M.K. (Eds.), Before the Wilderness: Environmental Management by Native Californians. Ballena Press, Menlo Park, California, pp. 55–116.
Little Jr, E.L., 1971. Atlas of United States trees. Volume 1. Conifers and important hardwoods. Miscellaneous publication 1146. US Dep. Agric. For. Serv., Washington, DC.
Lloret, F., López-Soria, L., 1993. Resprouting of Erica multiflora after experimental fire treatments. J. Veg. Sci. 4, 367–374.
Long, J., Lake, F., 2018. Escaping social-ecological traps through tribal stewardship on national forest lands in the Pacific Northwest, United States of America. Ecol. Soc. 23.
Long, J., Lake, F.K., Lynn, K., Viles, C., 2018. Tribal ecocultural resources and engagement. In: Spies, T.A., Stine, P.A., Gravenmier, R., Long, J.W., Reilly, M.J., tech. cords. (Eds.). 2018 Synth. Sci. to Inf. L. Manag. within Northwest For. Plan area. Gen. Tech. Rep. PNW-GTR-966. Portland, OR US Dep. Agric. For. Servi 966, 851–917.
Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K.J., Bolker, B.M., Brooks, M.E., 2017. glmmTMB: generalized linear mixed models using template model builder. R Packag version 0.1 3.
Mason, L., White, G., Morishima, G., Alvarado, E., Andrew, L., Clark, F., Durglo, M., Durglo, J., Eneas, J., Erickson, J., Friedlander, M., Hamel, K., Hardy, C., Harwood, T., Haven, F., Isaac, E., James, L., Kenning, R., Leighton, A., Pierre, P., Raish, C., Shaw, B., Smallsalmon, S., Stearns, V., Teasley, H., Weingart, M., Wilder, S., 2012. Listening and learning from traditional knowledge and Western science: a dialogue on contemporary challenges of forest health and wildfire. J. For. 110, 187–193.
Mason, O.T., Coville, F.V., 1904. Aboriginal American Basketry: Studies in a Textile Art without Machinery. US Government Printing Office, Washington DC.
Mathewson, M.S., 2007. California Indian basketweavers and the landscape. In: Li, J.L. (Ed.), To Harvest, to Hunt: Stories of Resource Use in the American West. Oregon State University Press, Corvallis, Oregon, pp. 40–56.
Mathewson, M.S., 1998. The Living Web: Contemporary Expressions of California Indian Basketry. PhD Dissertation. University of California, Berkeley.
Mazzocchi, F., 2006. Western science and traditional knowledge: Despite their variations, different forms of knowledge can learn from each other. EMBO Rep. 7, 463–466.
McLaughlin, A., Glaze, L., 2008. Gathering Hazel [WWW Document]. Karuk Tribe News. URL http://karuk.us/images/docs/newsletters/Summer08Newsletter.pdf (accessed 7.9.18).
Mockta, T.K., Fulé, P.Z., Meador, A.S., Padilla, T., Kim, Y.-S., 2018. Sustainability of culturally important teepee poles on Mescalero Apache Tribal Lands: characteristics and climate change effects. For. Ecol. Manage. 430, 250–258.
Moerman, D.E., 1998. Native American Ethnobotany. Timber Press, Portland, Oregon.
Norgaard, K., 2014. The politics of fire and the social impacts of fire exclusion on the Klamath. Humboldt J. Soc. Relat. 36, 77–101.
O'Neale, L., 1932. Yurok-Karok Basket Weavers. University of California Press, Berkeley, California.
Ortiz, B., 1998. Following the Smoke: Karuk indigenous basketweavers and the forest service. News Nativ. Calif. 11, 21–29.
Ortiz, B., 1993. Contemporary California Indian basketweavers and the environment. In: Blackburn, T.C., Anderson, M.K. (Eds.), Before the Wilderness: Environmental Management by Native Californians. Ballena Press, Menlo Park, California, pp. 195–211.
Pelc, B.D., Montgomery, R.A., Reich, P.B., 2011. Frequency and timing of stem removal influence Corylus americana resprout vigor in oak savanna. For. Ecol. Manage. 261, 136–142.
Peter, D.H., Harrington, T.B., Thompson, M., 2017. Effects of the light environment and stand history on beargrass (Xerophyllum tenax) morphology and demography. Northwest Sci. 91, 367–382.
Pickett, S.T.A., Kempf, J.S., 1980. Branching patterns in forest shrubs and understory trees in relation to habitat. New Phytol. 86, 219–228.
Quinn-Davidson, L.N., Varner, J.M., 2012. Impediments to prescribed fire across agency, landscape and manager: an example from northern California. Int. J. Wildl. Fire 21, 210–218.
Core Team, R., 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, pp. 2013.
Rentz, E.D., 2003. Effects of Fire on Plant Anatomical Structure in Native Californian Basketry Materials. San Francisco State University.
Rhoades, C.C., Fornwalt, P.J., 2015. Pile burning creates a fifty-year legacy of openings in regenerating lodgepole pine forests in Colorado. For. Ecol. Manage. 336, 203–209.
Robbins, M., McConnell, D., Stauffer, R., 2016. Indigenous Peoples Burning Network (IPBN) [WWW Document]. Conserv. Gatew. (The Nat. Conserv. URL https://www.conservationgateway.org/ConservationPractices/FireLandscapes/FireLearningNetwork/RegionalNetworks/Documents/IPBN-Poster-Apr2016.pdf (accessed 7.9.18).
Salberg, T.A., 2005. Hazel fuels reduction project: Integrating cultural resource management and hazardous fuels reduction. Evergr. Mag. Winter 72–73.
Sarna-Wojcicki, D.R., 2014. Ethics and epistemology: giving back in the Klamath. J. Res. Pract. 10, 21.
Scherjon, F., Bakels, C., MacDonald, K., Roebroeks, W., 2015. Burning the Land: an ethnographic study of off-site fire use by current and historically documented foragers and implications for the interpretation of past fire practices in the landscape. Curr. Anthropol. 56, 299–326.
Schoennagel, T., Nelson, C.R., Theobald, D.M., Carnwath, G.C., Chapman, T.B., 2009. Implementation of National Fire Plan treatments near the wildland–urban interface in the western United States. Proc. Natl. Acad. Sci. pnas.09009.
Schultz, C., Huber-Stearns, H., McCaffrey, S., Quirke, D., Ricco, G., Moseley, C., 2018. Prescribed Fire Policy Barriers and Opportunities: A diversity of challenges and

strategies across the West (No. 86). University of Oregon, Ecosystem Workforce Program Working Paper, Eugene, OR.
Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J., Bailey, J.D., Fettig, C.J., Fiedler, C.E., Harrod, R.J., Moghaddas, J.J., Outcalt, K.W., 2009. The national fire and fire surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecol. Appl. 19, 285–304.
Senos, R., Lake, F.K., Turner, N., Martinez, D., 2006. Traditional ecological knowledge and restoration practice. In: Apostol, D., Sinclair, M. (Eds.), Restoring the Pacific Northwest: The Art and Science of Ecological Restoration in Cascadia. Island Press, Washington DC, pp. 393–426.
Shanks, R.C., 2006. Indian baskets of Central California: Art, culture, and history: Native American basketry from San Francisco Bay and Monterey Bay north to Mendocino and east to the Sierras. Costaño Books, Novato, CA.
Shebitz, D.J., Kimmerer, R.W., 2005. Reestablishing roots of a Mohawk community and a culturally significant plant: Sweetgrass. Restor. Ecol. 13, 257–264.
Shebitz, D.J., Reichard, S.H., Dunwiddie, P.W., 2009. Ecological and cultural significance of burning beargrass habitat on the Olympic peninsula, Washington. Ecol. Restor. 27, 306–319.
Siefkin, N., Arguello, L., Kalt, J., 2002. Fire management of hazel for California Indian basketweaving. In: Paper presented at the Association for Fire Ecology Meeting, San Diego, California.
Skinner, C.N., Taylor, A.H., Agee, J.K., Briles, C.E., Whitlock, C.L., 2018. Klamath mountains bioregion. In: Wagtendonk, J. Van, Sugihara, N.G., Stephens, S.L., Thode, A.E., Shaffer, K.E., Fites-Kaufman, J. (Eds.), Fire in California's Ecosystems. University of California Press, Oakland, CA, pp. 171–194.
Smith, L.T., 1999. Decolonizing Methodologies: Research and Indigenous Peoples. Zed books, London.
Spencer, A.G., Schultz, C.A., Hoffman, C.M., 2015. Enhancing adaptive capacity for restoring fire-dependent ecosystems: the Fire Learning Network's Prescribed Fire Training Exchanges. Ecol. Soc. 20, 38.
Stapp, D.C., Burney, M.S., 2002. Tribal Cultural Resource Management: The Full Circle to Stewardship. Rowman Altamira, Lanham, MD.
Stephens, S.L., Collins, B.M., Biber, E., Fulé, P.Z., 2016. US federal fire and forest policy: emphasizing resilience in dry forests. Ecosphere 7, e01584.
Stewart, O., 2002. Forgotten Fires: Native Americans and the Transient Wilderness. University of Oklahoma Press, Norman, OK.
Taylor, A.H., Skinner, C.N., 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. For. Ecol. Manage. 111, 285–301.
Thaxton, J.M., Platt, W.J., 2006. Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. Ecology 87, 1331–1337.
Thomas, J.W., Franklin, J.F., Gordon, J., Johnson, K.N., 2006. The Northwest Forest Plan: origins, components, implementation experience, and suggestions for change. Conserv. Biol. 20, 277–287.
Thompson, L., 1991. To the American Indian: Reminiscences of a Yurok Woman. Heyday Press, Berkeley, California.
Thompson, R., Anderson, K., Pelltier, R., Strickland, L., Shafer, S., Bartlein, P., McFadden, A., 2015. Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America. US Geological Survey Professional Paper 1650–G.
Trauernicht, C., Brook, B., Murphy, B., Willimason, G., Bowman, D., 2015. Local and global pyrogeographic evidence that indigenous fire management creates pyrodiversity. Ecol. Evol. 5, 1908–1918.
Turner, N.J., 1998. Plant Technology of British Columbia First Peoples. University of British Columbia Press,, Vancouver and Royal British Columbia Museum, Victoria, BC.
Underwood, S., Arguello, L., Siefkin, N., 2003. Restoring ethnographic landscapes and natural elements in redwood national park. Ecol. Restor. 21, 278–283. https://doi.org/10.3368/er.21.4.278.
US Census Bureau, 2017. Cartographic Boundary Shapefiles – American Indian/Alaska Native Areas/Hawaiian Home Lands [WWW Document]. URL https://www.census.gov/geo/maps-data/data/cbf/cbf_aiannh.html (accessed 1.10.18).
USDA Forest Service, 2018. Toward Shared Stewardship Across Landscapes: An Outcome-based Investment Strategy [WWW Document]. FS-118. URL https://www.fs.fed.us/sites/default/files/toward-shared-stewardship.pdf (accessed 3.20.19).
USDA Forest Service PSW Region, 2018. Somes Bar Integrated Fire Management Project: Final Environmental Assessment [WWW Document]. URL https://www.fs.usda.gov/nfs/11558/www/nepa/106291_FSPLT3_4291171.pdf (accessed 6.1.19).
Vaillant, N.M., Reinhardt, E.D., 2017. An evaluation of the Forest Service hazardous fuels treatment program—are we treating enough to promote resiliency or reduce hazard? J. For. 115, 300–308.
Valladares, Fernando, Niinemets, U., 2007. The architecture of plant crowns: from design rules to light capture and performance. In: Pugnaire, F., Valladares, F. (Eds.), Functional Plant Ecology. Taylor and Francis, New York, pp. 101–149.
Vinyeta, K., Lynn, K., 2015. Strengthening the Federal-Tribal Relationship: A Report on Monitoring Consultation Under the Northwest Forest Plan. US Forest Service, Pacific Northwest Region, Portland, OR.
Waterman, T., 1920. Yurok geography. Univ. Calif. Publ. Am. Archaeol. Ethnol. 16, 177–314.
Williams, G.W., 2009. The US Forest Service in the Pacific Northwest: A History. Oregon State University Press, Corvallis, Oregon.
Wills, R., Stuart, J., 1994. Fire history and stand development of Douglas-fir/hardwood forests in northern California. Northwest Sci. 68, 205–212.
Wilson, S., 2008. Research is Ceremony: Indigenous Research Methods. Fernwood Publishing, Halifax and Winnipeg.
Wynecoop, M.D., Morgan, P., Strand, E.K., Trigueros, F.S., 2019. Getting back to fire sumêš: exploring a multi-disciplinary approach to incorporating traditional knowledge into fuels treatments. Fire Ecol. 15, 17.
Yurok GIS Program, 2015. Yurok Reservation and Surrounding Area [WWW Document]. URL http://www.yuroktribe.org/departments/infoservices/GIS/documents/Statistics_Map_August15.pdf (accessed 1.8.18).
Yurok Tribe, 2015. CFMC Sparks Comprehensive Fire Plan [WWW Document]. Yurok Today. URL http://www.yuroktribe.org/documents/APRIL_YUROK_NEWSLETTER_2015_WEB_000.pdf (accessed 8.1.18).
Zobel, D.B., 2002. Ecosystem use by indigenous people in an Oregon coastal landscape. Northwest Sci. 76, 304–314.

Marks-Block et al. Fire Ecology (2021) 17:6
https://doi.org/10.1186/s42408-021-00092-6

Fire Ecology

ORIGINAL RESEARCH Open Access

Revitalized Karuk and Yurok cultural burning to enhance California hazelnut for basketweaving in northwestern California, USA

Tony Marks-Block[1*], Frank K. Lake[2], Rebecca Bliege Bird[3] and Lisa M. Curran[4]

Abstract

Background: Karuk and Yurok tribes in northwestern California, USA, are revitalizing the practice of cultural burning, which is the use of prescribed burns to enhance culturally important species. These cultural burns are critical to the livelihoods of indigenous peoples, and were widespread prior to the establishment of fire exclusion policies. One of the major objectives of cultural burning is to enhance California hazelnut (*Corylus cornuta* Marsh var. *californica*) basketry stem production for Karuk and Yurok basketweavers. To evaluate cultural burning as a form of human ecosystem engineering, we monitored hazelnut basketry stem production, qualities, and shrub density in 48 plots (400 m^2) within two prescribed and 19 cultural burn sites. Socio-ecological variables that were analyzed included burn frequency, burn season, overstory tree (≥10 cm diameter at breast height) basal area, ungulate browse, and aspect. We also observed basketry stem gathering to compare travel distances, gathering rates, and basketweaver preferences across sites with different fire histories and land tenure.

Results: Hazelnut shrubs, one growing season post burn, produced a 13-fold increase in basketry stems compared with shrubs growing at least three seasons post burn ($P < 0.0001$). Basketry stem production and stem length displayed negative relationships with overstory tree basal area ($P < 0.01$) and ungulate browse ($P < 0.0001$). Plots burned at high frequency (at least three burn events from 1989 to 2019) had 1.86-fold greater hazelnut shrubs than plots experiencing less than three burn events ($P < 0.0001$), and were all located on the Yurok Reservation where land tenure of indigenous people is comparatively stronger. Basketweavers travelled 3.8-fold greater distance to reach gathering sites burned by wildfires compared with those that were culturally burned ($P < 0.01$). At cultural burn sites, wildfire sites, and fire-excluded sites, mean gathering rates were 4.9, 1.6, and 0.5 stems per minute per individual, respectively.

(Continued on next page)

* Correspondence: tony.marksblock@csueastbay.edu
[1]Department of Anthropology, Geography and Environmental Studies, California State University, East Bay, 25800 Carlos Bee Boulevard, Meiklejohn Hall 4036, Hayward, California 94542, USA
Full list of author information is available at the end of the article

© The Author(s). 2021 **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

(Continued from previous page)
Conclusions: Karuk and Yurok cultural fire regimes with high burn frequencies (*e.g.,* three to five years) promote high densities of hazelnut shrubs and increase hazelnut basketry stem production. This improves gathering efficiency and lowers travel costs to support the revitalization of a vital cultural practice. Our findings provide evidence of positive human ecosystem engineering, and show that increasing tribal sovereignty over fire management improves socio-economic well-being while at the same time supports measures of ecosystem structure and function.

Keywords: American Indians, basketry, California, *Corylus cornuta* var. *californica*, ecosystem engineering, indigenous peoples resource use, prescribed fire, resource management

Resumen

Antecedentes: Las tribus Karuk y Yurok del noroeste de California, EEUU, están revitalizando la práctica cultural de quemas, que es el uso del fuego prescripto para aumentar las especies culturalmente importantes. Estas quemas culturales son críticas para sustentar la vida de los pueblos indígenas, y fueron sumamente extendidas antes del establecimiento de las políticas de exclusión del fuego. Uno de los principales objetivos de las quemas culturales es aumentar la producción de tallos del avellano de California (*Corylus cornuta* Marsh var. *californica*) que es usado para la construcción de cestos por los fabricantes de cestos (cesteros) de las tribus Karuk y Yurok. Para evaluar las quemas culturales como una forma de ingeniería ecosistémica, monitoreamos la producción de cestos realizados con tallos de avellano, la calidad y densidad de esos tallos, en 48 parcelas (400 m^2) dentro de dos quemas prescriptas y en 19 lugares con quemas culturales. Las variables socio-ecológicas que fueron analizadas incluyeron la frecuencia de quemas, la estación de quemas, el área basal (≥10 cm de diámetro a la altura del pecho) de árboles del dosel superior, el ramoneo por ungulados, y la exposición. Observamos asimismo el lugar de colección de los tallos para comparar distancias recorridas, tasas de recolección, y las preferencias de quienes fabrican los cestos a través de sitios con diferentes historias de fuego y tenencia de la tierra.

Resultados: Una estación luego del fuego, los arbustos de avellano de California produjeron un incremento de 13 veces la producción de tallos factibles de ser usados en cestería comparados con arbustos creciendo al menos tres estaciones post fuego ($P < 0.0001$). La producción y el largo de los tallos desarrollaron relaciones negativas con el área basal de árboles del dosel superior ($P < 0.01$) y el ramoneo de ungulados ($P < 0.0001$). Las parcelas quemadas a alta frecuencia (al menos tres eventos de fuego de 1989 a 2019) tuvieron 1,86 veces más arbustos de avellano que aquellas parcelas que experimentaron menos de tres eventos de fuego ($P < 0.0001$), y fueron todos ubicados en la reservación de Yurok, donde la tenencia de la tierra por parte de la comunidad indígena es comparativamente más fuerte. Los fabricantes de cestos viajaron distancias 3,8 veces más largas para alcanzar lugares quemados por fuegos naturales comparados con aquellos que fueron sujetos a quemas cultuales prescriptas ($P < 0.01$). En los sitios quemados por prácticas culturales, por incendios naturales u aquellos lugares excluidos de fuegos, el tiempo promedio de recolección fue de 4,9, 1,6, y 0.5 tallos por minuto por individuo, respectivamente.

Conclusiones: Los regímenes de quemas culturales por parte de las tribus Karuk y Yurok con altas frecuencias de quema (*e,g,* de tres a cinco años), promueven una alta densidad de arbustos de avellano e incrementan la producción de tallos para cestería. Esto mejora la eficiencia en la recolección y reduce los costos del viaje, lo que ayuda a la revitalización de una práctica cultural vital. Nuestros hallazgos proveen evidencias positivas de ingeniería ecosistémica humana, y muestran que el incremento de la soberanía tribal sobre el manejo de fuego mejora las condiciones de bienestar socio-económico, mientras que al mismo tiempo aportan a la estructura y el funcionamiento del ecosistema.

Background

Across diverse ecosystems worldwide, prescribed burning by indigenous peoples, known colloquially as cultural burning, has been shown to impart positive effects on human and ungulate foraging returns, habitat diversity, and species abundance as well as the mitigation of wildfire spread by reducing fuel loads and fire intensities (Laris 2002; Bilbao et al. 2010; Bliege Bird et al. 2012; Fowler 2012; Seijo et al. 2015). Given the substantial shifts in ecosystem functioning generated by cultural burning practices of indigenous peoples, several authors have suggested that these practices provide critical ecosystem engineering functions that generate or maintain a distinctive suite of non-human species and

communities adapted to the pyrodiversity created by indigenous peoples' fire regimes (Jones et al. 1994; Smith 2011; Bliege Bird et al. 2013; Odling-Smee et al. 2013).

In California, USA, fire serves as a critical biophysical process (Sugihara et al. 2018). Preceding Spanish and American colonialism, fires set by California Indians imparted profound ecological effects by reducing fire severity and fuel continuity (Mallek et al. 2013; Taylor et al. 2016). These cultural fires enhanced California Indian subsistence and ceremonial resources and, thus, are integral to the culture and economy of California Indians (Lightfoot and Parrish 2009; Anderson 2018). However, in 1905, the USDA Forest Service initiated fire exclusion policies to protect timber commodities and built structures, and by the 1920s, these policies had solidified throughout the State of California to exclude cultural burning (Pinchot 1905; Ayres and Hutchinson 1931; Clar 1959; Cermak 2005). Fire exclusion policies reduced indigenous peoples' cultural burning practices and limited the availability of their key ecocultural resources (Huntsinger and McCaffrey 1995; Aldern and Goode 2014; Eriksen and Hankins 2014; Lake et al. 2017; Norgaard 2019). By the 1990s, US federal land management agencies revised their fire policies to recognize the potential benefits of prescribed fires as a management tool, generating opportunities to revive indigenous people's cultural burning practices (Butler and Goldstein 2010; Long and Lake 2018; Stephens and Sugihara 2018).

In northwestern California, indigenous peoples such as the Karuk, Yurok, and Hoopa Valley tribes (AKA Hupa), are leading efforts to re-introduce cultural burning by forming partnerships with public land and fire agencies as well as non-governmental organizations (Underwood et al. 2003; Levy 2005; Salberg 2005; Long and Lake 2018). In 2013, institutional support for cultural burning in northwestern California was initiated through the Prescribed Fire Training Exchanges (TREX; Terence 2016), and, in 2014, the Six Rivers National Forest began the Roots and Shoots project on the Lower Trinity, Orleans, and Ukonom ranger districts (Colegrove 2014). The TREX program falls under the Promoting Ecosystem Resilience and Fire Adapted Communities Together agreement between the USDA Forest Service and The Nature Conservancy that invests in cooperative and collaborative burning on private, tribal, and public lands across the United States (Butler and Goldstein 2010; Spencer et al. 2015). In Karuk and Yurok territory, TREX provides financial and logistical support to develop burn plans, process permits, supply equipment, and mobilize fire personnel to support intergovernmental, inter-agency, and civil society partnerships. (Harling 2015; Terence 2016). The Roots and Shoots project is a Six Rivers National Forest effort developed by the USDA Forest Service and Tribal members to burn 176 acres within 25 forest areas containing ecocultural resources integral to indigenous peoples (Colegrove 2014).

While cultural burns are utilized in different seasons and at different scales and intensities for a wide range of ecocultural species (Hankins 2013), in recent decades, one of the major objectives for conducting cultural burns in Karuk and Yurok ancestral territories (Fig. 1) has been to enhance the production of basketry materials for indigenous basketweavers (Hunter 1988; Ortiz 1998; Senos et al. 2006). California Indians use baskets in a wide range of contexts: child-rearing; food harvesting, processing, and storage; for everyday clothing; and in ceremonies (Johnson and Marks 1997; Bibby 2004; Shanks 2006; Mathewson 2007). Baskets are also economically important, sold both within and outside the indigenous community to supplement income (Cohodas 1997; Smith 2016). In turn, baskets provide spiritual connections to land and ancestors, through the materials used as well as the form of the basket design (Lang 1994; Johnson and Marks 1997; Smith 2016). Northwestern California Indian basketweaving exists as one of many manifestations of socio-ecological relationships within this fire-dependent culture (Lang 1991; Hillman and Salter 1997; Buckley 2002; Smith 2016; Baldy 2018).

One of the most highly valued and critically important species for basketweaving is California hazelnut (*Corylus cornuta* Marsh var. *californica*; Ortiz 1993; 1998; Smith 2016), a multi-stemmed, deciduous shrub. Hazelnut stems are integral to the weaving of baby baskets (cradles), which are composed of ~300 stems and currently are sold for ~$800. As Maggie Peters, a Yurok basketweaver, shared, "These baskets are in high demand by northwest California Indian families who want their children to begin their lives in a cultural way." Cultural burns for hazelnut are designed to manipulate the post-fire growth response of California hazelnut, stimulating it to re-sprout from underground buds (Fryer 2007; Clarke et al. 2013), and to produce straight, unbranched shoots suitable for use in basketweaving. Historically, cultural burning for hazelnut basketry stems occurred predominantly in the summer and fall months, although occasionally in the spring (Lake 2007). Hazelnut stem regrowth would then be harvested in the following spring (April and May) after one full growing season (spring burn, ten to12 months post burn; fall burn, 18 to 21 months post burn; Thompson 1991; O'Neale 1932; Lake 2007).

From the 1920s to the 2000s, fire exclusion policies and regulations against cultural burning increased the scarcity of suitable basketry stems for basketweavers (Heffner 1984; Ortiz 1993; Smith 2016). In response, some basketweavers developed alternative techniques to stimulate the

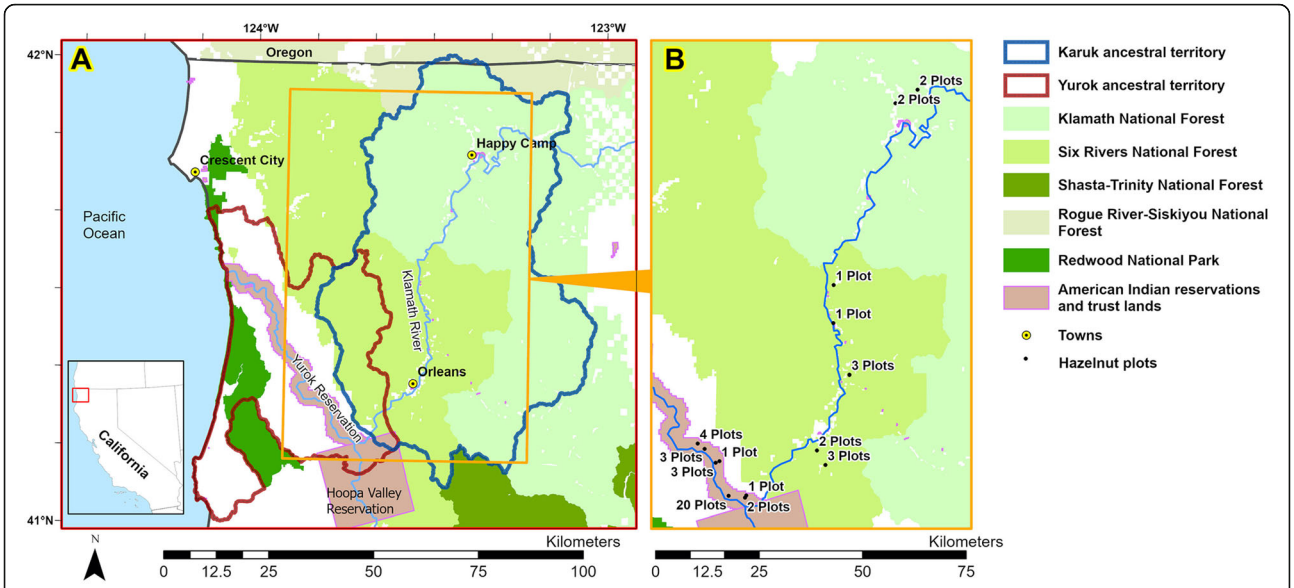


Fig. 1 (**A**) Study region with federal jurisdictional boundaries and Karuk and Yurok ancestral territories, northwestern California, USA. Ancestral territory boundaries, provided by the Karuk and Yurok Tribes, represent reconstructions, but currently are not fixed or rigid boundaries. Ancestral lands of other northwestern California Tribes (*e.g.,* Tolowa, Wiyot, Hupa, Shasta) are not included here, but their ancestral lands may partially overlap with the boundaries rendered here (Baumhoff, 1963). (**B**) Hazelnut monitoring plot locations. Forty-eight plots (each 400 m^2) were established and monitored at two prescribed burn sites and 19 cultural burn sites in Karuk and Yurok territory (2015 to 2019)

growth of hazelnut basketry stems, such as cutting (coppicing), propane torch burning, and pile burning (Heffner 1984; Hunter 1988; Ortiz 1998; Marks-Block et al. 2019). Others were able to maintain burning for basketry materials—albeit in limited areas—throughout the fire exclusion era (Bower 1978; Heffner 1984; Hunter 1988; Ortiz 1998). With the relatively recent expansion of cultural burning in this region initiated by TREX and the Roots and Shoots initiatives, opportunities emerged to evaluate the effects of cultural burning on hazelnut basketry stem production, shrub density, and basketweaver stem harvesting across sites with distinctive fire regimes and land tenure arrangements: for example, between sites with relatively short burning intervals in recent decades (*i.e.,* every three to ten years) in Yurok territory, and at sites in Karuk territory that only recently have been burned after years of fire exclusion.

Our study was motivated by three broad questions. First, is cultural burning by indigenous peoples a form of ecosystem engineering that has positive feedback on ecological and cultural processes? If so, we expected that cultural burning may increase basketry stem productivity, hazelnut shrub density, or reduce the harvesting costs (in search, collection, and travel time) of gathering suitable stems. Basketweaver ecological knowledge and previous experimental studies (O'Neale 1932; Ortiz 1998; Anderson 1999; Lake 2007; Marks-Block et al. 2019) led us to predict that basketry stem production and quality are affected by time since fire and shrub size (*i.e.,* shrub stem densities), and that burn characteristics (*e.g.,* season, severity, and frequency) and site characteristics (*e.g.*, canopy closure or solar access, aspect, forest stand structure, and deer browse) may be other important factors.

Second, does cultural burning alter species' assemblages, such that in the absence of such fire perturbation, plant communities may shift to alternative stable states (Beisner et al. 2003)? We hypothesized that repeated, short-interval cultural burning acts as a beneficial, culturally desired perturbation in hazelnut groves, and that cultural burning maintains high shrub densities and other forest stand characteristics (*e.g.,* relatively low overstory basal area; Anderson 1999; 2018). Following this, if burning is inconsistent or absent, then hazelnut vigor was expected to decline with reduced densities and basketry stems post burn.

Third, how does fire and resource governance in precolonial and contemporary contexts affect cultural fire geography, basketry stem availability, and gathering practices? Here, we examined how centralization in governance structures (Larson and Soto 2008) as well as differences in land tenure (Huntsinger and Diekmann 2010; Norgaard 2014) affected fire-enhanced resource use in Karuk and Yurok territory. We predicted that distinctive Karuk and Yurok land tenure history and current resource access configurations likely influence hazelnut basketry stem gathering decisions. These histories and configurations affect cultural fire frequencies, hazelnut shrub densities, and site productivity that also affect gathering rates of hazelnut basketry stems and travel

distance to gathering sites. The use of these rates and metrics were informed by human behavioral ecology and foraging theory, which suggested that resource acquisition decisions were informed by micro-economic costs and tradeoffs (Stephens and Krebs 1986; Winterhalder and Smith 2000) as well as property regimes and land tenure (Smith 1988; Aswani 1998).

Methods

Study area

Our study area was the 1919 km^2 ancestral territory of the Yurok Tribe and the 2728 km^2 ancestral territory of the Karuk Tribe (Fig. 1; Waterman 1920; Baumhoff 1963) in the mid-Klamath watershed of California. Settlements historically were concentrated along the Klamath River and the Pacific coast (Waterman 1920; Kroeber 1936), and hunting and gathering grounds for critical ecocultural resources were owned and tended by either families or individuals (Waterman 1920; Bettinger 2015). Today, the Yurok and Karuk tribes include approximately 6000 to 7000 members, and make up two of the most populous federally recognized tribes in California (currently 109 tribes; United States Census Bureau 2010). In Karuk territory, the federal government did not establish a reservation or ratify treaties, but instead unilaterally created Forest Reserves in the majority of their territory that are now the Klamath and Six Rivers national forests (Rawls 1986; Davies and Frank 1992; Conners 1998; Miller 2017). Currently, the Karuk Tribe has merely 3.83 km^2 of their ancestral territorial lands held in trust by the federal government, with the remainder largely under the jurisdiction of the USDA Forest Service and scattered private homesteads (Fig. 1; Davies and Frank 1992; Norgaard 2014; US Census Bureau 2017). In Yurok territory, multiple overlapping jurisdictions occur, including Redwood National Park (192 km^2; Underwood et al. 2003) and Six Rivers National Forest (577 km^2) outside of the reservation established by the federal government. The reservation is located along a 1.6 km buffer following the Klamath River from its estuary to ~80 km upriver near the confluence of the Klamath and Trinity rivers (~225 km^2; Huntsinger and Diekmann 2010). However, 106 km^2 (47%) of the reservation is under private timber company ownership (Yurok GIS Program 2015). While we did not formally collaborate with the neighboring Hoopa Valley Tribe, several Hoopa Tribal members collaborated on this project.

The Cultural Fire Management Council (CFMC) organizes cultural burns within Yurok territory, and all members are either basketweavers or have basketweavers within their families. When deciding and planning burn locations with limited resources, the presence of hazelnut groves increases the ranking of a potential CFMC burn site. The Hoopa Valley Fire Department also conducts burns for hazelnut stems (Salberg 2005), and the Karuk Tribe works directly with the Forest Service, the Orleans/Somes Bar Fire Safe Council, and private landowners to burn hazelnut groves (Senos et al. 2006; Long and Lake 2018).

Hazelnut basketry stem measurements and surveys

To evaluate whether cultural burning generates positive feedback to tribal members in the form of increased hazelnut basketry stem production, stem quality, and hazelnut shrub density, we established and monitored 48 20 × 20 m plots (each plot = 400 m^2) from January 2015 to March 2019. Given the unpredictability of cultural burns, plots were established when we learned of recent and potential burn locations. Limited resources and environmental variability prevented all plots and shrubs from being burned within and across burn sites each year.

Plots were placed in relatively high-density hazelnut groves (≥10 shrubs) within two prescribed burn sites and 19 cultural burn sites (Fig. 1). Plots were located >2 m from roads and fire control lines and established after identifying easily accessible hazelnut groves from burn unit perimeters or game trails. Multiple plots (two to five) were placed within burn units that contained numerous hazelnut groves to evaluate the effects of environmental heterogeneity on basketry stem productivity within those locations. After the plot was established, site aspect was measured with a compass and classed as: east (67.5° to 112.5°), southeast (112.5° to 157.5°), south (157.5° to 202.5°), southwest (202.5° to 247.5°), or west (247.5° to 292.5°). Slope and elevation were measured using a global positioning system. Canopy closure measurements were taken facing inward at the four corners of each plot using a spherical densiometer, and then averaged (Lemmon 1956; Fiala et al. 2006). Basal area of each plot was determined by measuring all trees (>10 cm diameter at breast height [dbh]) with the dominant overstory tree species designated by proportional basal area: black oak (*Quercus kelloggii* Newb.), Pacific madrone (*Arbutus menziesii* Pursh), bay laurel (*Umbellaria californica* [Hook. & Arn.] Nutt.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), and subsequently classified as conifer or broadleaf hardwood.

Plot surveys

In each plot, we recorded individual hazelnut shrub density; due to its multi-stemmed growth habit, a shrub was considered a single individual if it was a minimum of 15 cm from other shrubs. We randomly selected and tagged ten shrubs for long-term monitoring. We counted quality basketry stems and total stems in each of the ten tagged shrubs. We defined suitable quality basketry stems as straight and unbranched stems >10 cm in length. After the plot was established, we recorded and re-sampled shrub stem data every year in the dormant season (October to April), as

dormant stem morphology does not change until budbreak and gathering season in April or May. We grouped our hazelnut shrub and stem measurements according to growing seasons post burn based on a May to September growing season each year. We developed three post-burn temporal classes: one growing season post burn (5 to 20 months; n = 302 shrubs); two growing seasons post burn (21 to 30 months; n = 144 shrubs); and ≥3 growing seasons post burn (>31 months, n = 507 shrubs). The burn season affected the post-burn growing season time span before our post-burn survey because winter- and spring-burned shrubs re-sprouted quickly after the burn, whereas summer- and fall-burned shrubs did not re-sprout until the following spring. Given basketweaver interest in the effects of seasonality of burning on hazelnut stem re-growth, we classified burn season by Julian day, defining winter as days 355 through 78, spring as days 79 through 171, summer as days 172 through 265, and fall as days 266 through 354.

Because plant growth is influenced by prior rainfall, we also compiled precipitation (cm) records for a 12-month period beginning in August of the year preceding the survey from the closest Remote Automated Weather Station (RAWS) to the plot (Yurok, Slate Creek, Somes Bar, Dutch-Indy, and Slater Butte, California; https://raws.dri.edu/ncaF.html). We compiled fire frequency data (burn events from 1989 to 2019) within each plot to evaluate effects on shrub density. Fire frequency was converted into a dichotomous variable: less than three burn events or at least three burn events and was ascertained through conversations with landowners and fire managers, and by examining the California Department of Forestry and Fire Protection's prescribed fire GIS database (https://frap.fire.ca.gov/mapping/gis-data/).

One growing season post-burn surveys

Given that basketweavers prefer to gather in areas burned after only a single growing season, typically in April or May (10 to 20 months post burn), we recorded additional data from shrubs and plots (n = 36) within the one growing season post-burn temporal class. Because basketweavers select basketry stems based both on their diameter and length, we recorded the length of the longest basketry stem in each shrub, and we took the average of the largest and smallest diameters of basketry stems in each shrub. We also recorded the proportion of stems browsed by deer, elk, and other ungulates for each shrub, and the post-burn char height on trees (>10 cm dbh) to the nearest 0.5 m to evaluate whether fire severity affected hazelnut stem re-growth.

Hazelnut stem gathering observations

To supplement our ecological surveys, we monitored hazelnut basketry stem gathering to evaluate whether land tenure and fire governance differences as well as fire type (wildfire and cultural fire) effect resource acquisition decisions in Karuk, Yurok, and Hupa territories. From 2015 to 2019, we developed working collaborative relationships with basketweavers and hazelnut stem gatherers by attending 13 cultural fire planning meetings and 15 basketweaving classes, and by discussing our research interests at Karuk and Yurok Tribal government meetings. Through these collaborative exchanges, we attended hazelnut stem gathering trips, and requested and collected six gathering diaries from three basketweavers to evaluate where and why basketweavers select hazelnut stem gathering areas. Moreover, we conducted 13 in-depth semi-structured interviews (30 to 60 minutes per interview) with Karuk and Yurok resource users and seven fire managers about fire-enhanced resource use and cultural burning that included questions on hazelnut burning, hazelnut stem and nut gathering, basketweaving, and the type of property ownership at burn sites. Interviewees were identified and recommended by Karuk staff in the Department of Natural Resources and Yurok leaders on the Tribe's culture committee. The Karuk and Yurok Tribal councils and the Stanford University Institutional Review Board (IRB) approved these human subjects methods, and individuals provided consent to record gathering practices and statements surrounding hazelnut stem gathering.

During hazelnut stem gathering season (April and May of each year from 2015 to 2019), we attended 17 hazelnut stem gathering trips, during which we observed individuals gathering hazelnut stems and asked semi-structured and open-ended questions regarding basketry stem quality, basketweaver gathering site and stem preferences, and the availability and accessibility of hazelnut



Fig. 2 Three generations of Yurok Indians gathering hazelnut basketry stems at a cultural burn site near Weitchpec, California, USA (left to right): Phillis Donahue (mother), Chris Peters (son), and Nicki Peters (granddaughter). Cultural fires generate significant resources to sustain Karuk and Yurok basketweaving. Photo credit: F.K. Lake, taken *circa* 2010. Each of the three people in the photograph gave permission for their image to be used by the authors

basketry stems. Gathering hazelnut stems is an intergenerational activity that brings together friends and relatives, and basketweaving teachers and their students (Fig. 2). From 2015 to 2019, 90 people were observed gathering hazelnut stems. Observed hazelnut basketry stem harvesters were 75% women, and, on average, gathered in groups of three (range = 1 to 8 individuals). The majority (57%) of 30 gathering groups were intergenerational, with a mix of elders (>60 years), middle-aged gatherers (25 to 60 years), and youth (<25 years), and 66% of groups were composed of basketweaver mentors and their students (including familial mentorships). Of the 72 recorded gathering trips, those made by family-member groups were most common (63%), whereas trips made by groups of friends (21%), and trips made by individuals (17%) were less frequent.

During these trips, the sum of an individual's harvested stems and their time spent in a hazelnut grove were recorded to produce 55 independent gathering rates. Distances to hazelnut stem gathering areas recorded from these trips and from basketweaver reports were converted to a standard 80 km hr^{-1} rate, chosen conservatively due to winding mountainous roads with a 55 miles per hour (88 km hr^{-1}) automobile speed limit. The gathering site's fire history was also recorded and then classified either as a cultural fire site, wildfire site, or a fire-excluded site. We also recorded the site's land ownership (USDA Forest Service, private, or tribal) along with ancestral territory (Karuk, Yurok, Hupa) of the gathering site, and categorized site quality as relatively good or poor based on basketweaver post-harvest evaluations. From these data, we generated simulations of hazelnut stem foraging that included searching and gathering rates within cultural fire sites, wildfire sites, and unburned sites.

Statistical methods

To evaluate the effects of growing seasons post burn on hazelnut basketry stem production (quantity of basketry stems per shrub), we employed a negative-binomial generalized linear mixed model (GLMM) using the `glmmTMB` package in R (R Core Team 2014; Magnusson et al. 2017) and used Type III Wald Chi Square tests using the `car` package (Fox and Weisberg 2018) to perform backward model selection. Growing season post burn (class), aspect (class), elevation (meters above sea level), sample year, basal area (>10 cm dbh), precipitation (cm), dominant overstory tree (>10 cm dbh), and slope (degrees) were modeled as co-variate direct effects, and each plot was set as a random effect.

Given basketweaver preferences for harvesting stems one growing season post burn, we developed another negative-binomial GLMM that applied only to 30 plots surveyed one growing season post burn. Then, we performed a backward model selection process and analyzed additional variables. The initial model set the plot as a random effect and included the following direct effects as covariates: proportion of ungulate browse, burn char height, burn season (winter, spring, summer, and fall), pre-burn total stems, precipitation, canopy closure, basal area (>10 cm dbh), elevation, aspect (east, south, southwest, and west), dominant overstory tree (>10 cm dbh), sample year (2015 to 2019), and slope.

To assess the density of hazelnut shrubs, we applied a multi-variate gamma generalized linear model (GLM) using Type III Wald Chi Square tests to perform backward model selection using the `car` package in R (Fox and Weisberg 2018). Burn frequency (either less than three burn events or at least three burn events from 1989 to 2019), basal area (>10 cm dbh), canopy closure, dominant overstory tree (>10 cm dbh), elevation, aspect, and slope were all evaluated as potential explanatory variables. A univariate gamma GLM was also used to compare the relationship between basal area and shrub density, and a Wilcoxon rank sum test was employed in R (R Core Team 2014) to evaluate the relationship between territory (Karuk and Yurok) and shrub density.

To examine average stem diameter and length of basketry stems within shrubs surveyed after one growing season post burn, we selected gamma distributed GLMMs, as length and diameter distributions were skewed toward smaller sizes. Potential explanatory variables that were treated as direct effects in the initial stem diameter model were: basal area (>10 cm dbh), plot canopy closure, annual precipitation, aspect, slope, dominant overstory tree (>10 cm dbh), and burn season (*e.g.,* fall, winter, spring, summer). These explanatory variables were then included in the initial stem length model with the addition of ungulate browse proportions. As with other GLMMs, the plot was set as a random effect, and Type III Wald Chi Square tests were used to perform backward model selection.

Model diagnostics were analyzed using the `DHARMa` package in R (Hartig 2019). To analyze the differences within categorical predictor variables that showed significance in the GLMMs, estimated marginal means ($\bar{x}$) were generated and then 95% confidence intervals were compared using the Tukey method using the `emmeans` package (Lenth 2018). Estimated marginal $\bar{x}$ values for categorical values are averaged over the values of other significant model co-variates, which helps account for imbalances in sampling effort. The `sjPlot` package (Lüdecke 2019) was used to analyze and visualize the effects of significant continuous predictor variables in the GLMMs.

Foraging gains from basketweaver gathering trip observations were modeled as logistic functions using the `growthcurver` package in R (Sprouffske and Wagner 2016) based upon assumptions of the marginal value theorem and foraging theory that predict diminishing gathering returns resulting from the depletion of basketry stems through harvesting (Charnov 1976; Stephens and Krebs 1986).

Across observed gathering sites, we evaluated associations between gathering site fire type (wild, cultural) and territory (Karuk, Yurok, Hupa) by employing Pearson's Chi-square (χ^2) test of independence using R statistical software (R Core Team 2014). Separately, the travel distances to hazelnut gathering sites within cultural burn, wildfire, and unburned (fire excluded) locations were compared in R using a Wilcoxon rank sum test.

Results

Hazelnut basketry stem productivity

We found that fire strongly increased basketry stem productivity, but the effect declined rapidly over time (Fig. 3). Hazelnut shrubs one season post burn produced a 13-fold increase in basketry stems (estimated marginal $\bar{x}$ = 10.776, SE = 0.87), compared to shrubs three or more growing seasons post burn (estimated marginal $\bar{x}$ = 0.801, SE = 0.08), and six times more stems than shrubs two growing seasons post burn (estimated marginal $\bar{x}$ = 1.807, SE = 0.25, Fig. 3). Other covariates also emerged as important predictors: stem production declined with overstory tree basal area (Fig. 4), while sample years exhibited significant differences in basketry stems due to imbalances in yearly burning (χ^2 = 19.9, df = 4, P < 0.001).

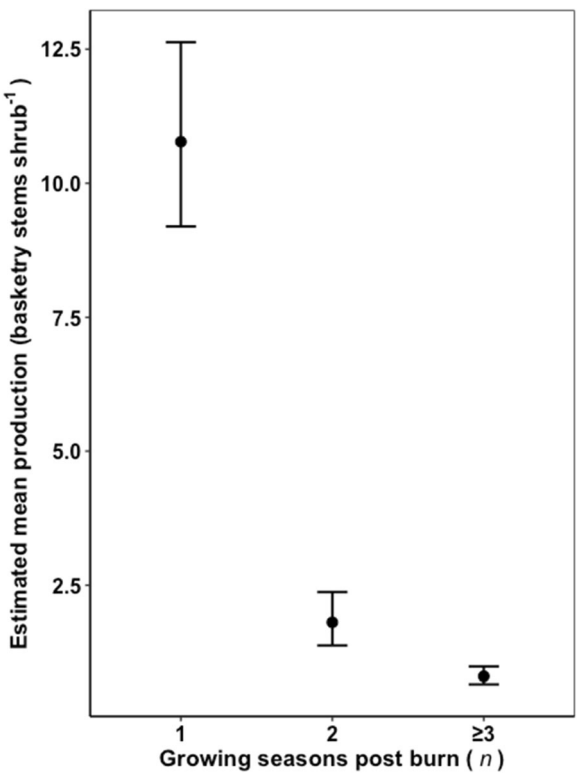


Fig. 3 Hazelnut basketry stem production (plus 95% confidence interval) with growing seasons post burn (2015 to 2019) in Karuk and Yurok territory, northwestern California, USA. Estimated marginal means are based on values generated from a negative-binomial generalized linear mixed model, and averaged over sample years due to imbalances in the data

Considering only shrubs growing one season post burn, a number of covariates significantly predicted basketry stem productivity (Table 1). Shrub vigor, measured by pre-burn total stems, had a strong positive relationship on basketry stem production (Table 1), whereas ungulate browse reduced basketry stems (estimate = −0.706, SE = 0.146, Z = −4.826; Fig. 5; Table 1). Burn season and aspect class also emerged as significant covariates in the single season post-burn model of best fit (Table 1).

Hazelnut shrub density

Hazelnut shrub density within plots was affected by burn frequency, aspect, and elevation (Table 2). Plots that were burned at least three times from 1989 to 2019 had 1.86 times more individual shrubs than plots burned less than three times (Fig. 6). Plots within eastern aspects had 2.2-fold higher density of hazelnut shrubs (estimated marginal $\bar{x}$ = 93.5, SE = 18.33) than those growing in southern (estimated marginal $\bar{x}$ = 43.5, SE = 3.99) and southwestern aspects (estimated marginal $\bar{x}$ = 42.5, SE = 4.86, P < 0.001; Table 2). Shrub densities also decreased with increased elevation (range = 170 to 934 m a.s.l, estimate = 0.000024, SE = 0.0000115, t = 2.13, P < 0.05; Table 2). Although territory was not a significant covariate in the multi-variate gamma GLM, shrub densities in Yurok territory were 2.19-fold greater than shrub densities within Karuk territory (Wilcoxon test statistic = 74, P < 0.001; Fig. 6). Additionally, overstory tree basal area was nonsignificant in the gamma GLM, but displayed a negative relationship with shrub density in univariate analysis (estimate = −0.00019, SE = 0.00007, t = 2.67, P < 0.05).

Basketry stem length and diameter

Basketry stem length and diameter was affected by burn season. Summer burns produced larger stem diameters (estimated marginal $\bar{x}$ = 4.54 mm, SE = 0.32) when compared with spring (estimated marginal $\bar{x}$ = 3.08 mm, SE = 0.25, P = 0.003) and winter burning (estimated marginal $\bar{x}$ = 3.64 mm, SE = 0.25, P = 0.037; Fig. 7). Spring burns also produced shorter stem lengths than all other burn seasons (estimated marginal $\bar{x}$ = 0.524 m, SE = 0.057, P < 0.05). The diameter and length of stems had an inverse relationship with overstory tree basal area (>10 cm dbh, P < 0.01; Figs. 7 and 8), and the proportion of ungulate browse was negatively correlated with stem length (estimate = −0.357, SE = 0.102, Z = −3.49, P < 0.001) in the gamma generalized linear mixed model. Furthermore, stems growing beneath canopies dominated by hardwoods were significantly longer (estimated marginal $\bar{x}$ = 0.83 m, SE = 0.062) than stems growing beneath coniferous canopies (estimated marginal $\bar{x}$ = 0.65 m, SE = 0.051; Fig. 8).

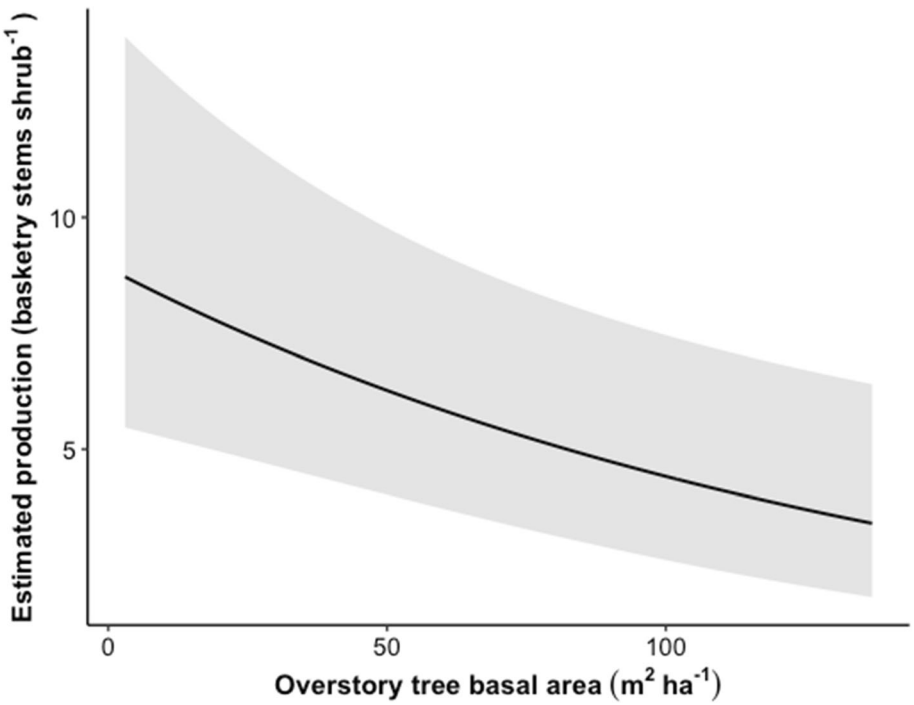


Fig. 4 Estimated hazelnut basketry stem production (plus 95% confidence interval, gray) with overstory tree (>10 cm dbh) basal area in Karuk and Yurok territory, northwestern California, USA, from 2015 to 2019. Estimates include shrubs in all temporal growing season classes (one, two, and three or more growing seasons post burn)

Hazelnut basketry stem gathering

All hazelnut basketry stems were gathered within a few weeks of bud break in the spring, between 20 March and early May, depending on the site aspect and elevation. The majority of basketweavers observed were either retired (14%) or employed by the Tribes, Forest Service, or local school districts (78%). While some employers provide flexible work hours that enable the gathering of ecocultural species like hazelnut, most hazelnut stem gathering observed here occurred on the weekends (84% of gathering trips). Basketweavers expressed that they would prefer to gather close to home, but few suitable burned hazelnut groves were located in close proximity to their residences. Three basketweavers noted that, despite the fact that they had relatively small patches (<500 m^2) of hazelnut on their landholdings that they burned regularly, these sites produced insufficient quantities of basketry stems to satisfy their needs. Thus, individuals with small hazelnut patches on their properties needed to gather at other burned sites to support their weaving.

Of all stem gatherers, we consistently recorded annual harvesting from six individuals from 2016 to 2019. Only one of these individuals gathered exclusively in Karuk territory while the other five individuals consistently gathered within Yurok territory. The five who gathered within Yurok territory, on average, gathered at 1.4 burn sites from 2016 to 2018 (range of total distinct sites = 3 to 5), and in 2019 visited 2.8 sites (six distinct sites visited). Four of these basketweavers reported that they engaged in five or more gathering trips within the hazelnut gathering season.

Gathering hazelnut stems requires a considerable commitment if burned areas are distant and the presence of quality hazelnut stems is unknown. Because some basketweavers now reside relatively far from ancestral territories and burned hazelnut groves, basketweavers were observed to travel considerable distances to gather. Based on 49 recorded trips to gathering patches, harvesters traveled a median distance of 34 km one way (range = 0 to 472 km) and an average of 60 km (±10.9 km). Basketweavers travelled 3.8-fold greater distances to reach wildfire gathering sites ($\bar{x}$ = 129 km, SE = 40 km) compared with cultural burn areas ($\bar{x}$ = 38 km, SE = 6 km, Wilcox test statistic = 72, $P < 0.01$).

From 2015 to 2019, basketweavers and stem gatherers selected 21 independent burn areas to gather hazelnut basketry stems; 76% of these sites were culturally burned and 24% were burned by wildfires. Of these sites, 29% were on US Forest Service land, 48% were privately owned, and 23% were tribally owned fee or trust lands (Yurok and Hoopa Valley reservations). Gathering trips in Yurok territory all occurred at culturally burned sites,

Table 1 Variables affecting hazelnut basketry stem production one growing season post-burn (2015 to 2019) in Karuk and Yurok territory, northwestern California, USA. Results of a Wald Type III Chi Square test (χ^2) on the significance of ungulate shrub browse proportion, pre-burn total stems, burn season (winter, spring, summer, and fall), and aspect class (east, southeast, south, southwest, and west) on basketry stem production generated from a negative-binomial generalized linear mixed model. Aspect classes included east (67.5° to 112.5°); southeast (112.5° to 157.5°); south (157.5° to 202.5°); southwest (202.5° to 247.5°); and west (247.5° to 292.5°). Only shrubs located in southern aspects (n = 124, estimated marginal $\bar{x}$ = 13.62, SE = 0.99) produced significantly different stems compared with those found in eastern aspects (n = 56, estimated marginal $\bar{x}$ = 8.01, SE = 1.23). Shrubs burned in the winter (n = 42, estimated marginal $\bar{x}$ = 15.54, SE = 1.73) produced 1.67-fold greater basketry stems than shrubs burned in the spring (n = 55, estimated marginal $\bar{x}$ = 9.32, SE = 1.05, P < 0.01), and 1.43-fold greater basketry stems than shrubs burned in the fall (n = 113, estimated marginal $\bar{x}$ = 10.89, SE = 0.92, P < 0.05). No other seasonal comparisons exhibited significant differences, and burn char height, dominant overstory tree, canopy closure, annual precipitation, elevation, and slope did not exhibit strong effects on basketry stem production and were removed from the model. Hazelnut shrub plots (n = 30; 400 m^2) are set as random effects. df = degree of freedom

Fixed effects	χ^2	df	*P*
Ungulate browse proportion (%)	23.29	1	<0.0001
Pre-burn total stems (*n*)	116.09	1	<0.0001
Burn season	13.41	3	0.003
Aspect class	10.04	3	0.018

whereas the 20 trips to gathering sites in Karuk and Hupa territories were more likely to occur at wildfire sites (Table 3).

Poor gathering sites (n = 12) tended to be sites gathered two or more growing seasons post burn, or sites that were heavily browsed by ungulates. Within five cultural burn sites on Forest Service land in Karuk territory, harvesters deemed stems to be poor quality due to heavy browsing. This was likely caused by the isolation of sites and lack of burning in surrounding areas, creating a strong patch-choice effect that attracted large numbers of browsers to the small area of the burn. Other sites that were assessed as relatively poor quality were those that were not burned at a sufficient intensity. At low-intensity burn sites, gatherers found that basketry stems were challenging to access given the limited consumption of underbrush and surface and ladder fuels (*e.g.,* down logs with branches, or small trees and shrubs).

Gatherers spent a mean 56 ±16 minutes per hazelnut stem gathering site. At cultural burn sites, mean gathering rates were significantly higher than gathering rates recorded at four wildfire locations and at a fire-excluded site (Fig. 9). While wildfires in this region burn hazelnut shrubs, basketweavers remarked that searching for hazelnut shrubs in these typically remote wildfire areas requires considerable additional time. Ms. Verna Reece, a renowned Karuk basketweaver and teacher, shared that she is one of the few gatherers who invests the necessary time and effort to drive the roads through wildfire areas in Karuk territory to scout and locate suitable hazelnut groves. Because Ms. Reece shares her knowledge of locations of hazelnut patches within wildfire areas, many of her students benefit from her initial reconnaissance and knowledge of local fire history.

Discussion

Basketry stem quality and ecology

Post-burn basketry stem qualities are important to basketweavers, who require a variety of stems of different lengths and diameters depending on what they intend to weave (Lake 2007: 243; O'Neale 1932). Longer stems provide enhanced functionality than shorter stems, as they can be cut depending upon the basketry project (V. Reece, personal communication). Therefore, measurements of stem diameter and length may assist both fire managers and basketweavers to identify and prioritize forest stand characteristics, burn season, and the frequency of cultural fires in hazelnut groves of interest across the landscape and, thus, promote socio-cultural values and ecological heterogeneity.

Overstory basal area was found to be negatively correlated to stem length, and hardwood overstories supported longer stem lengths when compared with coniferous overstories (on average 18 cm longer). These relationships may be attributed to greater understory light transmittance in forest stands with lower basal area, and broadleaf trees such as oaks (Fralish 2004; Barbier et al. 2008). Given that lower basal areas also support overall basketry stem production, canopy thinning in hazelnut groves would likely improve quality and quantity of basketry stems. Targeting relatively young coniferous trees for thinning would also support the recovery and growth of encroached hardwoods, whose populations have become compromised by Douglas-fir in the region (Hunter and Barbour 2001; Engber et al. 2011; Cocking et al. 2012; Schriver et al. 2018).

Shrubs that were burned in the spring produced significantly shorter stems compared to all other burn seasons. This result can be attributed to the truncated growing season caused by these burns, which occurred after bud break. For certain basketry projects that require longer stems (*e.g.,* baby cradles), these stems are less functional. However, shorter stems also tend to have smaller diameters, which is a desired quality for basketweavers producing baskets that require a tight weave (*e.g.,* basket caps; Johnson and Marks 1997). The stem

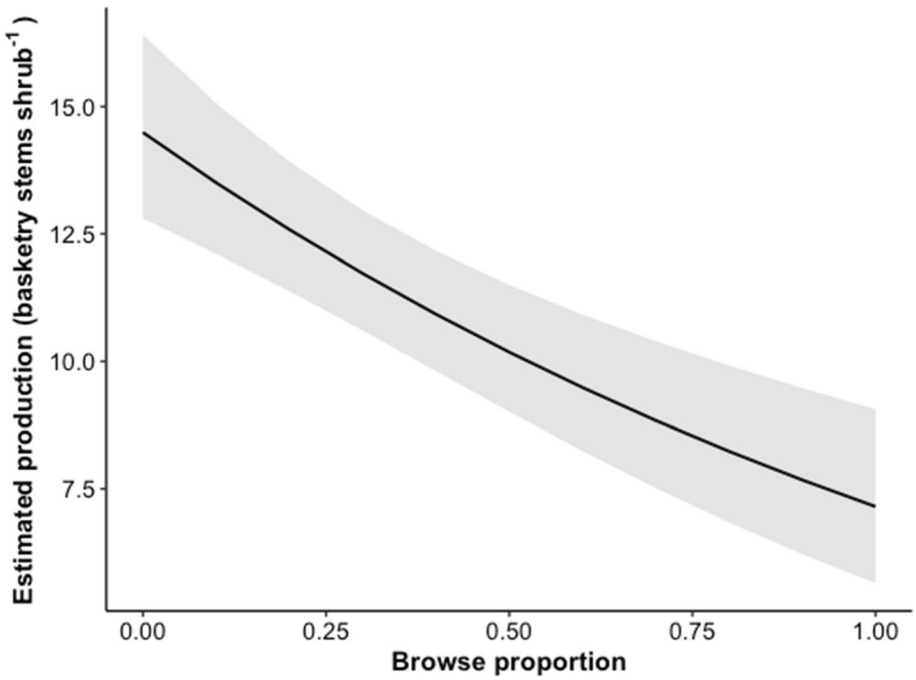


Fig. 5 Proportion of hazelnut shrub browsed with estimated basketry stem production values (plus 95% confidence interval, gray) from the one growing season post-burn temporal class in Karuk and Yurok territory, northwestern California, USA, from 2015 to 2019

wood to pith ratio is also different among spring- versus fall-burned hazelnut shoots, which affects the tensile strength and durability for use in weaving (Rentz 2003; Lake 2007). Moreover, spring burning raises concerns for some tribal members as burning during this season may negatively affect wildlife and was less common preceding colonialism (Knapp et al. 2009; Marks-Block et al. 2019). Tribal members have also taken advantage of recent winter droughts (Griffin and Anchukaitis 2014) and dry periods to increase cultural burning for hazelnut basketry stems. Stems produced from these burns also had a smaller diameter compared with those produced from summer burns, and were longer than stems burned in the spring. Hence, finding receptive burning opportunities in the winter may produce stems of desirable qualities, without the potential negative effects of burning in the spring.

Table 2 Variables affecting hazelnut shrub density (2015 to 2019) in Karuk and Yurok territory, northwestern California, USA. Results of a Wald Type III Chi Square test (χ^2) on the significance of burn frequency, elevation, and aspect class on hazelnut shrub density generated from a gamma generalized linear model. Aspect classes included east (67.5° to 112.5°); southeast (112.5° to 157.5°); south (157.5° to 202.5°); southwest (202.5° to 247.5°); and, west (247.5° to 292.5°). df = degree of freedom

Fixed effects	χ^2	df	*P*
Burn frequency	23.6	1	<0.0001
Elevation	4.8	1	0.027
Aspect class	21.9	4	<0.001

Ungulate browse also shortened stems and initiated lateral stem branching, reducing the functionality and quality of stems. When high proportions of stem browse occurred at cultural burn sites, basketweavers rated their quality as poor, and few basketweavers selected these sites for gathering. While browse occurs at all sites, if burning is conducted near residences, the nearby presence of dogs and people may discourage interspecies competition for post-burn hazelnut resprouts, and have the additional benefit of reducing wildfire hazards. Additionally, expanding the frequency and area (extent and place) of cultural burn sites, and managing wildfires to achieve resource objectives and socio-ecological benefits, may reduce interspecies competition for hazelnut resprouts by providing sufficient high-quality browse for ungulates across the landscape (Wan et al. 2014).

Ecology of basketry stem production and hazelnut shrub density

Our results clearly show that cultural burning optimizes the production of hazelnut basketry stems, but that this effect is the product of short fire intervals (*e.g.*, 3 to 5 yr). Because basketweavers can quickly exhaust a small hazelnut patch, optimizing basketry stem production requires a mosaic of recently burned patches, those regenerating from harvest, and those ready to be burned all within close proximity to residential locales. More

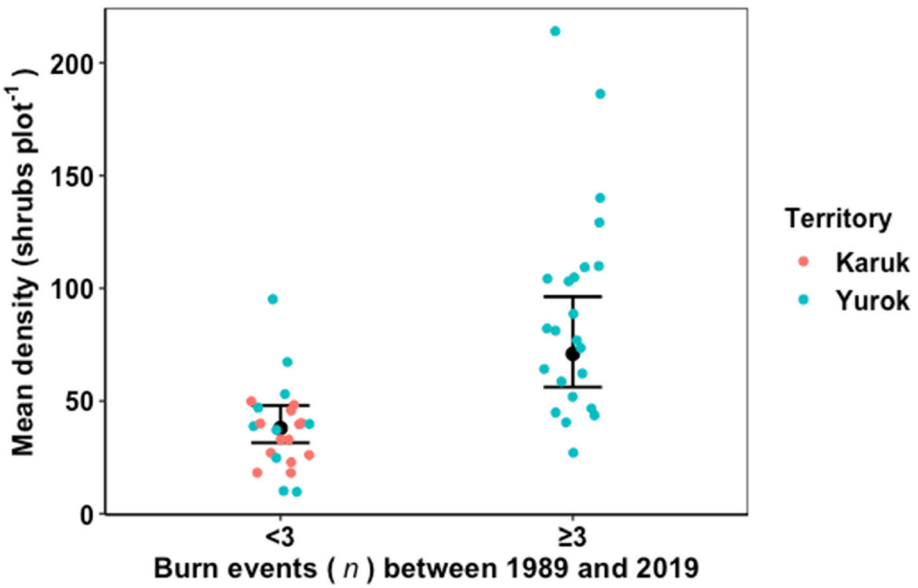


Fig. 6 Hazelnut shrub densities with number of burns in Karuk and Yurok territory, northwestern California, USA, from 1989 to 2019. Data was collected from 2015 to 2019. Scattered colored points are 400 m^2 plot shrub densities. Black points with 95% confidence intervals (bars) are estimated marginal means generated from a generalized linear model. Sites with less than three burn events had significantly greater hazelnut shrubs (estimated marginal $\bar{x}$ = 71.0, SE = 9.53) than plots burned less than three times (estimated marginal $\bar{x}$ = 38.1, SE = 4.02)

common fall burns do not produce basketry stems until ~18 months post burn; thus, different sites need to be burned annually to ensure annual harvests. This fire regime strongly concurs with California Indian basketweaver knowledge of hazelnut fire ecology and practice of cultural burning (O'Neale 1932; Thompson 1991; Ortiz 1998; Anderson 1999), and aids in the interpretation of regional fire history studies regarding fire frequency and seasonality (Taylor and Skinner 1998, 2003; Fry and Stephens 2006; F. Lake, USDA Forest Service,

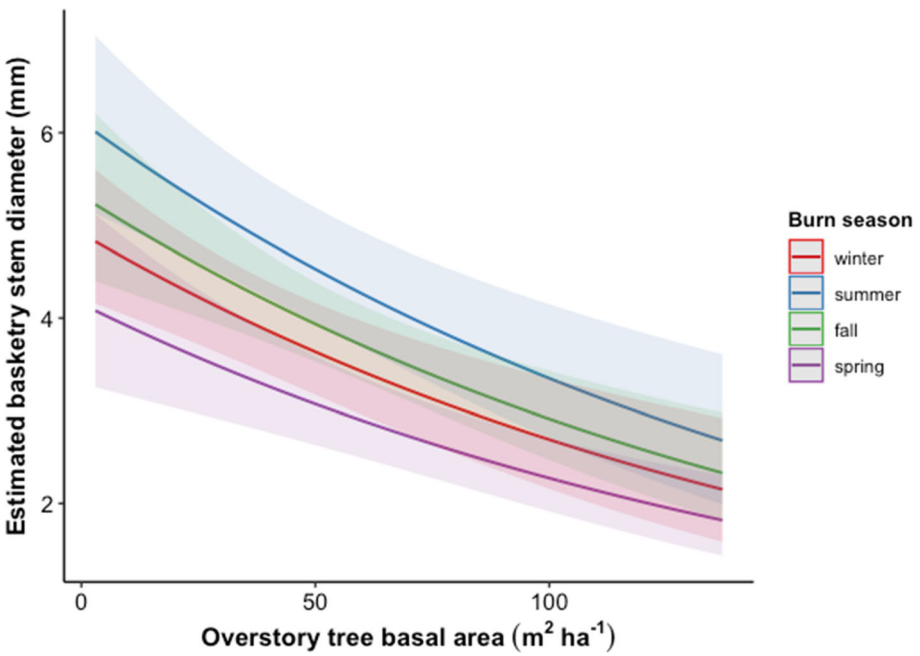


Fig. 7 Overstory tree (>10 cm dbh) basal area with estimated hazelnut basketry stem diameters (plus 95% confidence intervals) and burn season (summer, fall, winter, and spring) in Karuk and Yurok territory, northwestern California, USA, from 2015 to 2019

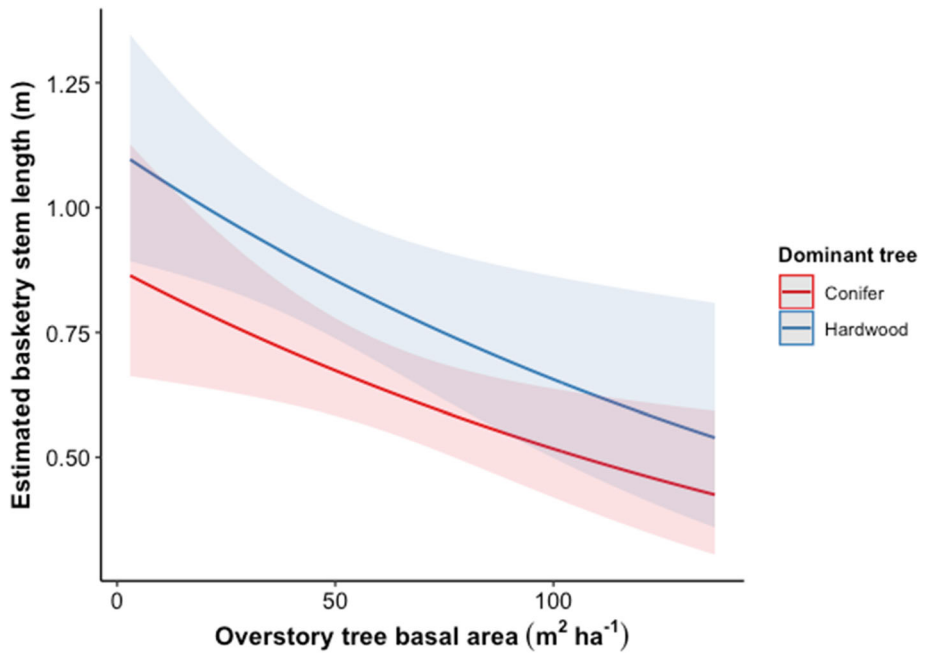


Fig. 8 Overstory tree (>10 cm dbh) basal area and dominant overstory tree with estimated hazelnut basketry stem length (plus 95% confidence intervals) one year post burn in Karuk and Yurok territory, northwestern California, USA, from 2015 to 2019

Arcata, and E. Knapp, USDA Forest Service, Redding, California, USA, unpublished data).

Higher hazelnut shrub densities occur in areas that have burned in ≥3 events within 30 years, increasing the density of basketry stems in these areas post burn compared with hazelnut groves where fire has been excluded and shrub densities are lower. Greater shrub density and basketry stem production in areas with relatively less overstory basal area also suggest that short-interval burning would benefit hazelnut shrubs, as these overstory conditions are promoted by frequent, low-intensity fire regimes (Stephens and Fulé 2005; Scholl and Taylor 2010). Given the vital importance of hazelnut stems in Karuk and Yurok culture, and for many other tribes regionally, burning for hazelnut undoubtedly affected the abundance of hazelnut across the pre-colonial landscape. Greater densities of hazelnut shrubs at lower elevations may be an artifact of the historical settlement of Karuk and Yurok villages along the Klamath River (Waterman 1920; Kroeber 1936), and the repeated cultural burning of hazelnut groves in close proximity to villages and favored resource camps.

Table 3 Hazelnut stem gathering trips by tribal territory and fire type in Yurok, Karuk, and Hoopa territory, northwestern California, USA. Trips were observed or reported by basketweavers and stem gatherers from 2014 to 2019. According to Pearson's χ^2 test, trips to gathering sites in Karuk and Hupa territories were significantly more likely to occur at wildfire sites compared with trips in Yurok territory ($\chi^2 = 41.03$, df = 2, $P < 0.0001$)

	Gathering trips (*n*) per territory		
Fire type	**Yurok**	**Karuk**	**Hupa**
Cultural fire	69	6	3
Wildfire	0	7	3

A staggered, low intensity, and frequent cultural fire regime, as proposed by Lightfoot and Parrish (2009), alters the species assemblage and maintains ecoculturally valuable hazelnut groves in a relatively stable ecological state (Botkin and Sobel 1975; Petraitis and Latham 1999, Beisner et al. 2003). This socio-ecological system is akin to the burned areas that Lewis and Ferguson (1988) referred to as "fire yards and corridors" that were regularly burned to maintain prairies. However, in this case, these yards are not anthropogenic prairies, but the park-like forests often described by early European settlers (Sudworth 1900; Leiberg 1902; Pyne 1982; Muir 2008). Unlike anthropogenic burning in the spinifex desert of Australia (Bliege Bird et al. 2008), or the swidden Mayan milpa that creates a shifting successional mosaic (Nigh and Diemont 2013), hazelnut groves are maintained by frequent low-intensity burning that inhibits successional processes. The focal ecocultural species in a hazelnut grove is woody and has a re-sprouting life history, which suggests that a distinctive burning regime is required to maintain hazelnut, compared to a "yard" of herbaceous perennials or annuals.

This socio-ecological model was described in 1916 by Lucy Thompson, a Yurok woman, who stated that, "The

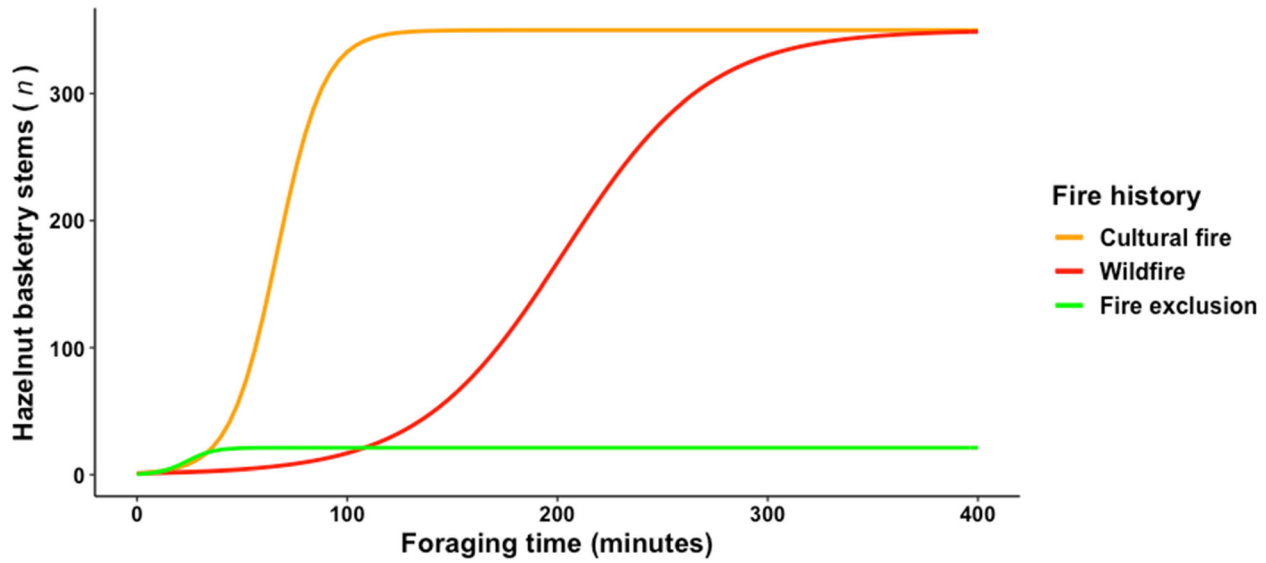


Fig. 9 Fire history and hazelnut basketry stem gathering rates modeled as logistic functions in Karuk and Yurok territory, northwestern California, USA, from 2015 to 2019. Foraging time includes travel and gathering time for stem harvesters. Gathering rates are based on average rates observed in 22 cultural burn areas (five stems per individual per minute), four wildfire areas (two stems per individual per minute), and one fire-excluded area (0.5 stems per individual per minute). Travel time to gathering areas was calculated from the mean distance travelled one way (34 km to cultural burn; 129 km to wildfire; 2 km to fire exclusion area) at a rate of 80 km hr^{-1}. This model assumes that a gatherer aims to harvest 350 stems, based upon the average harvest observed from trips to nine cultural burn areas

Douglas fir timber…has always encroached on the open prairies and crowded out the other timber; therefore they have continuously burned it" (Thompson 1991: 33). This finding was further developed and articulated as a state and transition model by Huntsinger and McCaffrey (1995) that included woodlands, but did not address important understory ecocultural species like hazelnut. Similarly, other ecological studies in northern California montane forests have found that repeated burning by lightning fires maintains steady shrubland states (Odion et al. 2010; Lauvaux et al. 2016), and that, in the absence of fire, oak woodlands transition to Douglas-fir stands (Hunter and Barbour 2001; Engber et al. 2011; Schriver et al. 2018). Hence, this fire-mediated dynamic is quite prevalent in the region, and supports the finding that hazelnut is less abundant in the absence of frequent fire.

Over the long term, positive feedbacks between cultural burning and hazelnut provide a niche-construction mechanism that improves landscapes in a wide variety of ways (Jones et al. 1994, 1997; Smith 2011; Odling-Smee et al. 2013; Bliege Bird 2015). Cultural burning increases stem production for basketweavers, but also increases quality forage for ungulates (Lawrence and Biswell 1972; Kie 1984; Long et al. 2008, Williamson and Weckerly 2020), and may also improve nut production for humans and wildlife (Lake 2007; Fine et al. 2013; Armstrong et al. 2018). Cultural burns may also increase wildlife habitat, supporting biodiversity (Martin and Sapsis 1992; Hankins 2009) and endangered species such as the California Condor (*Gymnogyps californianus* [Shaw, 1797]) and Spotted Owl (*Strix occidentalis* [Xántus de Vésey, 1860]) that feed in edge habitats and clearings (Cowles 1967; Franklin et al. 2000; Roberts et al. 2011; Nabhan and Martinez 2012; Eyes et al. 2017). The improvements in habitat and biodiversity that emerge from understory burning (Webster and Halpern 2010; Knapp et al. 2013; Wynecoop et al. 2019) have cascading effects on a wide range of other plant and animal species, which in turn sustain the cultural traditions, economic livelihoods, and social and physical well-being of the fire-dependent cultures that rely on these species and processes in their ancestral territories (Heffner 1984; Ortiz 1993; Mathewson 2007; Eriksen and Hankins 2015; Smith 2016).

Basketry stem gathering and fire governance

Cultural burning directly supports the maintenance and revitalization of northwestern California Indian basket-weaving by reducing the costs associated with basketry stem gathering. Foraging efficiencies are greatly improved by burning, and subsequently influence the selection of basketry stem gathering sites. Basketry stem gathering rates are 10-fold greater in cultural burn areas compared with fire-excluded hazelnut groves, leaving little incentive to gather in unburned areas (Anderson 1999). Without accounting for the increase in travel time to wildfire areas, cultural burn areas generated gathering rates that are 3-fold greater than those in wildfire areas,

which we attribute to greater shrub densities associated with repeated cultural burning. Accordingly, stem gatherers selected burn sites of higher quality more frequently than those areas of poor quality and lower shrub densities. These results offer strong evidence that stem-gatherer decision-making adheres to basic optimal foraging theories of maximizing efficiency (Stephens and Krebs 1986).

Land dispossession and limited tribal autonomy over burn practices have caused stem gatherers to select less than ideal harvesting sites. In Karuk territory, land dispossession was comparatively greater than in Yurok territory, thus, in recent decades, Tribal members have not been able to maintain as many hazelnut groves with consistent cultural burning. Collaborative burning between the Karuk Tribe and the USDA Forest Service tends to fluctuate with staff who are supportive of burning, but who may often transfer from the region (Diver 2016; Smith 2016). The sites where these collaborative burns occurred have predominantly been in remote locations where overstory basal area is relatively high, shrub densities are relatively low, and ungulate browse has been heavy. As a result, Karuk stem gatherers tend to gather in areas burned by wildfires, where they have found higher quality basketry stems. However, compared with culturally burned sites in Yurok territory, the gathering costs are higher due to increased travel and lower shrub densities. Despite USDA Forest Service policy changes that permit gathering by indigenous peoples (Kalt 2007), several basketweavers expressed that the persistence of racism, as well as its ongoing manifestations of harassment, imprisonment, and violence toward Indigenous peoples for gathering, hunting, and burning on their lands, makes them hesitant to gather hazelnut stems on national forests (Smith 2016; Norgaard 2019).

Gatherers generally do not harvest in hazelnut groves that they perceive as belonging to other families, or in tribal territories where they do not have social ties or permission. Hence, while higher quality groves occur in Yurok territory, individuals without Yurok ancestry or familial ties will gather at lower-quality hazelnut groves out of respect for land affiliations, unless they are invited. This social dynamic reflects the historically decentralized Karuk and Yurok governance structures preceding colonialism, in which usufruct rights to resource tracts were organized at the level of families and individuals (Waterman 1920; Thompson 1991; Huntsinger and Diekmann 2010; Bettinger 2015).

The centralization of resource and fire management by the US government and the fragmentation of tribal land ownership reduced access to ecocultural resources such as hazelnut basketry stems (Huntsinger and Diekmann 2010). Nonetheless, Karuk and Yurok Tribal members initiated successful burning programs that have reduced the relative scarcity of hazelnut stems and support cultural revitalization. To adjust to these new modes of governance, the Tribes developed their own natural resource departments and wildland fire departments, and established partnerships with the USDA Forest Service and non-governmental organizations such as fire safe councils and The Nature Conservancy, to co-manage fire and resources (Long and Lake 2018). Tribal basketweavers have also self-organized to form organizations such as the California Indian Basketweavers Association (LeBeau 1998; Kallenbach 2009) and Karuk Indigenous Basketweavers to address the need for cultural burn partnerships. In Karuk territory, these partnerships have supported the development of long-term cultural fire restoration projects that intend to initiate regular repeated burns in hazelnut groves (USDA Forest Service PSW Region 2018).

In Yurok territory, basketweavers and their families have initiated a successful cultural burning program that reduced the relative scarcity of hazelnut stems. The Cultural Fire Management Council (CFMC) began to burn hazelnut groves annually in 2013, and supported families and the Tribe to maintain regular burns. In 2019, the CFMC President, Margo Robbins (Yurok), shared that, "Ten years ago it wasn't often that you'd see a baby in a basket. Now there are lots of babies in baskets because of TREX." Basketweavers like Margo articulate a clear connection between burning and its role in supporting cultural revitalization.

Conclusion

Partnerships between tribes, non-governments organizations, and government agencies have supported the contemporary burning of hazelnut groves, much like collaborative burning projects in South America and Australia (Fache and Moizo 2015; Mistry et al. 2019; Neale et al. 2019), but increased tribal sovereignty and familial autonomy over burning in ancestral lands will ensure not only its maintenance, but its expansion (Baldy 2013; Robbins et al. 2016). Collaborations between fire managers and American Indian communities will support the revitalization of cultural burning and help achieve multiple socio-ecological management objectives (Lake et al. 2017; LeCompte 2018; Lewis et al. 2018; Long and Lake 2018; Wynecoop et al. 2019). Collaboration with basketweavers is vital when burning objectives include hazelnut basketry stems. Ideally, multiple hazelnut groves in a region will be burned frequently (every three to five years) in a staggered fashion, which will reduce obstacles to access (*e.g.,* downed logs and dense stands of small trees), support high shrub densities, and offer yearly harvesting opportunities.

The revitalization of Karuk and Yurok cultural burning provides an alternative model for restoring fire and

ecological function to landscapes that experienced fire exclusion and industrial timber extraction (Nikolakis and Roberts 2020). Compared with many non-tribal restoration initiatives focused upon conservation and hazardous fuel–fire risk reduction, California Indian initiatives primarily aim to restore socio-ecological relationships with ecocultural fire-enhanced species for cultural, ceremonial, and subsistence use. Because their practices were partially responsible for the historical fire regime, burning practices of indigenous and place-based fire-dependent cultures may be more effective at restoring the desired reference landscapes that conservation organizations and public land agencies intend to re-create (Kimmerer 2011; Lake 2013; Bliege Bird and Nimmo 2018). Moreover, tribes, resource users, and local entities appear to be well equipped to maintain burning over the long term, whereas limited budgets and complex political processes have constrained prescribed burning by land management agencies (Steelman and Burke 2007; North et al. 2015; Schultz and Moseley 2019). Cultural burns observed here indicate that this fire governance model exhibits considerable potential to support fire-adaptive socio-ecological communities (Abrams et al. 2015; Roos et al. 2016).

Acknowledgements
We truly appreciate the Karuk and Yurok Tribal Councils for their permission and continuing support to conduct this work on their lands and within their communities. Tribal GIS programs provided mapping data resources. Our research design benefited immeasurably from the critical input and generous involvement of Karuk and Yurok basketweavers, gatherers, and fire managers: E. Azzuz, C. Chook Hillman, L. Hillman, R. McConnell, R. McConnell Jr., K. McCovey, B. Peters, M. Peters, V. Reece, M. Robbins, B. Souza, and B. Tripp. We thank anonymous reviewers whose feedback greatly improved this paper, and N. Johnson (USDA Forest Service Pacific Southwest Research Station) for providing invaluable statistical contributions.
All opinions, findings, and conclusions or recommendations expressed here are those of the authors and do not necessarily reflect the views of the US National Science Foundation or Tribes, and should not be construed to represent any official USDA or US government determination or policy.

Authors' contributions
All authors contributed to study design and writing the manuscript. TMB implemented the study and analyzed the data. All authors read and approved the final manuscript.

Funding
Financial support instrumental in the initial development of this project was received from the US National Science Foundation's (NSF) Coupled Natural and Human Systems grant (DEB-1232319) to R. Bliege Bird and L. Curran at Stanford University. For this project and ongoing collaborative programs with the Tribes, L. Curran and T. Marks-Block received financial support from the US Joint Fire Science Program (#L17AC00214) and NSF Doctoral Dissertation Improvement Grant (1657569). T. Marks-Block was awarded additional support from NSF's Graduate Research Fellowship (DGE-114747), Stanford University's Department of Anthropology, Vice Provost for Graduate Education Diversity Dissertation Research Opportunity, and School of Humanities and Sciences Community Engagement grant. The USDA Forest Service also supported F. Lake with this research.

Availability of data and materials
Datasets used and analyzed during this study are available from the corresponding author upon request.

Ethics approval and consent to participate
Stanford University IRB approved this study (#33064), as did the Karuk and Yurok Tribal Councils.

Consent for publication
Consent for photographs on file.

Competing interests
All authors declare that they have no competing interests.

Author details
[1]Department of Anthropology, Geography and Environmental Studies, California State University, East Bay, 25800 Carlos Bee Boulevard, Meiklejohn Hall 4036, Hayward, California 94542, USA. [2]Pacific Southwest Research Station, Fire and Fuels Program, USDA Forest Service, 1700 Bayview Drive, Arcata, California 95521, USA. [3]Department of Anthropology, 323A Carpenter Building, Pennsylvania State University, University Park, State College, Pennsylvania 16802, USA. [4]Woods Institute for the Environment, Jerry Yang and Akiko Yamazaki Environment and Energy Building, 473 Via Ortega, Stanford University, Stanford, California 94305, USA.

Received: 4 August 2020 Accepted: 12 January 2021
Published online: 19 February 2021

References
Abrams, J. B., Knapp, M., Paveglio, T. B., Ellison, A., Moseley, C., Nielsen-Pincus, M., & Carroll, M. C. (2015). Re-envisioning community-wildfire relations in the U.S. West as adaptive governance. *Ecology and Society*, 20(3:34), 1-27. https://doi.org/10.5751/ES-07848-200334

Aldern, J.D., and R.W. Goode. 2014. The stories hold water: Learning and burning in North Fork Mono homelands. *Decolonization: Indigeneity, Education & Society* 3 (3): 26–51.

Anderson, M. K. (1999). The fire, pruning, and coppice management of temperate ecosystems for basketry material by California Indian tribes. *Human Ecology*, 27(1), 79-113. https://doi.org/10.1023/A:1018757317568

Anderson, M.K. 2018. The use of fire by Native Americans in California. In ***Fire*** *in California's ecosystems*, ed. J. van Wagtendonk, N.G. Sugihara, S.L. Stephens, A. E. Thode, K.E. Shaffer, and J. Fites-Kaufman, 381–397. Oakland, California: University of California Press.

Armstrong, C., Dixon, W., & Turner, N. (2018). Management and traditional production of Beaked Hazelnut (k'áp'xw-az', Corylus cornuta; Betulaceae) in British Columbia. *Human Ecology*, 46(4), 547-559. https://doi.org/10.1007/s10745-018-0015-x

Aswani, S. (1998). Patterns of marine harvest effort in southwestern New Georgia, Solomon Islands: resource management or optimal foraging? *Ocean & Coastal Management*, 40(2-3), 207-235. https://doi.org/10.1016/S0964-5691(98)00047-7

Ayres, R. W., & Hutchinson, W. I. (1931). *Forest Rangers' Catechism: Questions and Answers on the National Forests of the California Region*. Washington DC: US Department of Agriculture. https://doi.org/10.5962/bhl.title.65578

Baldy, C. R. (2013). Why we gather: traditional gathering in native Northwest California and the future of bio-cultural sovereignty. *Ecological Processes*, 2(1), 1-10. https://doi.org/10.1186/2192-1709-2-17

Baldy, C.R. 2018. *We Are Dancing for You: Native Feminisms and the Revitalization of Women's Coming-of-Age Ceremonies*. Seattle, Washington: University of Washington Press.

Barbier, S., Gosselin, F., & Balandier, P. (2008). Influence of tree species on understory vegetation diversity and mechanisms involved-a critical review for temperate and boreal forests. *Forest Ecology and Management*, 254(1), 1-15. https://doi.org/10.1016/j.foreco.2007.09.038

Baumhoff, M. 1963. Ecological determinants of aboriginal California populations. *American archaeology and ethnology* 49 (2): 155–236.

Beisner, B. E., Haydon, D. T., & Cuddington, K. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, 1(7), 376-382. https://doi.org/10.1890/1540-9295(2003)001[0376:ASSIE]2.0.CO;2

Bettinger, R. L. (2015). Orderly Anarchy: Sociopolitical Evolution in Aboriginal California. Oakland, California: University of California Press. https://doi.org/10.1525/9780520959194

Bibby, B. 2004. *Precious Cargo: California Indian Cradle Baskets and Childbirth Traditions*. Berkeley, California: Heyday Press.

Bilbao, B. A., Leal, A. V., & Méndez, C. L. (2010). Indigenous use of fire and forest loss in Canaima National Park, Venezuela. Assessment of and tools for alternative strategies of fire management in Pemón indigenous lands. *Human Ecology*, 38(5), 663-673. https://doi.org/10.1007/s10745-010-9344-0

Bliege Bird, R. (2015). Disturbance, complexity, scale: New approaches to the study of human-environment interactions. *Annual Review of Anthropology*, 44, 241-257. https://doi.org/10.1146/annurev-anthro-102214-013946

Bliege Bird, R., Bird, D. W., Codding, B. F., Parker, C. H., & Jones, J. H. (2008). The "fire stick farming" hypothesis: Australian Aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *Proceedings of the National Academy of Sciences of the United States of America*, 105(39), 14796-14801. https://doi.org/10.1073/pnas.0804757105

Bliege Bird, R., Codding, B., Kauhanen, P., & Bird, D. (2012). Aboriginal hunting buffers climate-driven fire-size variability in Australia's spinifex grasslands. *Proceedings of the National Academy of Sciences*, 109(26), 10287-10292. https://doi.org/10.1073/pnas.1204585109

Bliege Bird, R., & Nimmo, D. (2018). Restore the lost ecological functions of people. *Nature Ecology & Evolution*, 2, 1050-1052. https://doi.org/10.1038/s41559-018-0576-5

Bliege Bird, R., Tayor, N., Codding, B., & Bird, D. (2013). Niche construction and dreaming logic: aboriginal patch mosaic burning and varanid lizards (Varanus gouldii) in Australia. *Proceedings of the Royal Society B: Biological Sciences*, 280(1772), 20132297. https://doi.org/10.1098/rspb.2013.2297

Botkin, D.B., and M.J. Sobel. 1975. Stability in time-varying ecosystems. *The American Naturalist* 109 (970): 625–646 https://doi.org/10.1086/283034.

Bower, R.W. 1978. *Chronological History of the Klamath National Forest: People, Places, Programs, and Events*. Yreka, CA: USDA Forest Service, Klamath National Forest.

Buckley, T. (2002). *Standing Ground: Yurok Indian Spirituality, 1850-1990*. Berkeley, California: University of California Press. https://doi.org/10.1525/9780520936447

Butler, W. H., & Goldstein, B. E. (2010). The US fire learning network: Springing a rigidity trap through multi-scalar collaborative networks. *Ecology and Society*, 15(3), 21. https://doi.org/10.5751/ES-03437-150321

US Census Bureau. (2017). Cartographic Boundary Shapefiles - American Indian/Alaska Native Areas/Hawaiian Home Lands. https://www.census.gov/geo/maps-data/data/cbf/cbf_aiannh.html. Accessed 10 January 2018

Cermak, R. 2005. *Fire in the Forest: A History of Forest Fire Control on the National Forests in California, 1898-1956*. Vallejo, California: USDA Forest Service, Pacific Southwest Region.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorum. *Theoretical Population Biology*, 9(2), 129-136. https://doi.org/10.1016/0040-5809(76)90040-X

Clar, R.C. 1959. *California Government and Forestry*. Sacramento, California.: Division of Forestry, State of California.

Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., et al. (2013). Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist*, 197(1), 19-35. https://doi.org/10.1111/nph.12001

Cocking, M. I., Varner, J. M., & Sherriff, R. L. (2012). California black oak responses to fire severity and native conifer encroachment in the Klamath Mountains. *Forest Ecology and Management*, 270, 25-34. https://doi.org/10.1016/j.foreco.2011.12.039

Cohodas, M. 1997. *Basket Weavers for the California Curio Trade: Elizabeth and Louise Hickox*. Tucson, Arizona: University of Arizona Press.

Colegrove, N. 2014. *Decision Memo: Roots and Shoots (Traditional Cultural) Project*. Six Rivers National Forest: Lower Trinity/Orleans/Ukonom Ranger Districts.

Conners, P. 1998. *A History of Six Rivers National Forest...Commemorating the First 50 Years*. Eureka, California: USDA Forest Service, Pacific Southwest Region, Six Rivers National Forest https://foresthistory.org/wp-content/uploads/2017/01/HISTORY-OF-THE-SIX-RIVERS-NATIONAL-FOREST.pdf. Accessed 1 October 2018.

Core Team, R. 2014. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Cowles, R. B. (1967). Fire suppression, faunal changes and condor diets. In Proceedings of the 7th Tall Timbers Fire Ecology Conference (Vol. 9, pp. 217-224).

Davies, G., and F. Frank. 1992. *Stories of the Klamath National Forest: The First 50 Years*. Hat Creek, California: HiStory ink Books.

Diver, S. (2016). Co-management as a catalyst: Pathways to post-colonial forestry in the Klamath Basin, California. *Human Ecology*, 44(5), 533-546. https://doi.org/10.1007/s10745-016-9851-8

Engber, E. A., Varner III, J. M., Arguello, L. A., & Sugihara, N. G. (2011). The effects of conifer encroachment and overstory structure on fuels and fire in an oak woodland landscape. *Fire Ecology*, 7(2), 32-50. https://doi.org/10.4996/fireecology.0702032

Eriksen, C., & Hankins, D. L. (2014). The retention, revival, and subjugation of indigenous fire knowledge through agency fire fighting in eastern Australia and California. *Society & Natural Resources*, 27(12), 1288-1303. https://doi.org/10.1080/08941920.2014.918226

Eriksen, C., and D.L. Hankins. 2015. Colonisation and fire: Gendered dimensions of indigenous fire knowledge retention and revival. In *The Routledge Handbook of Gender and Development*, 129–137. New York: Routledge.

Eyes, S. A., Roberts, S. L., & Johnson, M. D. (2017). California Spotted Owl (Strix occidentalis occidentalis) habitat use patterns in a burned landscape. *The Condor: Ornithological Applications*, 119(3), 375-388. https://doi.org/10.1650/CONDOR-16-184.1

Fache, E., & Moizo, B. (2015). Do burning practices contribute to caring for country? Contemporary uses of fire for conservation purposes in indigenous Australia. *Journal of Ethnobiology*, 35(1), 163-182. https://doi.org/10.2993/0278-0771-35.1.163

Fiala, A. C. S., Garman, S. L., & Gray, A. N. (2006). Comparison of five canopy cover estimation techniques in the western Oregon Cascades. *Forest Ecology and Management*, 232(1-3), 188-197. https://doi.org/10.1016/j.foreco.2006.05.069

Fine, P. V. A., Misiewicz, T. M., Chavez, A. S., & Cuthrell, R. Q. (2013). Population genetic structure of California hazelnut, an important food source for people in Quiroste Valley in the Late Holocene. *California Archaeology*, 5(2), 353-370. https://doi.org/10.1179/1947461X13Z.00000000019

Fowler, C. 2012. *Ignition Stories: Indigenous Fire Ecology in the Indo-Australian Monsoon Zone*. Durham, North Carolina: Carolina Academic Press.

Fox, J., and S. Weisberg. 2018. *An R Companion to Applied Regression*. Thousand Oaks, California: Sage Publications.

Fralish, J.S. 2004. The keystone role of oak and hickory in the central hardwood forest. In *Upland oak ecology symposium: History, current conditions, and sustainability. US Forest Service General Technical Report SRS-73*, 78–87. Asheville, North Carolina: U.S. Department of Agriculture, Forest Service, Southern Research Station.

Franklin, A. B., Anderson, D. R., Gutiérrez, R. J., & Burnham, K. P. (2000). Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs*, 70(4), 539-590. https://doi.org/10.1890/0012-9615(2000)070[0539:CHQAFI]2.0.CO;2

Fry, D., & Stephens, S. (2006). Influence of humans and climate on the fire history of a ponderosa pine-mixed conifer forest in the southeastern Klamath Mountains, California. *Forest Ecology and Management*, 223(1), 428-438. https://doi.org/10.1016/j.foreco.2005.12.021

Fryer, J. (2007). Corylus cornuta. Fire Effects Information System, [Online]. https://www.fs.fed.us/database/feis/plants/shrub/corcor/all.html. Accessed 9 July 2018

Griffin, D., & Anchukaitis, K. J. (2014). How unusual is the 2012-2014 California drought? *Geophysical Research Letters*, 41(24), 9017-9023. https://doi.org/10.1002/2014GL062433

Hankins, D.L. 2009. The Effects of Indigenous Prescribed Fire on Herpetofauna and Small Mammals in Two Central Valley California Riparian Ecosystems. *The California Geographer* 49: 31–50.

Hankins, D. L. (2013). The effects of indigenous prescribed fire on riparian vegetation in central California. *Ecological Processes*, 2(1), 1-9. https://doi.org/10.1186/2192-1709-2-24

Harling, W. 2015. Learning together, burning together. *Wildfire Magazine* 24 (1): 26–30 https://www.iawfonline.org/article/learning-together-burning-together/.

Hartig, F. (2019). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. *R package version* 0.2.4. http://florianhartig.github.io/DHARMa/

Heffner, K. 1984. *"Following the Smoke": Contemporary plant procurement by the Indians of Northwest California*. Eureka, California: Manuscript on file, Heritage Resource Program, Six Rivers National Forest.

Hillman, L., and J.F. Salter. 1997. Environmental management: American Indian knowledge and the problem of sustainability. *Forests, Trees and People Newsletter* 34: 20–26.

Hunter, J. C., & Barbour, M. G. (2001). Through-growth by Pseudotsuga menziesii: A mechanism for change in forest composition without canopy gaps. *Journal of Vegetation Science*, 12(4), 445-452. https://doi.org/10.2307/3236996

Hunter, J.E. 1988. Prescribed burning for cultural resources. *Fire Management Notes* 49 (2): 8–9.

Huntsinger, L., and L. Diekmann. 2010. Virtual reservation: Land distribution, natural resource access, and equity on the Yurok forest. *Natural Resources Journal* 50 (2): 341–370.

Huntsinger, L., & McCaffrey, S. (1995). A forest for the trees: Forest management and the Yurok environment, 1850 to 1994. *American Indian Culture and Research Journal*, 19(4), 155-192. https://doi.org/10.17953/aicr.19.4.cv0758kh373323h1

Johnson, R., and C.K. Marks. 1997. *Her Mind Made Up: Weaving Caps the Indian Way*. Arcata, California: Ron Johnson, Humboldt State University.

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69(3), 373-386. https://doi.org/10.2307/3545850

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78(7), 1946-1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2

Kallenbach, E. 2009. The California Indian Basketweavers Association: Advocates for the use of museum collections by contemporary weavers. *Museum Anthropology Review* 3 (1): 1–13.

Kalt, J. 2007. Public lands traditional gathering policy finalized. *News from Native California* 20 (4): 7–8.

Kie, J. G. (1984). *Deer habitat use after prescribed burning in northern California. Res. Note PSW-RN-369*. Berkeley, California: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. https://doi.org/10.2737/PSW-RN-369

Kimmerer, R. W. (2011). Restoration and reciprocity: the contributions of traditional ecological knowledge. In D. Egan, E. Hjerpe, & J. Abrams (Eds.), *Human Dimensions of Ecological Restoration* (pp. 257-276). New York: Springer. https://doi.org/10.5822/978-1-61091-039-2_18

Knapp, E. E., Estes, B. L., & Skinner, C. N. (2009). Ecological effects of prescribed fire season: a literature review and synthesis for managers. Gen. Tech. Rep. PSW-GTR-224. Albany, California: USDA Forest Service, Pacific Southwest Research Station. https://doi.org/10.2737/PSW-GTR-224

Knapp, E. E., Skinner, C. N., North, M. P., & Estes, B. L. (2013). Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management*, 310, 903-914. https://doi.org/10.1016/j.foreco.2013.09.041

Kroeber, A.L. 1936. *Karok Towns*. Berkeley, California: University of California Press.

Lake, F.K. 2007. *Traditional Ecological Knowledge to Develop and Maintain Fire Regimes in Northwestern California*. Klamath-Siskiyou Bioregion: Management and Restoration of Culturally Significant Habitats. PhD Dissertation. Oregon State University, Corvallis, Oregon.

Lake, F.K. 2013. Trails, trials and tribulations: Tribal resource management and research issues in northern California. *Occasion* 5: 1–22.

Lake, F. K., Wright, V., Morgan, P., McFadzen, M., McWethy, D., & Stevens-Rumann, C. (2017). Returning fire to the land-celebrating traditional knowledge and fire. *Journal of Forestry*, 115(5), 343-353. https://doi.org/10.5849/jof.2016-043R2

Lang, J. 1991. The basket and world renewal. *Parabola* 16 (3): 83–85.

Lang, J. 1994. *Ararapikva: Creation Stories of the People: Traditional Karuk Indian Literature from Northwestern California*. Berkeley, California: Heyday Press.

Laris, P. (2002). Burning the seasonal mosaic: Preventative burning strategies in the wooded savanna of Southern Mali. *Human Ecology*, 30(2), 155-186. Accessed 14 October 2015 https://doi.org/10.1023/A:1015685529180

Larson, A. M., & Soto, F. (2008). Decentralization of natural resource governance regimes. Annual Review of Environment and Resources, 33, 213-239. https://doi.org/10.1146/annurev.environ.33.020607.095522

Lauvaux, C. A., Skinner, C. N., & Taylor, A. H. (2016). High severity fire and mixed conifer forest-chaparral dynamics in the southern Cascade Range, USA. *Forest Ecology and Management*, 363, 74-85. https://doi.org/10.1016/j.foreco.2015.12.016

Lawrence, G., & Biswell, H. (1972). Effect of forest manipulation on deer habitat in Giant Sequoia. *The Journal of Wildlife Management*, 36(2), 595-605. https://doi.org/10.2307/3799092

LeBeau, M. 1998. Federal land management agencies and California Indians: a proposal to protect native plant species. *Environs: Environmental Law & Policy Journal* 21 (2): 27–47.

LeCompte, J. 2018. Restoration, Risk, and the (Non) Reintroduction of Coast Salish Fire Ecologies in Washington State. In *Fire Otherwise: Ethnobiology of burning for a changing world (pp. 128-150)*, ed. C.T. Fowler and J.R. Welch. University of Utah Press.

Leiberg, J. B. (1902). *Forest conditions in the northern Sierra Nevada, California (Vol. U.S. Geolo)*. Washington, D.C., USA: US Government Printing Office. https://doi.org/10.3133/pp8

Lemmon, P.E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science* 2 (4): 314–320.

Lenth, R. 2018. Emmeans: Estimated marginal means, aka least-squares means. *R package version* 1 (4): 6 https://cran.r-project.org/web/packages/emmeans/index.html.

Levy, S. (2005). Rekindling native fires. *BioScience*, 55(4), 303-308. https://doi.org/10.1641/0006-3568(2005)055[0303:RNF]2.0.CO;2

Lewis, H., & Ferguson, T. A. (1988). Yards, corridors, and mosaics: How to burn a boreal forest. *Human Ecology*, 16(1), 57-77. https://doi.org/10.1007/BF01262026

Lewis, M., Christianson, A., & Spinks, M. (2018). Return to flame: Reasons for burning in Lytton First Nation, British Columbia. *Journal of Forestry*, 116(2), 143-150. https://doi.org/10.1093/jofore/fvx007

Lightfoot, K., & Parrish, O. (2009). *California Indians and Their Environment: An Introduction*. Berkeley, California: University of California Press. https://doi.org/10.1525/9780520942288

Long, J., & Lake, F. K. (2018). Escaping social-ecological traps through tribal stewardship on national forest lands in the Pacific Northwest, United States of America. *Ecology and Society*, 23(2), 10. https://doi.org/10.5751/ES-10041-230210

Long, R. A., Rachlow, J. L., Kie, J. G., & Vavra, M. (2008). Fuels reduction in a western coniferous forest: effects on quantity and quality of forage for elk. *Rangeland Ecology & Management*, 61(3), 302-313. https://doi.org/10.2111/07-046.1

Lüdecke, D. (2019). sjPlot: Data visualization for statistics in social science. R package version 2.7.0. https://cran.r-project.org/package=sjPlot

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., et al. (2017). glmmTMB: generalized linear mixed models using template model builder. R package version 0.1.

Mallek, C., Safford, H., Viers, J., & Miller, J. (2013). Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. *Ecosphere*, 4(12), 1-28. https://doi.org/10.1890/ES13-00217.1

Marks-Block, T., Lake, F. K., & Curran, L. M. (2019). Effects of understory fire management treatments on California Hazelnut, an ecocultural resource of the Karuk and Yurok Indians in the Pacific Northwest. *Forest Ecology and Management*, 450, 117517. https://doi.org/10.1016/j.foreco.2019.117517

Martin, R.E., and D.B. Sapsis. 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. In *Proceedings of the Symposium on Biodiversity of Northwestern California: October 28 - 30, 1991, Santa Rosa, California*, ed. R.R. Harris, D.C. Erman, and H.M. Kerner, 150–157. Berkeley, California: Wildland Resources Center, Division of Agriculture and Natural Resources, University of California.

Mathewson, M.S. 2007. California Indian basketweavers and the landscape. In *To Harvest, to Hunt: Stories of Resource Use in the American West*, ed. J.L. Li, 40–56. Corvallis, Oregon: Oregon State University Press.

Miller, L.K. 2017. Native American land ownership in California's National Forests. *Forest History Today* 23 (2): 3–13.

Mistry, J., Schmidt, I. B., Eloy, L., & Bilbao, B. (2019). New perspectives in fire management in South American savannas: the importance of intercultural governance. *Ambio*, 48(2), 172-179. https://doi.org/10.1007/s13280-018-1054-7

Muir, J. 2008. *The Mountains of California*. London, United Kingdom: Penguin.

Nabhan, G. P., & Martinez, D. (2012). Traditional ecological knowledge and endangered species recovery: Is ethnobiology for the birds? *Journal of Ethnobiology*, 32(1), 1-6. https://doi.org/10.2993/0278-0771-32.1.1

Neale, T., Carter, R., Nelson, T., & Bourke, M. (2019). Walking together: a decolonising experiment in bushfire management on Dja Dja Wurrung country. *Cultural Geographies*, 26(3), 341-359. https://doi.org/10.1177/1474474018821419

Nigh, R., & Diemont, S. A. W. (2013). The Maya milpa: fire and the legacy of living soil. *Frontiers in Ecology and the Environment*, 11(s1), e45-e54. https://doi.org/10.1890/120344

Nikolakis, W., & Roberts, E. (2020). Indigenous fire management: a conceptual model from literature. *Ecology and Society*, 25(4). https://doi.org/10.5751/ES-11945-250411

Norgaard, K.M. 2014. The politics of fire and the social impacts of fire exclusion on the Klamath. *Humboldt Journal of Social Relations* 36 (1): 77–101.

Norgaard, K. M. (2019). Salmon and Acorns Feed Our People: Colonialism, Nature, and Social Action. New Brunswick, New Jersey: Rutgers University Press. https://doi.org/10.36019/9780813584225

North, M. P., Stephens, S. L., Collins, B. M., Agee, J. K., Aplet, G., Franklin, J. F., & Fulé, P. Z. (2015). Reform forest fire management. *Science*, 349(6254), 1280-1281. https://doi.org/10.1126/science.aab2356

Odion, D. C., Moritz, M. A., & Dellasala, D. A. (2010). Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology*, 98(1), 96-105. https://doi.org/10.1111/j.1365-2745.2009.01597.x

Odling-Smee, J., Erwin, D. H., Palkovacs, E. P., Feldman, M. W., & Laland, K. N. (2013). Niche Construction Theory: A Practical Guide for Ecologists. *The Quarterly Review of Biology*, 88(1), 3-28. https://doi.org/10.1086/669266

O'Neale, L. 1932. *Yurok-Karok Basket Weavers*. Berkeley, California: University of California Press.

Ortiz, B. 1993. Contemporary California Indian basketweavers and the environment. In *Before the Wilderness: Environmental management by Native Californians*, ed. T.C. Blackburn and M.K. Anderson, 195–211. Menlo Park, California: Ballena Press.

Ortiz, B. 1998. Following the smoke: Karuk indigenous basketweavers and the forest service. *News from Native California* 11 (3): 21–29.

Petraitis, P., & Latham, R. (1999). The importance of scale in testing the origins of alternative community states. Ecology, 80(2), 429-442. https://doi.org/10.1890/0012-9658(1999)080[0429:TIOSIT]2.0.CO;2

Pinchot, G. 1905. *Use of the National Forest Reserves: Regulations and Instructions*. Washington DC: USDA Forest Service.

Pyne, S. 1982. *Fire in America. A cultural history of wildland and rural fire*. Princeton, New Jersey: Princeton University Press.

Rawls, J.J. 1986. *Indians of California: The changing image*. Norman, Oklahoma: University of Oklahoma Press.

Rentz, E. D. (2003). Effects of Fire on Plant Anatomical Structure in Native Californian Basketry Materials. Masters Thesis. San Francisco State University, San Francisco, California.

Robbins, M., D. McConnell, and R. Stauffer. 2016. Indigenous Peoples Burning Network (IPBN). *Conservation Gateway (The Nature Conservancy)* https://www.conservationgateway.org/ConservationPractices/FireLandscapes/FireLearningNetwork/RegionalNetworks/Documents/IPBN-Poster-Apr2016.pdf. Accessed 9 July 2018.

Roberts, S. L., van Wagtendonk, J. W., Miles, A. K., & Kelt, D. A. (2011). Effects of fire on spotted owl site occupancy in a late-successional forest. *Biological Conservation*, 144(1), 610-619. https://doi.org/10.1016/j.biocon.2010.11.002

Roos, C.I., A.C. Scott, C.M. Belcher, W.G. Chaloner, J. Aylen, R.B. Bird, et al. 2016. Living on a flammable planet: Interdisciplinary, cross-scalar and varied cultural lessons, prospects and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371 (1696): 20150469 https://doi.org/10.1098/rstb.

Salberg, T.A. 2005. *Hazel fuels reduction project: Integrating cultural resource management and hazardous fuels reduction*, 72–73. Winter: Evergreen Magazine.

Scholl, A. E., & Taylor, A. H. (2010). Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. *Ecological Applications*, 20(2), 362-380. https://doi.org/10.1890/08-2324.1

Schriver, M., Sherriff, R. L., Varner, J. M., Quinn-Davidson, L., & Valachovic, Y. (2018). Age and stand structure of oak woodlands along a gradient of conifer encroachment in northwestern California. *Ecosphere*, 9(10), e02446. https://doi.org/10.1002/ecs2.2446

Schultz, C. A., & Moseley, C. (2019). Collaborations and capacities to transform fire management. *Science*, 366(6461), 38-40. https://doi.org/10.1126/science.aay3727

Seijo, F., Millington, J. D. A., Gray, R., Sanz, V., Lozano, J., García-Serrano, F., et al. (2015). Forgetting fire: Traditional fire knowledge in two chestnut forest ecosystems of the Iberian Peninsula and its implications for European fire management policy. *Land Use Policy*, 47, 130-144. https://doi.org/10.1016/j.landusepol.2015.03.006

Senos, R., F.K. Lake, N. Turner, and D. Martinez. 2006. Traditional ecological knowledge and restoration practice. In *Restoring the Pacific Northwest: The art and science of ecological restoration in Cascadia*, ed. D. Apostol and M. Sinclair, 393–426. Washington DC: Island Press.

Shanks, R.C. 2006. In *Indian Baskets of Central California: Art, Culture, and History*, ed. L.W. Shanks. Novato, CA: Costaño Books.

Smith, B. D. (2011). General patterns of niche construction and the management of "wild" plant and animal resources by small-scale pre-industrial societies. Philosophical Transactions of the Royal Society of London. *Series B, Biological Sciences*, 366(1566), 836-848. https://doi.org/10.1098/rstb.2010.0253

Smith, C.A. 2016. *Weaving pikyav (to-fix-it): Karuk Basket Weaving in-Relation-with the Everyday World*. UC Berkeley, Berkeley, California: PhD Dissertation.

Smith, E. 1988. Risk and uncertainty in the'original affluent society': evolutionary ecology of resource-sharing and land tenure. *Hunters and gatherers: history, evolution, and social change* http://faculty.washington.edu/easmith/EAS_1988_R+U.PDF. Accessed 22 October 2015.

Spencer, A. G., Schultz, C. A., & Hoffman, C. M. (2015). Enhancing adaptive capacity for restoring fire-dependent ecosystems: the Fire Learning Network's Prescribed Fire Training Exchanges. *Ecology and Society*, 20(3), 38. https://doi.org/10.5751/ES-07847-200338

Sprouffske, K., & Wagner, A. (2016). Growthcurver: an R package for obtaining interpretable metrics from microbial growth curves. *BMC bioinformatics*, 17(1), 172. https://doi.org/10.1186/s12859-016-1016-7

Steelman, T. A., & Burke, C. A. (2007). Is wildfire policy in the United States sustainable? *Journal of Forestry*, 105(2), 67-72. https://doi.org/10.2139/ssrn.1931057

Stephens, D., and J. Krebs. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.

Stephens, S.L., and P.Z. Fulé. 2005. Western pine forests with continuing frequent fire regimes: possible reference sites for management. *Journal of Forestry* 103 (7): 357–362.

Stephens, S.L., and N. Sugihara. 2018. Fire management and policy since European settlement. In *Fire in California's Ecosystems*, ed. J. Van Wagtendonk, N. Sugihara, S. Stephens, A. Thode, K. Shaffer, and J. Fites-Kaufman, 399–410. Oakland, California: University of California Press.

Sudworth, G.B. 1900. Stanislaus and Lake Tahoe Forest Reserves, California and adjacent territory. In *Annual reports of the Department of the Interior, 21st annual report of the U.S. Geological Survey, Part 5*, 505–561. Washington DC: US Government Printing Office.

Sugihara, N., J. van Wagtendonk, and J. Fites-Kaufman. 2018. Fire as an ecological process. In *Fire in California's Ecosystems*, ed. J. van Wagtendonk, 2nd ed., 57–70. Oakland, CA: University of California Press.

Taylor, A. H., & Skinner, C. N. (1998). Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecology and Management*, 111(2), 285-301. https://doi.org/10.1016/S0378-1127(98)00342-9

Taylor, A. H., & Skinner, C. N. (2003). Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecological Applications*, 13(3), 704-719. https://doi.org/10.1890/1051-0761(2003)013[0704:SPACOH]2.0.CO;2

Taylor, A. H., Trouet, V., Skinner, C. N., & Stephens, S. L. (2016). Socioecological transitions trigger fire regime shifts and modulate fire-climate interactions in the Sierra Nevada, USA, 1600-2015 CE. *Proceedings of the National Academy of Sciences*, 113(38), 13684-13689. https://doi.org/10.1073/pnas.1609775113

Terence, M. (2016, November 3). Unleashing the TREX: Why officials think controlled burns can save California from wildfire. North Coast Journal, Eureka, California. November 3, pp. 16-23. http://www.northcoastjournal.com/humboldt/unleashing-the-trex/Content?oid=4132514

Thompson, L. 1991. *To the American Indian: Reminiscences of a Yurok Woman*. Berkeley, California: Heyday Press.

Underwood, S., L. Arguello, and N. Siefkin. 2003. Restoring ethnographic landscapes and natural elements in Redwood National Park. *Ecological Restoration* 21 (4): 278–283 https://doi.org/10.3368/er.21.4.278.

United States Census Bureau. (2010). 2010 Census interactive population map. http://www.census.gov/2010census/popmap/. Accessed 20 October 2016

USDA Forest Service PSW Region. (2018). Somes Bar Integrated Fire Management Project: Final Environmental Assessment. https://www.fs.usda.gov/nfs/11558/www/nepa/106291_FSPLT3_4291171.pdf. Accessed 1 June 2019

Wan, H.Y., A.C. Olson, K.D. Muncey, and S.B.S. Clair. 2014. Legacy effects of fire size and severity on forest regeneration, recruitment, and wildlife activity in aspen forests. *Forest ecology and management* 329: 59–68 https://doi.org/10.1016/j.foreco.2014.06.006.

Waterman, T. 1920. Yurok geography. *University of California Publications in American Archaeology and Ethnology* 16 (5): 177–314.

Webster, K. M., & Halpern, C. B. (2010). Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. *Ecosphere*, 1(5), 1-27. https://doi.org/10.1890/ES10-00018.1

Williamson, L. H., & Weckerly, F. W. (2020). Elk forage response to prescribed fire in Boyes meadow, Prairie Creek Redwoods State Park, California. California Fish and Wildlife, 106(3), 93-102.

Winterhalder, B., & Smith, E. A. (2000). Analyzing adaptive strategies: Human behavioral ecology at twenty-five. *Evolutionary Anthropology Issues News and Reviews*, 9(2), 51-72. https://doi.org/10.1002/(SICI)1520-6505(2000)9:2<51::AID-EVAN1>3.0.CO;2-7

Wynecoop, M. D., Morgan, P., Strand, E. K., & Trigueros, F. S. (2019). Getting back to fire sumés: exploring a multi-disciplinary approach to incorporating

traditional knowledge into fuels treatments. *Fire Ecology*, 15(1), 17. https://doi.org/10.1186/s42408-019-0030-3

Yurok GIS Program. (2015). Yurok Reservation and Surrounding Area. http://www.yuroktribe.org/departments/infoservices/GIS/documents/Statistics_Map_August15.pdf. Accessed 8 January 2018

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Submit your manuscript to a SpringerOpen journal and benefit from:

► Convenient online submission
► Rigorous peer review
► Open access: articles freely available online
► High visibility within the field
► Retaining the copyright to your article

Submit your next manuscript at ► springeropen.com

ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/242078159

The Relationships among In-Channel Sediment Storage, Pool Depth, and Summer Survival of Juvenile Salmonids in Oregon Coast Range Streams

Article *in* North American Journal of Fisheries Management · August 2004

DOI: 10.1577/M03-073.1

CITATIONS
89

READS
155

2 authors:



Christine L. May
James Madison University
33 PUBLICATIONS **1,721** CITATIONS
SEE PROFILE



Danny C. Lee
US Forest Service
55 PUBLICATIONS **1,871** CITATIONS
SEE PROFILE

All content following this page was uploaded by Christine L. May on 03 September 2014.

The user has requested enhancement of the downloaded file.

North American Journal of Fisheries Management 24:761–774, 2004
© Copyright by the American Fisheries Society 2004

The Relationships among In-Channel Sediment Storage, Pool Depth, and Summer Survival of Juvenile Salmonids in Oregon Coast Range Streams

CHRISTINE L. MAY* AND DANNY C. LEE

U.S. Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, California 95521, USA

Abstract.—The influence of channel aggradation on water availability and salmonid survival was investigated during the summer dry season in two Oregon Coast Range streams. Deep pools and a deformable streambed of coarse gravel were present in highly aggraded stream reaches. However, these thick, highly porous alluvial deposits caused surface flow to become intermittent, which stranded fish in drying channels. In gravel-bed reaches with thinner alluvial deposits, pool depth was limited by the underlying bedrock, but pools were sustained by hyporheic flow throughout the summer dry season. In these moderately aggraded reaches, pool depth and area decreased throughout the summer, resulting in severe crowding of fish trapped in pools formed over small patches of exposed bedrock and isolated by dry, gravel-bed riffles. Bedrock-dominated stream reaches had slightly smaller pools but were most likely to contain continuous surface flow throughout the summer dry season; these reaches exhibited the smallest decreases in pool depth and area. Repeated snorkel surveys indicated that fish abundance in pools decreased by 59% during the summer, significantly higher losses occurring in gravel-bed pools. Streambed substrate and partitioning of surface and subsurface flow may also have important implications for fish energetics due to differences in water temperature and food availability.

Stream channels in mountainous terrain can progressively build up (aggrade) or erode (degrade) the streambed in response to changes in sediment supply (Lisle 1982) or hydraulic controls such as large, in-stream wood (Nakamura and Swanson 1993; Montgomery et al. 1996; Buffington and Montgomery 1999). These processes are important to natural resource and fisheries managers, in part because: (1) land-use practices and wildfires, particularly preceding large storms, can be associated with massive inputs of sediment to stream channels (Swanson 1981; Madej and Ozaki 1996; Benda and Dunne 1997a; May and Gresswell 2003), and (2) the condition of stream channels may strongly affect the population viability of highly valued endangered species, such as coho salmon *Oncorhynchus kisutch*.

Although many studies have investigated the direct effects of fine sediment on the habitat and physiology of salmonids (e.g., Cooper 1965; Beschta and Jackson 1979; Tappel and Bjornn 1983; Lisle 1989; Lake and Hinch 1999), the effects of coarse sediment inputs have not been established. Many of the effects of fine sediment occur only during the egg-to-fry-emergence stage or when fine sediment is suspended in water during periods of high stream discharge. Because fluxes of coarse sediment can change the overall morphology of the channel, their effects are more persistent. Changes in channel morphology caused by large influxes of sediment may be particularly important during periods of extremely low stream discharge, when salmonids face challenging conditions for survival and growth, and during the incubation period, when stable spawning gravels are necessary. Thus, coarse sediment dynamics are highly likely to significantly affect population viability.

In the Oregon Coast Range, a large proportion of the channel network in mountainous terrain is susceptible to channel aggradation based on reach-scale transport and storage capacity (Montgomery et al. 2003). In this region, stream channels typically have a thin layer of highly mobile alluvium that is composed primarily of coarse gravel that resides directly over the underlying bedrock. The presence of a bedrock or alluvial reach morphology depends on the balance between local transport capacity and coarse sediment supply (Montgomery et al. 1996). This relationship can be influenced by log jams that trap sediment, local variations in sediment supply, and bedload-clast lithology (Montgomery et al. 1996; Massong and Montgomery 2000). Large influxes of sediment from landslides and debris flows can overwhelm the local transport capacity and can lead to sub-

* Corresponding author: cmay@seismo.berkeley.edu

Received April 20, 2003; accepted October 6, 2003

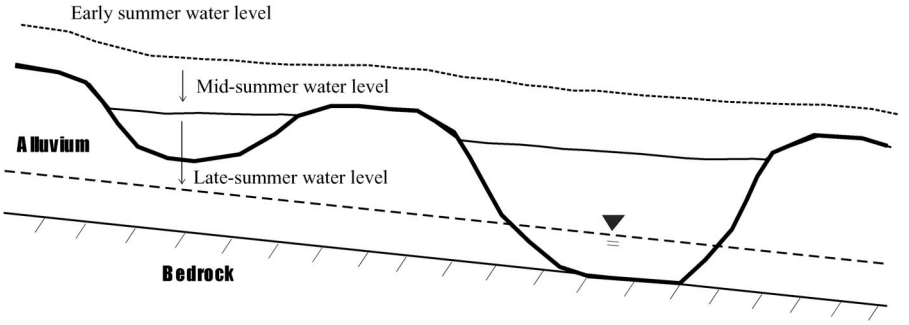


FIGURE 1.—Conceptual diagram of the influence of channel aggradation on water availability during the summer dry season.

stantial aggradation of the channel (Reeves et al. 1995; Benda and Dunne 1997b; Hogan et al. 1998).

Deep pools have the potential to form in aggraded reaches because of a deformable bed created by the stored alluvium. In reaches with less sediment in storage, the underlying bedrock typically limits pool depth (Reeves et al. 1995). Many studies have suggested that large, deep pools create optimal habitat for salmonids (Reeves et al. 1993; McIntosh et al. 1994; Bisson et al. 1997); however, expectations of habitat quality are often based on observations of large numbers of fish occupying deep pools. Such observations may be a misleading indicator of habitat quality because they do not consider how fish survival or growth varies among different pool types.

As an alternative to the conventional view of deep pools, we propose a hypothesis that deep pools formed in areas of thick alluvial deposits have a greater likelihood of going dry during the summer dry season, thereby posing a detriment to fish survival. In deep, highly porous substrates, streamflow levels can drop below the bed elevation during low-flow periods in late summer (Figure 1). This interaction with the hyporheic zone is created by surface water infiltrating through the gravel bed into the interstitial areas in the subsurface. Hyporheic flow eventually returns to the surface of the stream, particularly where patches of bedrock are exposed. There is a growing recognition that the hyporheic zone is an important and dynamic component of aquatic ecosystems (e.g., Hynes 1983; Stanford and Ward 1988, 1993; Findlay 1995; Edwards 1998; Wondzell and Swanson 1999). However, the volume of the hyporheic zone can be greatly increased by changes in sediment supply and retention (Edwards 1998). Alternatively, in areas of low sediment storage, smaller pools may form but these pools may have a higher likelihood of remaining wet throughout the summer because they intercept subsurface flow traveling across the bedrock surface. Patterns of pool drying thus provide a first-order control on fish survival during the summer dry season.

This study had four objectives: (1) to quantify the area and depth of pools in bedrock and aggraded stream reaches, (2) to document which pools persisted throughout the summer dry season, (3) to compare fish survival estimates between bedrock-controlled pools and pools formed in thick deposits of alluvium, and (4) to predict areas susceptible to channel aggradation and pool drying.

Study Basins

The Oregon Coast Range consists of rugged mountains at low elevations (<500 m) that are deeply dissected by an extensive drainage network of steep, V-shaped valleys. The topography is similar to the ridge and ravine topography described by Hack (1960). Landslides and debris flows are important processes in landform development and are dominant mechanisms for routing sediment from hill slopes and headwater streams into mainstem river valleys (Dietrich and Dunne 1978).

Segments of two streams with a mixture of bedrock and alluvial reaches were selected for investigation (Table 1; Figure 2). These sites were selected because they provided examples of channels that experienced recent influxes of coarse sediment and because their disturbance histories were well documented (Reeves et al. 1995; Benda and Dunne 1997a, 1997b; May and Gresswell 2004). Tertiary marine sedimentary rocks of the Tyee Formation (Baldwin 1964) underlie both basins. Harvey Creek, a tributary to the lower Umpqua River, has a history of minimal logging and road construction. Knowles Creek is a tributary to the Siuslaw

TABLE 1.—Channel and basin characteristics of Harvey and Knowles creeks, Oregon.

Variable	Harvey Creek	Knowles Creek
Channel length surveyed (m)	2,990	3,595
Drainage area of surveyed channel (km^2)	8.2–17.8	5.1–19.8
Number of		
Gravel-bed pools	65	18
Gravel pools with bedrock contact	9	22
Bedrock pools	13	26
Gravel-bed glides	7	15
Gravel glides with bedrock contact	0	8
Bedrock glides	2	19

River and is managed for commercial timber production. Two extremely large storms in 1996 triggered more than 20 debris flows in each basin (May 2002; May and Gresswell 2004).

The sandstone lithology of the southern and central Oregon Coast Range produces a unique particle-size distribution. Gravel and sand are the dominant particle sizes, and larger cobbles and boulders are typically limited to discrete patches associated with landslide and debris-flow deposits (Benda 1990). The low abundance of silt and clay produced from this lithology, combined with the loose gravel and sand, produce a highly porous substrate and a strong potential for hyporheic exchange.

The region has a maritime climate characterized by wet, relatively warm winters and dry summers. Average annual precipitation ranges from 165 to 229 cm, falling mostly as winter rain. The summer season is a period of extensive drought that typically persists from June through September. Mean monthly discharge for August at a nearby stream gauge on the undammed Siuslaw River was 4.5 m^3/s for the 26-year period of record. Mean August discharge during the study period (June–August 2002) was 4.1 m^3/s, which is only slightly below average. No increases in streamflow occurred during the sampling period (total June–August precipitation at North Bend Airport was less than 6 mm; National Weather Service, unpublished data).

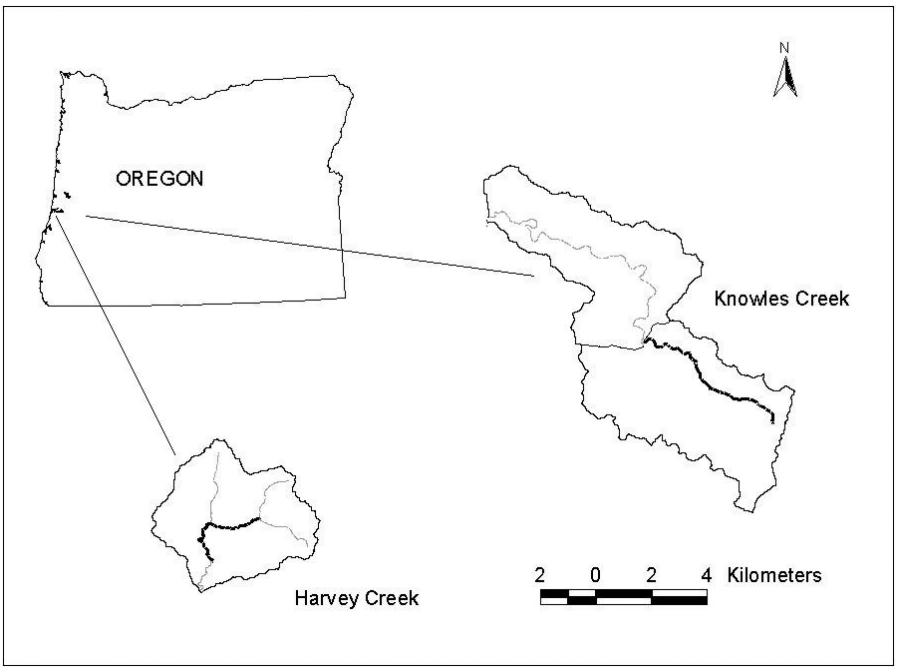


FIGURE 2.—Location of the study basins (Harvey and Knowles creeks) in the Oregon Coast Range, Oregon. Bold lines represent the study reaches.

TABLE 2.—Midsummer (24 June–11 July) and late-summer (25–30 August) connectivity of pools and glides in Harvey and Knowles creeks, Oregon, during 2002. Pools with high connectivity had sufficient streamflow between upstream or downstream riffles to allow fish passage. Low connectivity classifications only considered inflow from upstream in order to assess the potential for invertebrate drift.

Habitat type	Midsummer connectivity			Late-summer connectivity		
	High (%)	Low (%)	None (%)	High (%)	Low (%)	None (%)
Bedrock dominated	83	73	17	5	44	54
Gravel with bedrock contact	76	86	14	2	33	65
Gravel bed	32	37	63	0	1	99

Fish species present during the summer include juvenile coho salmon *Oncorhynchus kisutch*, juvenile steelhead *O. mykiss*, cutthroat trout *O. clarki*, sculpins *Cottus* spp., and dace *Rhinichthys* spp. The dominant forest type is Douglas-fir *Pseudotsuga menziesii* in the uplands; red alder *Alnus rubra* are common in riparian zones.

Methods

Surveys of habitat types and fish abundance were conducted during the dry season in midsummer (24 June–11 July 2002) and late summer (25–30 August 2002). All habitat units within the study area were censused and classified as pools, glides, or riffles (Bisson et al. 1982). Three pool types were identified: (1) pools scoured into alluvium, with no bedrock contact (gravel-bed pools), (2) pools scoured into alluvium, with a bedrock contact at the pool bottom (gravel pools with bedrock contact), and (3) pools formed by bedrock depressions that had little or no alluvium in storage (bedrock pools). Pools included in the survey were at least as long as the bank-full channel width, and at least 30 cm in maximum depth. Glides were classified as low-gradient, shallow (<30-cm maximum depth), homogenous channel units. Glides were similarly classified into three categories of bedrock and alluvial substrates and were included in all analyses except those based on residual pool dimensions. Because habitat classification is a subjective measure, observer bias can seriously compromise the repeatability, precision, and transferability of surveys (Hankin and Reeves 1988; Poole et al. 1997). To increase consistency of the surveys, a single individual, who was highly trained and experienced, classified all habitat units.

Residual pool depth and residual area were measured during midsummer for each pool by use of standard survey equipment and standard protocol (Lisle 1987). Residual depth is defined as the difference in bed elevation between the bottom-most point in a pool and the downstream riffle crest (Lisle 1987). Residual pool depth and area are useful metrics for quantifying pool dimensions because they are independent of discharge. Dimensions of the wetted channel and the maximum pool depth were recorded for each habitat unit during both sampling periods to assess the change in available habitat.

Connectivity to upstream or downstream habitats was documented for each habitat unit. Pools and glides that were completely isolated by dry riffles on the upstream and downstream ends were classified as having no connectivity. Pools and glides with inflow from shallow, upstream riffles that were impassable for fish but that still had the potential to provide a conduit for invertebrate drift were classified as having low connectivity. Pools and glides attached to upstream or downstream riffles that had sufficient flow to allow fish movement were classified as having high connectivity. Two standards were used. In coarse substrate, riffles less than 5 cm deep were considered barriers to fish passage. Coarse substrate provided intermittent pockets of water between individual grains, and no consistent fish passage corridors were apparent in these shallow riffles. For riffles with a bedrock substrate, a minimum of 2 cm of continuous flow was required for passage. This change in criteria was based on our observations of fish passing through extremely shallow riffles with a bedrock substrate where a continuous flow path was present. Because pools or glides with low connectivity on the upstream end could also be classified as having high connectivity on the downstream end, the row sums in Table 2 will not necessarily equal 100%.

The relative abundance of salmonids was estimated by snorkel surveys in each pool and glide during the midsummer and late-summer sampling periods. The midsummer survey was timed to coincide with the period when the majority of pools were becoming isolated, so that fish observed in an individual pool were presumably trapped there for the remainder of the summer. Riffles were usually too shallow for divers and were not included

in the surveys. Divers entered each habitat unit at the downstream end and proceeded slowly upstream. All observations of fish were made between 0900 and 1600 hours on days with little or no cloud cover. Divers identified salmonids as either juvenile coho salmon or juvenile trout. Sculpins and dace could not be estimated reliably because they commonly occupied benthic habitats.

Estimates of fish mortality, presumably due to desiccation, were based on the number of fish observed rearing in midsummer pools and glides that were dry by late summer. Mortality estimates were based on two underlying assumptions: (1) physical isolation of pools by midsummer prevented movement of fish among pools, and (2) all fish stranded in dry pools died. Because streamflow did not increase during the sampling period, we assumed that there were no opportunities for movement between isolated pools.

Stream temperature data were collected at 30-min intervals from 26 to 30 August in three pools within a 1-km section of Harvey Creek. We used Onset Stowaway temperature sensors, which have an accuracy of ±0.2°C. Prior to deploying the sensors in the field, we tested them for accuracy in the laboratory. Each sensor was located in a pool with different substrate and streamflow conditions.

Statistical analyses.—One-way analysis of variance (ANOVA) was used to detect significant differences among pool dimensions for each pool type. If a difference was detected, a Kruskal–Wallis multiple comparison procedure was used to identify which groups differed. The influence of residual pool depth on the likelihood of pools remaining wet throughout the summer was tested with the log-likelihood test in logistic regression.

Changes in fish abundance (i.e., survival from midsummer to late summer) and fish density in each pool type were tested by use of ANOVA, followed by a Kruskal–Wallis multiple comparison procedure to detect significant differences among groups. Data from pools that went dry during the summer were omitted from the analysis of fish density in order to assess the degree of crowding in remnant pools that persisted throughout the summer.

The likelihood of stream reaches going dry and the presence of gravel-bed pools were tested with logistic regression. The initial model included four reach-scale and basin-scale variables: (1) basin, (2) longitudinal distance upstream from the mouth of the basin to the headwaters (calculated from 10-m-resolution digital elevation models), (3) recent debris-flow deposits (identified during field surveys), and (4) depositional reaches that plotted below an empirically derived threshold of drainage area and channel slope (predicted by Montgomery et al. 1996). Reach-scale channel gradient was measured in the field with a clinometer, and drainage area was calculated from 10-m-resolution digital elevation models. Variables included in the final model were selected by the probability level of the parameter (those with $P < 0.05$ were included).

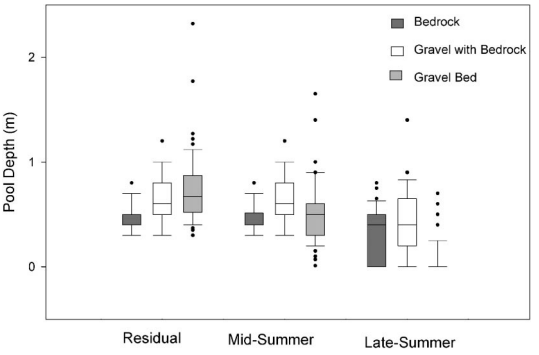


FIGURE 3.—Box-and-whisker plot of residual, midsummer (24 June–11 July), and late-summer (25–30 August) pool depths for three pool types in Harvey and Knowles creeks, Oregon, during 2002. The lower boundary of each box represents the 25th percentile, the midline represents the median, and the upper boundary represents the 75th percentile. The lower whisker represents the 10th percentile, the upper whisker represents the 90th percentile, and circles represent outlying points.

Results

Pool Size and Surface Water Availability

A total of 6.6 km of stream length was surveyed, which contained a total of 153 pools and 51 glides (Table 1). Residual pool depth (Figure 3) was significantly lower in bedrock pools than in the other pool types ($P = 0.0001$, one-way ANOVA). Median depth in each of the three pool types was less than 1 m. A few deep pools were measured in gravel-bed reaches (maximum depth = 2.3 m) and gravel pools with bedrock contact (maximum depth = 1.2 m); these depths were outside the range observed for bedrock pools (maximum depth = 0.8 m). Residual pool area (Figure 4) was slightly larger for gravel pools with bedrock contact than for other pool types ($P = 0.01$, one-way ANOVA).

Twenty-five percent of gravel-bed pools were already dry by midsummer, whereas no pools with bedrock contact were dry during this period (Figure 5). Pools with a bedrock control were more likely to persist throughout the summer dry season

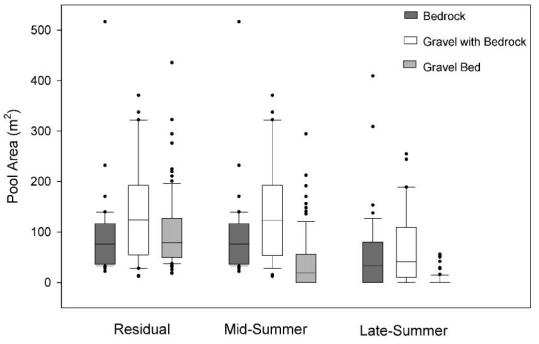


FIGURE 4.—Box-and-whisker plot of residual, midsummer (24 June–11 July), and late-summer (25–30 August) pool area for three pool types in Harvey and Knowles creeks, Oregon, during 2002. The lower boundary of each box represents the 25th percentile, the mid-line represents the median, and the upper boundary represents the 75th percentile. The lower whisker represents the 10th percentile, the upper whisker represents the 90th percentile, and circles represent outlying points.

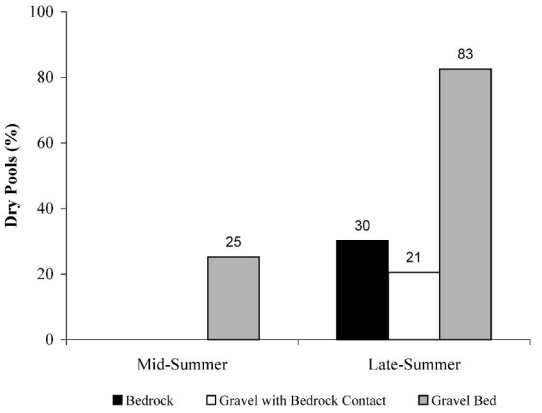


FIGURE 5.—Percentages of three pool types in Harvey and Knowles creeks, Oregon, that were dry by midsummer (24 June–11 July) and late summer (25–30 August) in 2002. Numeric values above the bars represent the actual percentages.

and exhibited the smallest individual decreases in pool depth and area. Seventy percent of bedrock pools remained wet by late summer, and the median decreases in pool depth and pool area were 17% and 40%, respectively. Seventy-nine percent of gravel pools with bedrock contact remained wet by late summer, and the median decreases in pool depth and area were 29% and 50%, respectively. Only 17% of gravel-bed pools persisted through late summer, accompanied by a 100% reduction in median residual pool depth and area.

Among pool types, deeper pools did not have a greater likelihood of remaining wet throughout the summer ($P = 0.05$, log-likelihood test in logistic regression). Within pool types, there was a positive correlation between residual pool depth and the likelihood of remaining wet throughout the summer for gravel-bed pools ($P = 0.02$, log-likelihood test in logistic regression).

Based on residual pool area, the greatest proportion of the total habitat area in both study basins consisted of gravel-bed pools. The majority of this habitat was unavailable, however, during late summer due to a lack of water (Figure 6). Bedrock pools had greater water availability and progressively became the dominant form of available habitat during the summer. By the end of the summer, connectivity was extremely limited for all pool types (Table 2), but the potential for invertebrate drift was highest in bedrock reaches due to the presence of continuous surface flow.

Depositional reaches (hereafter referred to as free-formed alluvial reaches) that plotted below an empirically derived threshold of drainage area and channel slope (Montgomery et al. 1996), recent debris-flow deposits, longitudinal distance from the mouth to the headwaters, and river basin were explanatory variables used to predict the occurrence of dry pools. Debris-flow deposits (a) and free-formed alluvial reaches (b) were highly significant variables ($P = 0.0001$, log-likelihood test) in a logistic regression model ($y = -0.73 + 2.50a + 3.02b$) that correctly predicted the occurrence of 70% of all dry units. No consistent longitudinal pattern ($P = 0.20$, log-likelihood test) or basin effect was detected ($P = 0.06$, log-likelihood test). Pools in free-formed alluvial reaches were 21

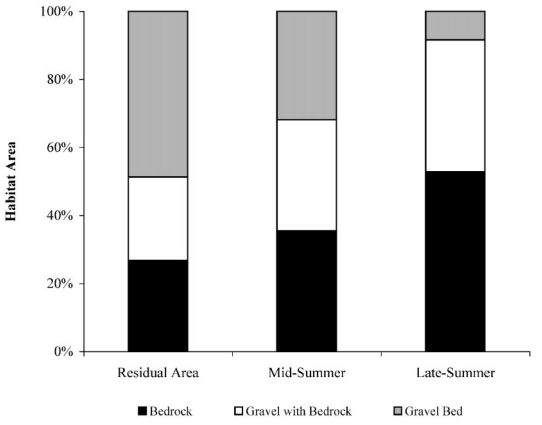


FIGURE 6.—Percentages of available residual, midsummer (24 June–11 July), and late-summer (25–30 August) pool habitat composed of three pool types in Harvey and Knowles creeks, Oregon, 2002.

TABLE 3.—Juvenile salmon abundance and density (SDs in parentheses) in three pool types during midsummer (24 June–11 July) and late summer (25–30 August) of 2002 in Harvey and Knowles creeks, Oregon. Fish densities were calculated based on wetted area.

Pool type	Total number of fish observed midsummer	Residual area median fish density (fish/m^2)	Midsummer median fish density (fish/m^2)	Total number of fish observed in late summer	Late-summer median fish density (fish/m^2)
Bedrock dominated	4,890	0.80 (0.95)	0.80 (0.73)	2,550	0.97 (0.85)
Gravel with bedrock contact	4,050	0.70 (1.20)	0.76 (1.11)	2,260	1.06 (0.91)
Gravel bed	5,110	0.75 (0.65)	1.02 (1.00)	880	1.39 (0.87)

times more likely to go dry than other stream reaches (odds ratio, logistic regression), and pools in debris-flow deposits were 12 times more likely to go dry (odds ratio, logistic regression). In addition to predicting areas susceptible to pool drying, free-formed alluvial reaches and debris-flow deposits correctly predicted the occurrence of 67% of gravel-bed pools in the study streams.

Changes in Fish Abundance

Divers observed a total of 14,050 salmonids (82% juvenile coho salmon, 18% trout) during the midsummer survey. Juvenile coho salmon were evenly distributed during the midsummer sampling period (present in 99% of pools and glides). Trout were less abundant and had a patchy distribution (present in 67% of pools and glides).

Due to the high variability in fish density among pool types (Table 3), no significant differences were detected during either time period ($P = 0.3$ based on midsummer wetted area, $P = 0.4$ based on late-summer wetted area, one-way ANOVA). Fish density remained relatively constant in bedrock pools throughout the summer. Pools in aggraded reaches progressively shrank throughout the summer, resulting in a 46% increase in fish density. This increase in density resulted in substantial crowding of fish in remnant pools. The seasonal increase in fish density was significantly higher in gravel-bed pools and gravel pools with bedrock contact than in bedrock pools (assessed as the change in density between midsummer and late summer within pool types, $P = 0.014$, one-way ANOVA).

Fish abundance decreased substantially in all pool types by late summer (Figure 7); however, the only statistically significant difference was detected for gravel-bed pools ($P = 0.0001$, one-way ANOVA). The decrease in fish abundance, presumably due solely to the desiccation of fish in dry pools, was 36% of the initial population. Mortality of fish desiccated in gravel-bed pools was a minimum estimate, because 25% of pools were already dry during the initial sampling period. Total fish abundance in the study areas decreased by 59% by late summer.

Stream Temperature

The partitioning of surface and subsurface flow in aggraded and bedrock reaches suggests that stream temperature could vary substantially among the different pool types. Our direct investigation was extremely limited, but in the three pools monitored, strong differences in stream temperature were observed (Figure 8). Diurnal temperature patterns fluctuated most in a bedrock pool that received surface flow from a shallow bedrock riffle upstream. In contrast, a bedrock pool that received no surface flow from upstream but that was recharged by subsurface flow discharging from fractured bedrock had relatively low water temperatures and almost no diurnal fluctuation. A gravel pool with bedrock contact that received a mixture of surface flow and hyporheic flow from an upstream riffle containing a thin veneer of alluvium over bedrock was intermediate between the two extremes. The observed temperature patterns should be considered a localized effect and not the result of longitudinal variation within the 1-km section of stream that the pools were located in. This is evident because the pool with the highest water temperature was situated upstream of the pools with lower temperatures. Additionally, there were no significant tributary inputs between the pools that were monitored for temperature.

Discussion

In Mediterranean climates, the summer dry season can be an extremely stressful period for aquatic organisms because of the scarcity of water and potentially high water temperatures. Although the occurrence of a summer drought is very predictable, its magnitude and extent are highly variable. Because the severity of the 2002 dry season was typical for low-flow conditions in the study area, our results have important implications for fish habitat, and inferences drawn from this study are not limited to extremely dry years.

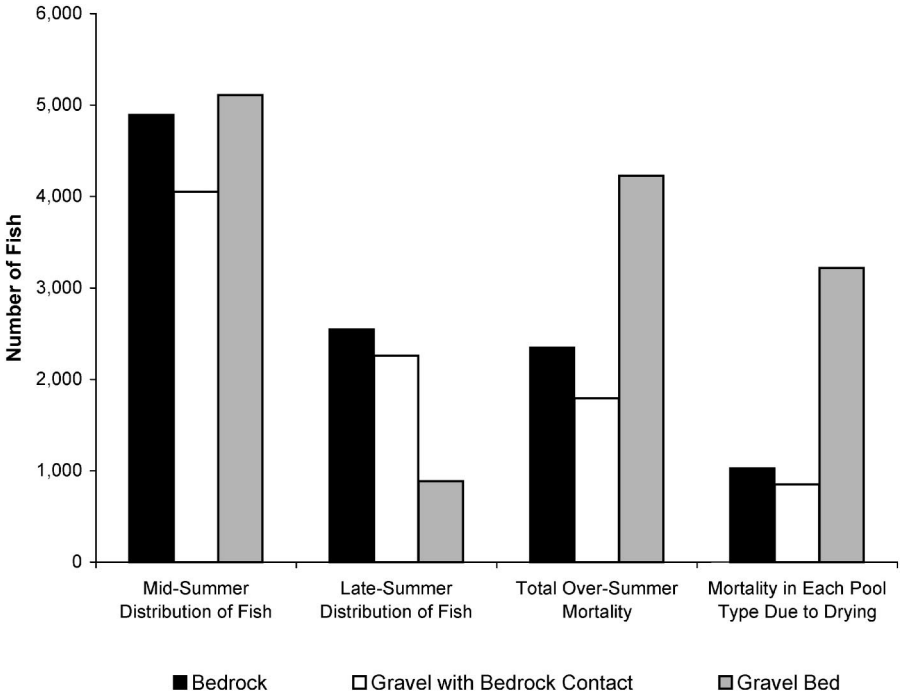


FIGURE 7.—Salmonid abundance in midsummer (24 June–11 July) and late summer (25–30 August), total summer mortality, and desiccation mortality within three pool types in Harvey and Knowles creeks, Oregon, 2002.

Available habitat for salmonids rearing during the summer dry season was strongly correlated with in-channel sediment storage. Residual pool depth was greatest in aggraded reaches; however, the lack of water made the majority of these deep pools unavailable during the summer, and substantial fish mortality occurred when streamflow in gravel-bed pools shifted to subsurface flow. Water was present in these channels for the duration of the summer, but was unavailable at the surface because it passed underneath the streambed as hyporheic flow. In contrast, pools with a bedrock contact had a greater likelihood of remaining wet than pools in aggraded reaches. Small, remnant pools persisted in aggraded reaches when pools were deep enough to contact subsurface flow or when sediment depth was relatively thin, allowing pools to scour to the underlying bedrock. Field evidence suggested that the size of remnant pools was proportional to the area of exposed bedrock at the pool bottom.

A common expectation in coastal regions of the Pacific Northwest is that winter rearing habitat constitutes the primary limiting factor for juvenile coho salmon production (Tschaplinski and Hartman 1983; Nickelson et al. 1992). Results of this study indicate that the summer dry season can also be a period of extremely high mortality in the life cycle of coho salmon and that water availability is one of the primary limitations for survival. Total fish abundance by late summer was 59% lower than midsummer abundance estimates, suggesting that the summer season can be a period of very high mortality. Although estimates of fish abundance based on snorkel surveys can lack the precision of other sampling methods (Hankin and Reeves 1988; Hillman et al. 1992), the magnitude of the difference suggests meaningful biological differences.

To interpret the effects of pool drying on fish survival, we must evaluate several alternative explanations for the change in fish abundance. Indirect effects of pool drying on fish survival include severe crowding and the loss of habitat area, which could cause high levels of physiological stress and/or increased risk of predation. As a direct effect, pool drying could result in acute mortality of fish due to desiccation. However, we cannot rule out the possibility that fish can burrow into the underlying substrate and seek refuge in the hyporheic zone. The effectiveness of the hyporheic zone as a refuge from drying is highly uncertain (Edwards 1998), and this alternative explanation seems unlikely because pools were dry

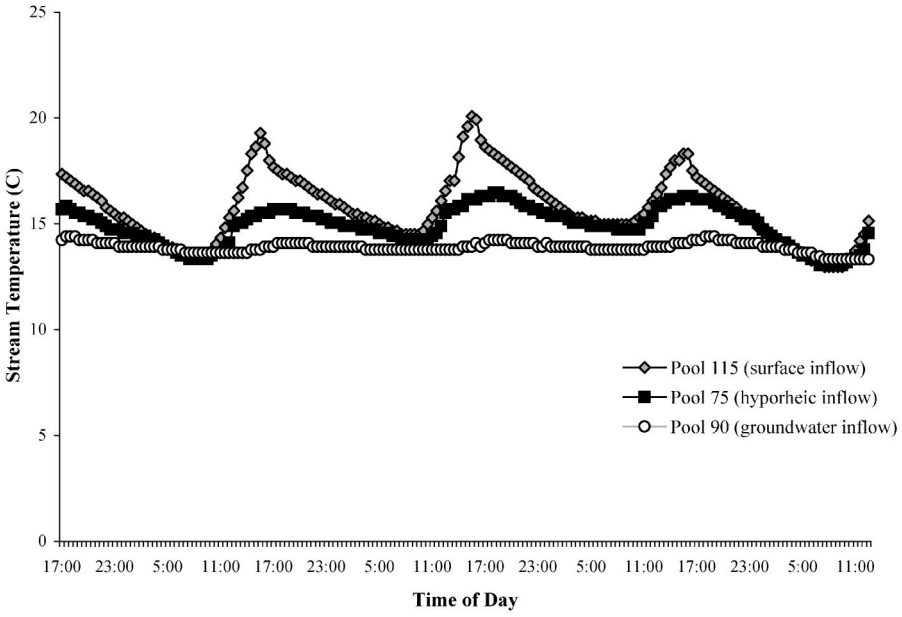


FIGURE 8.—Fluctuations in stream temperature for pools with different substrate and streamflow conditions within a 1-km reach of Harvey Creek, Oregon, during 26–30 August 2002. Pool 115 (bedrock-dominated) was located at the upstream end of the study reach and received surface flow from a shallow bedrock riffle. Pool 90 (a gravel pool with bedrock contact) was located 515 m downstream of pool 115 and received subsurface flow that emerged from fractured bedrock. Pool 75 (a gravel pool with bedrock contact) was located 735 m downstream of pool 115 and received a mixture of surface and subsurface flow from a riffle with a thin veneer of gravel over the underlying bedrock.

for an extended time period (weeks to months). Connectivity between pools was also very limited, so movement of fish to areas that had persistent surface water throughout the summer was also unlikely. Fish abundance did not increase between midsummer and late summer in any of the pools we observed, which suggests that movement was severely limited and that fish were not able to congregate in persistent pools.

The fraction of the initial population of salmonids that were lost to desiccation in dry pools by late summer was proportional to the fraction of bedrock pools and gravel pools with bedrock contact that went dry, suggesting that fish were evenly distributed among these pool types. In contrast, the proportion of gravel-bed pools that went dry (83%) was greater than the proportion of fish desiccation mortalities (63%). Midsummer fish density in gravel-bed pools that persisted throughout the summer was 43% higher (1.09 fish/m^2 residual area) than in gravel-bed pools that eventually went dry (0.62 fish/m^2 residual area). Within the gravel-bed pool type, deeper pools had a greater likelihood of remaining wet throughout the summer, and fish may have preferentially utilized these pools. Similarly, Labbe and Fausch (2000) observed that deeper pools had a higher probability of persisting through the summer dry season in an intermittent stream underlain by thick alluvial deposits. However, it is important to note that shallower bedrock pools had a greater overall likelihood of remaining wet throughout the summer than the deeper gravel-bed pools.

Field observations suggest that three factors influenced water availability in pools: (1) gravel depth, (2) bedrock topography, and (3) subsurface flow paths through fractured bedrock. Gravel depth influenced surface water availability by increasing the proportion of the low-flow stream water that traveled through the hyporheic zone. The relatively small size of pools in the study area suggests that scour was inadequate to create pool contact with the underlying bedrock in alluvial deposits greater than 1 m deep. The uneven surfaces of the underlying bedrock also compounded the problem of predicting water availability. When bedrock was exposed at the bottom of a pool, we could not determine whether the bedrock contact was (1) a slightly elevated ledge within the bank-full channel or (2) a trough where the low-flow stream water

collected. Presumably, this could explain why some of the gravel pools with bedrock contact went dry. In addition, a few bedrock-dominated stream reaches also had intermittent surface flow. Impervious sandstone layers typically formed the channel bed, but the sandstone layers were interbedded with more erosive, more porous siltstone layers. Sandstone layers commonly had large fractures that allowed all or a portion of the streamflow to travel beneath the bedrock surface. Bedrock pools are typically formed by plucking, a process whereby fractures produce loosened blocks that are entrained and transported (Whipple et al. 2000). Plucking of large blocks exposed the porous siltstone layers, and subsurface flow was observed emerging from bedrock ledges. Infiltrating and emerging flow paths through the fractured bedrock have also been observed during studies of hillslope hydrology in this area (Anderson et al. 1997).

In some regions, broad valley floors that contain thick alluvial and glacial deposits function as recharge areas for the hyporheic zone (Stanford and Ward 1993). In upwelling zones, hyporheic exchange has the potential to greatly enhance summer habitat. However, this broad-scale pattern has not been observed in the Oregon Coast Range, where mountain streams are typically constrained within narrow valleys and where the hyporheic zone appears to be limited to the aggraded zone of the bank-full channel.

Predicting Areas Susceptible to Channel Aggradation and Pool Drying

This study established a direct linkage between physical channel structure and ecologically significant habitat characteristics. Two areas subject to pervasive channel aggradation were: (1) stream reaches that fell below a drainage area and channel slope threshold (Montgomery et al. 1996), and (2) thick sediment accumulations stored behind massive log jams that were delivered by debris flows. Based on these predictions, juvenile fish survival during the summer dry season can be estimated or modeled over a broader area.

Montgomery et al. (1996) identified an inverse relationship between drainage area and channel slope that separates bedrock reaches from free-formed alluvial reaches. The threshold is affected by the local influence of log jams, sediment supply, and clast lithology (Montgomery et al. 1996; Massong and Montgomery 2000). Alluvial reaches consistently plot at a lower average slope for a given drainage area, and are therefore expected to exhibit predictable and persistent alluvial bed morphology. Alluvial reaches are inherently depositional and are susceptible to pervasive, long-term channel aggradation. In contrast, stream reaches that plot above the threshold are limited to localized sediment accumulations stored behind log jams, boulder accumulations, and debris-flow deposits (Montgomery et al. 2003). Specific sites of aggradation in these areas are therefore transient and less predictable.

Similar to free-formed alluvial reaches, debris-flow deposits also had a high likelihood of going dry. These results indicate that temporal dynamics of sediment and wood supply, in addition to spatially explicit models based on slope–area relationships, are important considerations for predicting channel aggradation. In the Oregon Coast Range, landslides and debris flows can deliver large volumes of coarse sediment to river channels. These mass wasting processes can form extensive accumulations of wood that completely dam the channel and valley floor; the associated sediment deposits can be several meters thick and can inundate hundreds of meters of stream channel (May 2001, 2002). The architecture of these deposits is unique in small, coastal streams that lack the capacity to transport large volumes of wood by fluvial processes, because wood is typically large relative to channel size (Bilby and Ward 1989). Wood delivered from riparian forests adjacent to the channel typically create in-stream wood structures that consist of individual pieces or small accumulations. Alluvial deposits stored behind wood accumulations are typically thin because the depth of sediment is limited by the height of the wood accumulation; therefore, substantial channel aggradation is not possible in such areas. Debris-flow deposits may assume a greater relative importance in log-jam formation for streams bordered by industrial forests because of decreases in the size of wood recruited from the local riparian area (Montgomery et al. 2003) and increases in debris-flow frequency and magnitude associated with timber harvest and roads (May 2002).

A logistic regression model that included the location of free-formed alluvial reaches and recent debris-flow deposits accurately predicted the presence of 70% of dry pools at the reach scale, and identified the spatial occurrence of 67% of gravel-bed pools. Contrary to a common expectation that the likelihood of pool persistence throughout the summer would increase in a downstream direction due to increased drainage area, no consistent longitudinal pattern in water availability was detected

by the logistic regression model. Patterns of pool drying were also similar between the two study basins.

Discontinuous Flow Patterns and Fish Energetics

Habitat connectivity is an important consideration for fish because it influences movement and the availability of food resources supplied from upstream sources. Pools that lack connectivity may provide only limited opportunities for growth because of the lack of invertebrate drift from upstream. Previous research in the Napa River, California, found that discontinuous flow patterns of dry riffles alternating with wet pools, as well as high water temperatures, resulted in low to negative growth of juvenile steelhead (Stillwater Sciences 2002). In three western Washington streams with a high degree of connectivity, juvenile coho salmon moved out of smaller and shallower habitat units, and fish that moved among habitat units grew faster than fish that remained in the same habitat unit (Kahler et al. 2001). These results indicate that small-scale, habitat- and growth-related movements are important components of summer rearing.

Limited sampling of stream temperature suggests that surface and subsurface flow paths substantially influence stream temperature at very fine spatial scales. The diversity of flow paths creates thermal heterogeneity, allowing fish inhabiting individual pools to experience different environmental conditions. High water temperatures can increase metabolic rates (Brett 1971) and therefore have a direct effect on growth. Based on the differences in temperature and connectivity among the different pool types we investigated, there may be a strong potential for differential growth among the pool types. Bedrock reaches appeared to have a greater supply of food because a higher proportion of riffles remained wet and had the potential to deliver invertebrate drift, whereas isolated pools were limited to in situ production and localized terrestrial inputs. The net effect of potentially greater food availability and increased fish metabolic costs (due to higher water temperatures) in bedrock reaches could not be determined in this study but is an important consideration for future research.

Patterns of seasonal growth and survival of salmonids in the Pacific Northwest are highly uncertain. Previous research has documented a positive correlation between summer streamflow and survival of juvenile coho salmon (Mathews and Olson 1980); however, no underlying mechanisms have been investigated. Summer growth of juvenile salmonids may be critical to population viability because larger fish generally have higher overwinter survival rates than do smaller individuals (Quinn and Peterson 1996). Larger smolts also have a greater likelihood of surviving the ocean phase of their life history (Yamamoto et al. 1999; Zabel and Williams 2002). In the Pacific Northwest, winter growth is often restricted by cold water temperatures, reduced primary production, and the need for juvenile fish to seek cover from high stream velocities (Bilby and Bisson 1992). In coastal streams of northern California, extremely low growth rates of juvenile coho salmon have been observed during the winter, followed by substantial increases in growth during spring (Bell 2001). If food or foraging opportunities are limited in the summer and winter, salmonid fishes may be highly dependent on growth accrued during spring and autumn for achieving a larger body size.

Summary and Implications for Land Management

Field investigations of channel aggradation and water availability during the middle of the summer dry season indicated that areas of high sediment storage were associated with slightly deeper pools. Late-summer surveys revealed that the majority of gravel-bed pools went dry because the streambed was extremely porous and allowed streamflow to drop below the bed elevation. Aggradation caused surface flow to become intermittent, which stranded fish in drying channels. In areas of low sediment storage, pool depth was limited by the underlying bedrock, but these pools were sustained by hyporheic flow and were more likely to persist throughout the summer dry season. These results illuminate an important temporal dynamic that occurs during the summer dry season, and serve as a reminder that field measurements taken at a single point in time can be a misleading indication of habitat quality when habitat conditions are spatially and temporally dynamic (Van Horne 1983).

Our results also address an important question about the influence of large influxes of sediment and wood on aquatic habitat, a subject that is currently undergoing a great deal of speculation. Because channel aggradation was directly linked to water availability and fish survival, this study demonstrates that increases in coarse sediment supply can be associated with sharp reductions in salmonid habitat and productivity. Land-use practices, such as timber harvest and road construction, are often associated with large influxes of coarse

sediment in forested mountain streams, particularly through increases in landslide and debris-flow activity (Swanson and Dyrness 1975; Swanson et al. 1982; Madej and Ozaki 1996; May 2002). Similarly, severe wildfires, which are a major component of the disturbance regime in the Oregon Coast Range (Long et al. 1998), can also result in an accelerated rate of coarse sediment input (Swanson 1981; Meyer et al. 2001; May and Gresswell 2003). However, river systems are dynamic, and disturbance events that result in a short-term loss of habitat may be required to create productive habitat conditions over the long term (Reeves et al. 1995; Labbe and Fausch 2000). Aggraded channels may create important habitat for other life history stages during other seasons. For example, aggraded reaches can create spawning areas in channels that otherwise may be too coarse (Buffington and Montgomery 1999).

Reeves et al. (1995) hypothesized that the most complex habitat conditions and fish assemblages would form in watersheds that are at intermediate stages of disturbance and reorganization. Channels that are interposed between gravel rich and gravel poor may provide optimal habitat conditions, because deep pools can form in the stored alluvium and contact with the underlying bedrock provides consistent water availability and lower water temperatures. However, the biotic interactions caused by increased crowding of fish trapped in isolated pools and the lower food availability associated with discontinuous surface flow may offset the favorable abiotic conditions. Tradeoffs between short- and long-term effects of disturbance remain uncertain, but mountain streams that are susceptible to catastrophic disturbances like fires and debris flows will produce a dynamic condition in which not all habitats are suitable for salmonid production at a specific point in time.

Acknowledgments

Funding for this research was provided by the National Fire Plan, an interagency program supported in part by the U.S. Department of Agriculture Forest Service. We are especially grateful to the watershed sciences team at the Redwood Sciences Laboratory in Arcata, California, Robert Gresswell with the U.S. Geological Survey, and Sherri Johnson with the Pacific Northwest Research Station for providing logistical support and field assistance. Dave Montgomery generously provided slope–area data for Knowles Creek. Bret Harvey contributed substantially to this paper through numerous discussions, analytical insight, and critical reviews of the draft manuscript. Dan Isaak and two anonymous reviewers provided a thorough critique of the submitted manuscript, and their efforts are greatly appreciated.

References

Anderson, S. P., W. E. Dietrich, D. R. Montgomery, R. Torres, M. E. Conrad, and K. Loague. 1997. Subsurface flow paths in a steep, unchanneled catchment. Water Resources Research 33:2637–2653.

Baldwin, E. M. 1964. Geology of Oregon. University of Oregon, Eugene.

Bell, E. 2001. Survival, growth and movement of juvenile coho salmon (*Oncorhynchus kisutch*) overwintering in alcoves, backwaters, and main channel pools in Prairie Creek, California. Master's thesis. Humboldt State University, Arcata, California.

Benda, L. E. 1990. The influence of debris flows on channels and valley floors in the Oregon Coast Range, U.S.A. Earth Surface Processes and Landforms 15:457–466.

Benda, L. E., and T. Dunne. 1997a. Stochastic forcing of sediment supply to channel networks from landsliding and debris flows. Water Resources Research 33:2849–2863.

Benda, L. E., and T. Dunne. 1997b. Stochastic forcing of sediment routing and storage to channel networks. Water Resources Research 33:2865–2880.

Beschta, R. L., and W. L. Jackson. 1979. The intrusion of fine sediment into a stable gravel bed. Journal of the Fisheries Research Board of Canada 36:204–210.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clearcut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.

Bilby, R. E., and J. W. Ward. 1989. Changes in characteristics and function of woody debris with increasing size of streams in western Washington. Transactions of the American Fisheries Society 118: 368–378.

Bisson, P. A., J. L. Nielsen, R. A. Palmason, and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62–73 *in* N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Bethesda, Maryland.

Bisson, P. A., G. H. Reeves, R. E. Bilby, and R. J. Naiman. 1997. Watershed management and Pacific salmon: desired future conditions. Pages 447–474 *in* D. J. Stouder, P. A. Bisson, and R. J. Naiman, editors. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Brett, J. R. 1971. Energetic responses of salmon to temperature. a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). American Zoologist 11:99–113.

Buffington, J. M., and D. R. Montgomery. 1999. Effects

of hydraulic roughness on surface textures of gravel-bed rivers. Water Resources Research 35: 3507–3521.

Cooper, A. C. 1965. The effect of transported stream sediment on the survival of sockeye and pink salmon eggs and alevin. International Pacific Salmon Fisheries Commission Bulletin 18.

Dietrich, W. E., and T. Dunne. 1978. Sediment budget for a small catchment in mountainous terrain. Zeitschrift fuer Geomorphologie N. F 29:191–206.

Edwards, R. T. 1998. The hyporheic zone. Pages 399–429 *in* R. J. Naiman, and R. E. Bilby, editors. River ecology and management: lessons from the Pacific coastal ecoregion. Springer, New York.

Findlay, S. 1995. Importance of surface–subsurface exchange in stream ecosystems: the hyporheic zone. Limnology and Oceanography 40:159–164.

Hack, J. T. 1960. Interpretation of erosional topography in humid temperate climates. American Journal of Science 258A:80–97.

Hankin, D. G., and G. H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimates. Canadian Journal of Fisheries and Aquatic Sciences 45:834–844.

Hillman, T. W., J. W. Mullan, and J. S. Griffith. 1992. Accuracy of underwater counts of juvenile Chinook salmon, coho salmon, and steelhead. North American Journal of Fisheries Management 12:598–603.

Hogan, D. L., S. A. Bird, and M. Hassan. 1998. Spatial and temporal evolution of small coastal gravel-bed streams: influence of forest management on channel morphology and fish habitats. Pages 365–392 *in* P. C. Klingeman, R. L. Beschta, P. D. Komar, and J. B. Bradley, editors. Gravel-bed rivers in the environment. Water Resources Publications, Highlands Ranch, Colorado.

Hynes, H. B. N. 1983. Groundwater and stream ecology. Hydrobiologia 100:93–99.

Kahler, T. H., P. Roni, and T. P. Quinn. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:1947–1956.

Labbe, T. E., and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774–1791.

Lake, R. G., and S. G. Hinch. 1999. Acute effects of suspended sediment angularity on juvenile coho salmon. Canadian Journal of Fisheries and Aquatic Sciences 56:862–867.

Lisle, T. E. 1982. Effects of aggradation and degradation on riffle–pool morphology in natural gravel channels, northwestern California. Water Resources Research 18:1643–1651.

Lisle, T. E. 1987. Using 'residual depths' to monitor pool depths independently of discharge. U.S. Forest Service Research Note PSW-394.

Lisle, T. E. 1989. Sediment transport and resulting deposition in spawning gravels, north coastal California. Water Resources Research 25:1303–1319.

Long, C. J., C. Whitlock, P. J. Bartlein, and S. H. Millspaugh. 1998. A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. Earth Surface Processes and Landforms 28:774–787.

Madej, M. A., and V. Ozaki. 1996. Channel response to sediment wave propagation and movement, Redwood Creek, California, USA. Earth Surface Processes and Landforms 21:911–927.

Massong, T. M., and D. R. Montgomery. 2000. Influence of sediment supply, lithology, and wood debris on the distribution of bedrock and alluvial channels. Geological Society of America Bulletin 112:591–599.

Mathews, S. B., and F. W. Olson. 1980. Factors affecting Pudget Sound coho salmon. Canadian Journal of Fisheries and Aquatic Sciences 37:1373–1378.

May, C. L. 2001. Spatial and temporal dynamics of sediment and wood in headwater streams of the Oregon Coast Range. Doctoral dissertation. Oregon State University, Corvallis.

May, C. L. 2002. Debris flow characteristics through different forest age classes in the central Oregon Coast Range. Journal of the American Water Resources Association 38:1097–1113.

May, C. L., and R. E. Gresswell. 2003. Processes and rates of sediment and wood accumulation in headwater streams of the Oregon Coast Range, U.S.A. Earth Surface Processes and Landforms 28:409–424.

May, C. L., and R. E. Gresswell. 2004. Spatial and temporal patterns of debris-flow deposition in the Oregon Coast Range, USA. Geomorphology 57: 135–149.

McIntosh, B. M., J. R. Sedell, J. E. Smith, R. C. Wissmar, S. E. Clark, and G. H. Reeves. 1994. Historical changes in fish habitat for selected river basins of eastern Oregon and Washington. Northwest Science 68:36–53.

Meyer, G. A., J. L. Pierce, S. H. Wood, and A. J. Jull. 2001. Fire, storms, and erosional events in the Idaho batholith. Hydrological Processes 15:3025–3038.

Montgomery, D. R., T. B. Abbe, J. M. Buffington, N. P. Peterson, K. M. Schmidt, and J. D. Stock. 1996. Distribution of bedrock and alluvial channels in forested mountain drainage basins. Nature (London) 381:587–589.

Montgomery, D. R., T. M. Massong, and C. S. Hawley. 2003. Influence of debris flows and log jams on the location of pools and alluvial channel reaches, Oregon Coast Range. Geological Society of America Bulletin 115:78–88.

Nakamura, F., and F. J. Swanson. 1993. Effects of coarse woody debris on morphology and sediment storage of a mountain stream system in western Oregon. Earth Surface Processes and Landforms 18:43–61.

Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:783–789.

Poole, G. C., C. A. Frissell, and S. C. Ralph. 1997. In-

stream habitat unity classification: inadequacies for monitoring and some consequences for management. Journal of the American Water Resources Association 33:879–896.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555–1564.

Reeves, G. H., F. H. Everest, and J. R. Sedell. 1993. Diversity of juvenile anadromous salmonid assemblages in coastal Oregon basins with different levels of timber harvest. Transactions of the American Fisheries Society 122:309–317.

Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionary significant units of anadromous salmonids in the Pacific Northwest. Pages 334–349 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Stanford, J. A., and J. V. Ward. 1988. The hyporheic habitat of river ecosystems. Nature (London) 335: 64–66.

Stanford, J. A., and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. Journal of the North American Benthological Society 12:48–60.

Stillwater Sciences. 2002. Napa River watershed limiting factors analysis. Final Technical Report. Berkeley, California. Available: http://www.stillwatersci.com/publications.htm.

Swanson, F. J. 1981. Fire and ecoystem processes. U.S. Forest Service General Technical Report WO-26.

Swanson, F. J., and C. T. Dyrness. 1975. Impact of clearcutting and road construction on soil erosion by landslides in the western Cascade Range, Oregon. Geology 3:393–396.

Swanson, F. J., R. L. Fredricksen, and F. M. McCorison. 1982. Material transfer in a western Oregon forested watershed. Pages 267–291 *in* R. L. Edmonds, editor. Analysis of coniferous forest ecosystems in the western United States. Hutchinson Ross, New York.

Tappel, P. D., and T. C. Bjornn. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. North American Journal of Fisheries Management 3:123–135.

Tschaplinski, P. J., and G. F. Hartman. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Canadian Journal of Fisheries and Aquatic Sciences 40:452–461.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Whipple, K. X., G. S. Hancock, and R. S. Anderson. 2000. River incision into bedrock: mechanics and relative efficacy of plucking, abrasion, and cavitation. Geological Society of America Bulletin 112: 490–503.

Wondzell, S. M., and F. J. Swanson. 1999. Floods, channel change, and the hyporheic zone. Water Resources Research 35:555–567.

Yamamoto, S., K. Morita, and A. Goto. 1999. Marine growth and survival of white-spotted charr, *Salvelinus leucomaenis*, in relation to smolt size Ichthyological Research 46:85–92.

Zabel, R. W., and J. G. Williams. 2002. Selective mortality in Chinook salmon: what is the role of human disturbance? Ecological Applications 12:173–183.

frontiers in Forests and Global Change

ORIGINAL RESEARCH
published: 05 November 2020
doi: 10.3389/ffgc.2020.594274

Large Trees Dominate Carbon Storage in Forests East of the Cascade Crest in the United States Pacific Northwest

David J. Mildrexler[1], Logan T. Berner[2], Beverly E. Law[3], Richard A. Birdsey[4] and William R. Moomaw[4,5]*

[1] Eastern Oregon Legacy Lands, Joseph, OR, United States, [2] EcoSpatial Services L.L.C., Flagstaff, AZ, United States, [3] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, United States, [4] Woodwell Climate Research Center, Falmouth, MA, United States, [5] The Fletcher School and Global Development and Environment Institute, Tufts University, Medford, MA, United States

OPEN ACCESS

Edited by:
Isabel Cañellas, Centro de Investigación Forestal (INIA), Spain

Reviewed by:
Jurij Diaci, University of Ljubljana, Slovenia
Thomas J. Dean, Louisiana State University, United States

***Correspondence:**
David J. Mildrexler
d.mildrexler@gmail.com

Specialty section:
This article was submitted to Forest Management, a section of the journal Frontiers in Forests and Global Change

Received: *12 August 2020*
Accepted: *16 October 2020*
Published: *05 November 2020*

Citation:
Mildrexler DJ, Berner LT, Law BE, Birdsey RA and Moomaw WR (2020) Large Trees Dominate Carbon Storage in Forests East of the Cascade Crest in the United States Pacific Northwest. Front. For. Glob. Change 3:594274. doi: 10.3389/ffgc.2020.594274

Large-diameter trees store disproportionally massive amounts of carbon and are a major driver of carbon cycle dynamics in forests worldwide. In the temperate forests of the western United States, proposed changes to Forest Plans would significantly weaken protections for a large portion of trees greater than 53 cm (21 inches) in diameter (herein referred to as "large-diameter trees") across 11.5 million acres (∼4.7 million ha) of National Forest lands. This study is among the first to report how carbon storage in large trees and forest ecosystems would be affected by a proposed policy. We examined the proportion of large-diameter trees on National Forest lands east of the Cascade Mountains crest in Oregon and Washington, their contribution to overall aboveground carbon (AGC) storage, and the potential reduction in carbon stocks resulting from widespread harvest. We analyzed forest inventory data collected on 3,335 plots and found that large trees play a major role in the accumulated carbon stock of these forests. Tree AGC (kg) increases sharply with tree diameter at breast height (DBH; cm) among five dominant tree species. Large trees accounted for 2.0 to 3.7% of all stems (DBH ≥ 1" or 2.54 cm) among five tree species; but held 33 to 46% of the total AGC stored by each species. Pooled across the five dominant species, large trees accounted for 3% of the 636,520 trees occurring on the inventory plots but stored 42% of the total AGC. A recently proposed large-scale vegetation management project that involved widespread harvest of large trees, mostly grand fir, would have removed ∼44% of the AGC stored in these large-diameter trees, and released a large amount of carbon dioxide to the atmosphere. Given the urgency of keeping additional carbon out of the atmosphere and continuing carbon accumulation from the atmosphere to protect the climate system, it would be prudent to continue protecting ecosystems with large trees for their carbon stores, and also for their co-benefits of habitat for biodiversity, resilience to drought and fire, and microclimate buffering under future climate extremes.

Keywords: carbon, climate mitigation, eastside screens, forests, global change, large-diameter trees, 21-inch rule

INTRODUCTION

Forest carbon accumulation is crucial for mitigating ongoing climatic change, with individual large trees storing a substantial portion of the overall carbon in living trees. Globally, forests store about 862 Gt carbon in live and dead vegetation and soil, with 42% of it stored in live biomass (above- and belowground; Pan et al., 2011). Globally, forests removed the equivalent of about 30% of fossil fuel emissions annually from 2009 to 2018 (Friedlingstein et al., 2019), and 44% of that was by temperate forests. Temperate forests of the United States are the largest category of land sinks in the country, consistently offsetting about 14% of the Nation's CO_2 emissions (EPA, 2020). Projections indicate that ecological systems have significant additional climate mitigation potential, with forest carbon accumulation serving as a central component of a natural climate solutions framework (Griscom et al., 2017; Fargione et al., 2018; Moomaw et al., 2019; Cook-Patton et al., 2020).

Large-diameter trees constitute about half of the mature forest biomass worldwide and are key to the ability of forests to accumulate substantial amounts of carbon needed to mitigate climate change (Luyssaert et al., 2008; Lutz et al., 2018). Trees exceeding 60 cm (23.6 in) diameter at breast height (DBH) comprise ∼41% of the world's aboveground live tree biomass (Lutz et al., 2018). Furthermore, on average, 50% of the live tree biomass carbon in all types of forests globally is stored in the largest 1% of trees, but the value for the United States is lower, ∼30% in the largest 1% of trees due to widespread historical logging of large trees (Lutz et al., 2018). A single large tree can add the same amount of carbon to the forest within a year as is contained in a single mid-sized tree of the same species (Stephenson et al., 2014). The relationship between large-diameter trees and overall forest biomass suggests that forests cannot accumulate aboveground carbon (AGC) to their ecological potential without large trees (Lutz et al., 2018). Recognition of the importance of large-diameter trees in determining global atmospheric carbon stocks has led to management recommendations to conserve existing large-diameter trees and those that will soon reach large diameters (Lindenmayer et al., 2014; Lutz et al., 2018; Moomaw et al., 2019).

In addition to comprising a substantial portion of forest carbon storage and accumulation, large-diameter trees fulfill a variety of unique ecological roles such as increasing drought-tolerance, reducing flooding from intense precipitation events, altering fire behavior, redistributing soil water, and acting as focal centers of mycorrhizal communication and resource sharing networks (Bull et al., 1997; Brooks et al., 2002; Brown et al., 2004; Luyssaert et al., 2008; Beiler et al., 2015; Lindenmayer and Laurance, 2017). In the United States Pacific Northwest (PNW), carbon dense old growth forests buffer against increasing temperatures by creating microclimates that shelter understory species from rising temperatures (Frey et al., 2016; Davis et al., 2019a). Forests with large-diameter trees often have high tree species richness, and a high proportion of critical habitat for endangered vertebrate species, indicating a strong potential to support biodiversity into the future and promote ecosystem resilience to climate change (Lindenmayer et al., 2014; Buotte et al., 2020).

In the PNW region of the United States a 21-inch (∼53 cm) diameter criteria (USDA Forest Service, 1995) was enacted in 1994 to slow the loss of large, older trees and old forest patches in national forests east of the Cascade Mountains crest in Oregon and Washington. The forests under consideration shall be referred to as "eastside forests" to be consistent with United States Forest Service (USFS) terminology. In our study, we refer to trees that equal or exceed this value to be "large-trees" or "large-diameter trees." Extensive studies determined that the large tree component of old forest structure had decreased due to human uses, and that sensitive wildlife species associated with old growth forest such as the American Marten and the Northern Goshawk were also in decline (Interior Columbia Basin Ecosystem Management Project, 2000; Wisdom et al., 2000; Bull et al., 2005; Greenwald et al., 2005). Site-specific exceptions have allowed removal of some trees ≥21 in DBH. However, the 21-inch rule has prevented large-scale harvest of trees ≥21 in DBH. For example, the 2010 Snow Basin Vegetation Management Project proposed harvesting over 43,000 trees ≥21 in DBH but was stopped by litigation [League of Wilderness Defenders, et al., v. Connaughton, et al., No. 3:12-cv-02271-HZ (D. Or. Dec. 9, 2014)]. Recently restoration of these forests was claimed to be inhibited by the 21-inch rule that protects large trees from logging (Hessburg et al., 2020). The rationale for harvesting large trees is premised upon the use of historical baselines of stand structure and species composition as management targets, and assuming that by removing large shade-tolerant species like grand fir and Douglas-fir it will promote resilience to future drought and disturbance (Johnston et al., 2018; Merschel et al., 2019; Hessburg et al., 2020). However, ongoing climate change and many other anthropogenic stressors such as habitat fragmentation, invasive species, and declines in biodiversity, heighten concerns over use of historical conditions as management targets (Millar et al., 2007; IPCC, 2018; Ripple et al., 2020). Proposed amendments to the 21-inch diameter limit would allow widespread harvesting of the larger trees up to 30 in DBH (76.2 cm) across six National Forests of eastern Oregon and southwestern Washington with major implications for forest carbon dynamics and important environmental co-benefits (**Figure 1**).

Carbon storage is an increasingly important management objective for National Forest Lands in the United States (Depro et al., 2008; Dilling et al., 2013; Dugan et al., 2017). USFS Forest Inventory and Analysis (FIA) data have been used to develop baseline stocks and trends of forest carbon for every region and individual National Forest, including assessment of the main disturbance, management, and environmental factors that drive changes (Birdsey et al., 2019). Western United States forests show considerable potential to accumulate additional carbon over the coming century, especially forests within the PNW that are projected to have relatively low to moderate vulnerability to future drought and fire (**Figure 1**; Buotte et al., 2020). Strategies to mitigate climate change effects on forests require careful examination of the tradeoffs of proposed forestry practices on forest carbon stock accumulation, water cycling, and additional environmental co-benefits of forests, such as biodiversity and

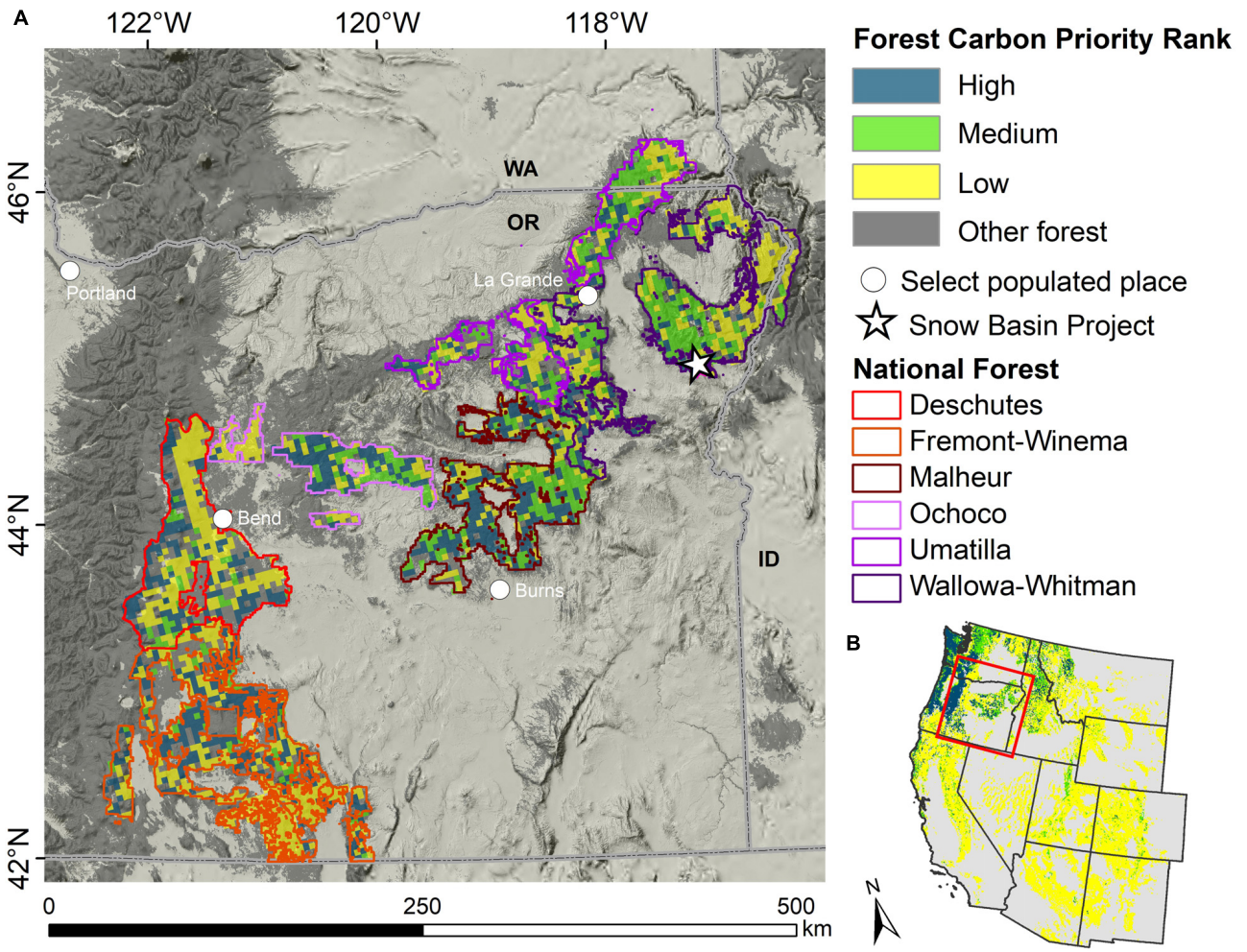


FIGURE 1 | Locations of the six national forests in eastern Oregon, southeastern Washington, and western Idaho, and the proposed Snow Basin Project area **(A)**. The forest carbon conservation priority rank is shown for the national forests and **(B)** for the broader western United States. The forest carbon conservation priority rank is from Buotte et al. (2020) and was derived from simulations of potential forest carbon sequestration and vulnerability to drought and fire over the 21st century. Forest extent is from Ruefenacht et al. (2008).

microclimatic buffering (McKinley et al., 2011; Law et al., 2018; Sheil, 2018; Buotte et al., 2020).

The potential effects of changing the 21-inch rule on carbon storage of eastside forests have not been adequately considered. Proposed changes to the management of large trees should be carefully assessed prior to adoption of new rules given that forest carbon storage is critically important in the context of a warming climate, and that large trees disproportionately store more accumulated carbon, keeping it out of the atmosphere. The objective of this study is to evaluate the potential impact of removal of the 21-inch rule on forest carbon stocks and carbon stock accumulation in eastside forests (**Figure 1**). We examine the relationship between tree DBH and AGC storage at tree to population scales for selected dominant tree species in eastside forests, focusing on the following questions:

1. How does AGC storage change with tree diameter among the dominant eastside tree species?
2. How common are large trees across the eastside forests by species and what proportion of each species total AGC do they account for?
3. What are the potential consequences on carbon stores of widespread removal of large trees in eastside forest restoration projects?

MATERIALS AND METHODS

Study Area

Our study area included the six national forests in eastern Oregon, two of which extend slightly into southwestern Washington and western Idaho (**Figure 1**). Located within the East Cascades and Blue Mountains ecoregions, these national forests together cover approximately 11.5 million acres (4.7 million ha) of complex mountainous terrain, characterized by a broad range of environmental gradients in climate regimes and

TABLE 1 | Summary of forest inventory data and climate conditions for the six National Forests included in the analysis.

National forest	Forest inventory			Climate conditions			
	N. Plots	DBH (cm)	AGC (kg)	Annual precipitation (mm)	Temperature (°C)		
					Annual	Jan.	July
Deschutes	474	16 (187)	131 (11359)	817 (170)	6.1 (0.6)	−1.5 (1.9)	16.1 (1.8)
Fremont-Winema	740	17 (204)	145 (14269)	681 (156)	6.3 (0.6)	−1.4 (1.9)	16.6 (1.8)
Malheur	687	15 (145)	108 (8392)	571 (104)	5.9 (0.7)	−2.9 (2.0)	17.2 (2.1)
Ochoco	253	16 (188)	119 (13462)	484 (101)	7.1 (0.6)	−1.0 (1.9)	17.6 (1.9)
Umatilla	487	14 (139)	99 (8759)	802 (121)	6.8 (0.7)	−1.5 (1.8)	17.5 (2.0)
Wallowa-Whitman	694	13 (164)	91 (8301)	792 (119)	6.0 (0.7)	−3.0 (1.8)	17.3 (2.1)

Forest inventory data were from the USFS Forest Inventory and Analysis program for the period 2000 to 2018. The variables include number of inventory plots and the average (max) diameter at breast height (DBH) and aboveground carbon (AGC) of trees on inventory plots. Average (±1 SD) climate conditions were based on the 40-year period from 1981 to 2019 and derived from 4-km resolution gridded PRISM data (Daly et al., 2008).

associated forest types (Johnson and Clausnitzer, 1992; Peterson and Waring, 1994; Berner and Law, 2015). The Blue Mountains ecoregion functions ecologically and floristically as a transverse bridge between the Cascade Mountains to the west and the Rocky Mountains to the east (Kerns et al., 2017). This "mega-corridor" links together some of the most intact habitat remaining in the PNW region and is of great importance to regional-scale connectivity and carbon storage in response to a warming climate (McGuire et al., 2016; Buotte et al., 2020).

Climatic conditions from 1981 to 2019 were similar across National Forests with regard to January and July average temperatures but show substantial variation in annual precipitation (**Table 1**). The Deschutes and Fremont-Winema National Forests are in the eastern Cascade Mountains and thus receive relatively high annual precipitation (817 mm and 681 mm) due to orographic uplift. National Forests in the southwestern Blue Mountains receive less precipitation (Malheur, 571 mm; Ochoco, 484 mm) due to their location within the rainshadow of the Cascade Mountains. In the northeastern portion of our study area annual precipitation increases to 802 mm and 792 mm, respectively, for the Umatilla and Wallowa Whitman National Forests due to the intrusion of moisture-laden air masses through the Columbia River Gorge. The region's complex precipitation patterns are similarly reflected in the distribution of forest types and biophysical characteristics.

Forest Inventory and Analysis Dataset

We relied on forest inventory measurements from the USFS FIA program and our own selection of biomass equations to evaluate relationships between tree diameter and AGC storage, as well as assess potential effects of tree removal proposed as part of the 2010 Snow Basin project. The FIA conducts systematic forest inventories across the United States, with one field sampling plot for every ∼2,400 hectares (6,000 acres) of forest (O'Connell et al., 2017). In the western United States, the FIA surveys 10% of sampling plots each year, meaning that each sampling plot is revisited every 10 years. At each sampling plot, field crews collect data on tree species, tree size, and other forest attributes. These inventory data are available online through the FIA DataMart[1].

[1]https://apps.fs.usda.gov/fia/datamart/

We downloaded the latest FIA data (FIADB_1.8.0.02) for Oregon, Washington, and Idaho, and then identified inventory plots that occurred within the six national forests based on a spatial overlay with national forest boundaries (n = 3,973 plots). To maintain landowner privacy the FIA plot coordinates available to the public are slightly altered ("fuzzed"), thus our spatial overlay may include some plots just outside the national forests or miss some plots that occur around the edges of these forests. We selected the latest inventory measurements from each surveyed plot for the years 2010 to 2018 (the most recent year available). We filtered these data to include only live trees of the five tree species of interest. A total of 54,651 individual trees were measured on the microplots, subplots, and macroplots, which represented 636,520 trees after applying the expansion factors for each type of plot. Overall, we used data from 3,335 plots in this analysis. A summary of FIA plot conditions within our study area shows that relatively small variations in average DBH across National Forests, between 13 cm and 17 cm, translate into substantial differences in AGC (**Table 1**). The Fremont Winema National Forest had the largest average DBH (∼17 cm) and the largest average AGC stores (∼145 kg), whereas the Wallowa-Whitman had the smallest average DBH (∼13 cm) and the smallest average AGC stores (∼91 kg).

We performed the analysis using the statistical software R (v. 3.6.1; R Core Team, 2020) with add-on packages including data.table (Dawle and Srinivasan, 2019), ggplot2 (Wickham, 2016), maptools (Bivand and Lewin-Koh, 2019), raster (Hijmans, 2019), and rgdal (Bivand et al., 2019).

Estimating Tree Aboveground Carbon Storage

We estimated AGC storage (AGC; kg C) for each tree on the FIA inventory plots using tree biometric measurements from FIA along with species- and component-specific biomass allometric models and traits (**Supplementary Tables 1, 2**). Using species-specific allometric models that include height measurements are essential to capture climate and site effects on taper and height (volume), and reduce uncertainty compared to estimates that are diameter-based and generalized models. For example, Van Tuyl et al. (2005) found that generalized models underestimated

biomass by 50% on the eastside. Specifically, for each tree we estimated AGC as the sum of carbon stored in stem, branch, bark, and foliage biomass. To estimate stem biomass, we first derived stem volume using species-specific allometric models that incorporated tree diameter and height (Cochran, 1985; **Supplementary Table 1**). We then converted stem volume to biomass using published information on the wood density of each species, which we found was important to reducing uncertainty in estimates (Van Tuyl et al., 2005; Ross, 2010; Berner and Law, 2015). We also estimated branch, bark, and foliage biomass using species-specific allometric models, substituting equations for similar species where necessary (Gholz et al., 1979; Means et al., 1994; Jenkins et al., 2004). We assumed dry stem, branch, and bark biomass was 47.6 to 52.5% carbon depending on species (Lamlom and Savidge, 2003) and that dry foliage biomass was 46.1 to 51.4% carbon depending on species (Berner and Law, 2016). For trees smaller than 10 cm DBH, total aboveground biomass was estimated from tree height and then converted to AGC assuming wood carbon content.

Tree-Level Analysis of Relationship Between Tree Diameter and Aboveground Carbon

To better understand how carbon storage varies with tree size in eastside forests, we examined relationships between tree diameter (DBH; cm) and aboveground carbon (AGC; kg) among trees sampled on the FIA plots. Specifically, we rounded the DBH of each tree to the nearest centimeter and then computed the average AGC of trees within each 1-cm size class. To account for sampling uncertainty, we repeatedly computed these metrics using a resampling approach where each draw ($n = 10^4$) utilized data from a random 25% of inventory plots sampled with replacement. We computed the median across these 10^4 draws as our best-estimate of these metrics and also derived 95% confidence intervals.

Population-Level Analysis of Tree Diameter and Aboveground Carbon

We evaluated how the cumulative percentage of tree stems and AGC varied with tree diameter across the six national forests of our study area using forest inventories. This involved quantifying the cumulative percentage of tree stems and total AGC by DBH for each tree species, as well as pooled across tree species. To account for sampling uncertainty, we again implement a resampling approach ($n = 10^4$ draws).

Snow Basin Case Study: Carbon Consequences of Proposed Large Tree Removal

To estimate the carbon consequences of large tree removal we utilized USFS National Environmental Policy Act (NEPA) documentation from the Snow Basin Vegetation Management Project located on the Wallowa-Whitman National Forest, Whitman Ranger District, Baker County, Oregon (**Figure 1**). The project area includes 10,721 ha (26,493 acres) of National Forest land and primarily encompasses two main subwatersheds (Paddy Creek-Eagle Creek and Little Eagle Creek). Elevations within the project area range from approximately 1,340 m (4,400 feet) on the southern boundary to approximately 1,980 m (6,500 feet) at the northern boundary near the border with the Eagle Cap Wilderness. The USFS's preferred alternative plan was to remove over 43,000 large trees (DBH $\geq$ 21 in or 53.3 cm) from the project area. The large tree removal was prevented by litigation, but the project nonetheless provides a realistic framework to evaluate the carbon cost of large tree removal associated with dry forest landscape-scale restoration projects.

The Snow Basin NEPA document estimated the number of large trees to be removed or retained per acre by biophysical environment (Snow Basin DEIS). The USFS's preferred alternative proposed removal of grand fir from cool/moist and warm/dry grand fir biophysical environments, as well as removal of ponderosa pine, Douglas-fir, and western larch from mixed ponderosa pine and Douglas-fir biophysical environments (**Table 2**). Based on this information we computed the total number of large trees proposed for removal vs. retention across the project area by biophysical environment. To evaluate the potential carbon consequences of large tree removal, it was necessary to know tree size class distribution. The FIA only surveyed 13 plots in the Snow Basin project area between 2010 and 2018, of which 12 plots included large trees. After an initial analysis, we deemed this inadequate for rigorous assessment of tree size class distribution and therefore used tree measurements from all FIA plots in the Wallowa-Whitman National Forest that included large trees for the species of interest ($n = 217$ plots). To estimate the size class distribution of large trees, we computed the fraction of large trees that occurred at 0.1 cm DBH intervals between 53.3 cm and the largest observed DBH for grand fir, and after combining ponderosa pine, Douglas-fir, and western larch into a mixed-species group. For each biophysical environment, we then distributed the large trees proposed for removal or retention among these size classes in proportion to the occurrence of trees in each size class. Lastly, we estimated the total large tree AGC that would be removed or retained by multiplying the number of trees in each size class by the mean AGC of trees in that size class and then summing AGC across size classes. To account for sampling uncertainty, we again computed these metrics using a resampling approach where each of 10^4 draws utilized data from a random 25% of inventory plots sampled with replacement. As before, we computed the median across these 10^4 draws as our best-estimate and derived 95% confidence intervals. For verification, we also performed this assessment using only FIA plots in the Snow Basin Project area rather than across the Wallowa-Whitman National Forest and present these findings in the **Supplementary Material**.

RESULTS

Relationships Between Tree Diameter and Aboveground Carbon

Average tree aboveground carbon (AGC; kg) rapidly increased with tree diameter at breast height (DBH; cm) among dominant tree species measured on USFS inventory plots located in the

TABLE 2 | The total number of trees ≥21 in DBH proposed for removal and retention across the Snow Basin project area as reported in the NEPA plan prepared by the USFS (Table 53 of Snow Basin Vegetation Management Project DEIS, 2011).

Biophysical environment	Acres treated	Species removed	Mean number of large trees per acre		Total number of large trees	
			Removed	Retained	Removed	Retained
Cool/moist grand fir	973	Grand fir	5	9	4,865	8,757
Warm/dry grand fir	5,262	Grand fir	5	5	26,310	26,310
Warm/dry Douglas-fir and ponderosa pine Warm/moist Douglas-fir	6,136	Douglas-fir, ponderosa pine, western larch	2	3	12,272	18,408
Grand total	12,371	–	–	–	43,447	53,475

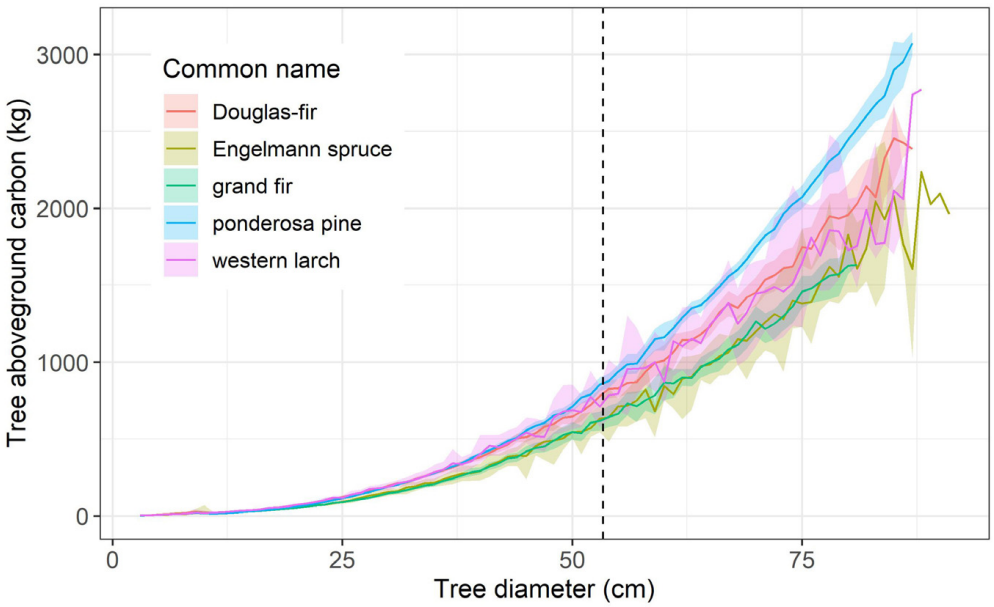


FIGURE 2 | Average tree aboveground carbon (AGC; kg) increases sharply with tree diameter at breast height (DBH; cm) for five dominant tree species measured on USFS inventory plots located in the six eastside national forests. The 21-inch (53.3 cm) DBH limit of the Eastside Screens (vertical dash line) is shown for reference. Tree AGC (≥10 cm DBH) was estimated from tree diameter and height using regional species-specific allometric equations, wood density, and carbon content. Similarly, sapling AGC (DBH = 3–9.9 cm) was estimated from sapling height using regional species-specific allometry and wood carbon content. These estimates and 95% confidence intervals were derived by resampling ($n = 10^4$) measurements from inventory plots (n = 3,335). For visual clarity, the tree diameter limit for each species excludes the largest 0.5% of trees, generally those larger than 80 to 88 cm DBH.

six eastside national forests (**Figure 2**). For instance, an average 25 cm (∼10") diameter tree stored 90–121 kg of AGC depending on tree species, while a 50 cm (∼20") diameter tree stored 541–683 kg of AGC. Thus, doubling tree diameter over this range led to a 5.3–6.2-fold increase in AGC. Similarly, tripling tree diameter from 25 cm to 75 cm led to a 13.8–18.2-fold increase in AGC, with the largest increase observed for ponderosa pine. For any given diameter, ponderosa pine, Douglas-fir and western larch tended to store more AGC than an Engelmann spruce or grand fir.

These results clearly showed that for large trees, a small increase in diameter corresponds to a massive increase in additional carbon storage relative to a small tree increasing by the same diameter increment. Overall, as trees grow larger, each additional centimeter of stem diameter corresponds with a progressively larger increase in tree carbon storage.

Tree Diameter and Aboveground Carbon Storage Within Tree Populations

Large trees (DBH ≥ 21 in or 53.3 cm) accounted for a small percentage of each species' tree stems, but a substantial percentage of the total AGC stored by each species on FIA inventory plots located in the six eastside national forests (**Figure 3** and **Table 3**). Specifically, large trees accounted for ∼2.0 to ∼3.7% of all stems (DBH ≥ 1" or 2.54 cm) among the five dominant tree species; however, these trees held ∼33.3 to ∼45.8% of the total AGC stored by each species (**Table 3**). Grand

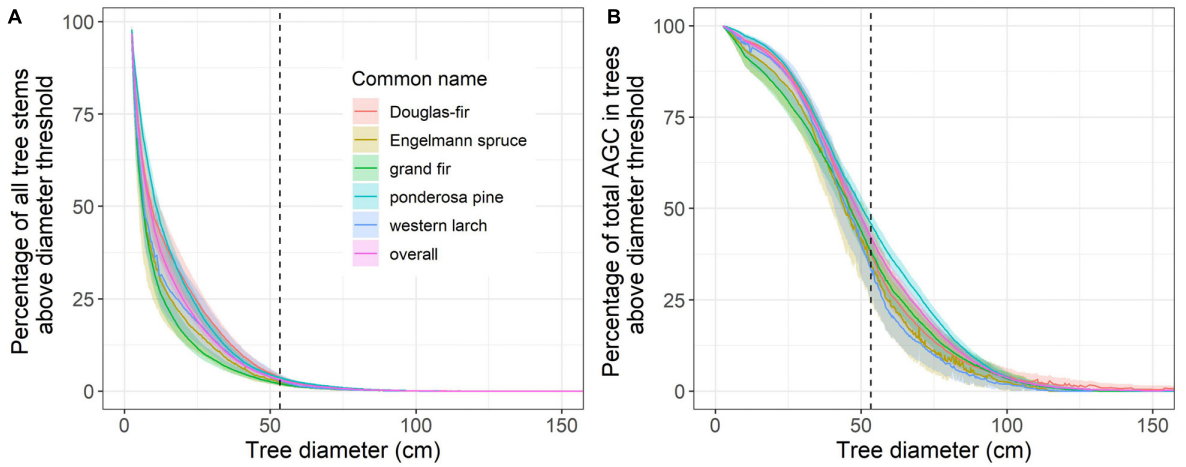


FIGURE 3 | Percentage of **(A)** all tree stems and **(B)** total aboveground carbon that occur in trees above a given diameter threshold by species based on measurements from USFS inventory plots located in the six eastside national forests. The dashed vertical lines represent a 21 in (53.3 cm) tree DBH. These estimates and 95% confidence intervals were derived by resampling ($n = 10^4$) measurements from inventory plots (n = 3,335). For example, trees with ≥21 in diameter represent 3.7 [3.2, 4.2]% of all ponderosa pine and account for 45.8 [42.8, 48.8]% of all aboveground carbon stored by this species on these inventory plots. Only ∼0.002% of trees exceeded 150 cm diameter, so for visual clarity we limited the *x*-axis to 150 cm.

TABLE 3 | Percentage of all trees stems and total aboveground carbon (AGC) occurring in trees above and below the 21 in DBH threshold based on measurements from USFS inventory plots located in the six eastside national forests.

Common name	Number of trees in the population	% of total species stems in trees. . .		% of total species AGC in trees. . .	
		<21 in	≥21 in	<21 in	≥21 in
Douglas-fir	100021	96.3 [95.4, 97.1]	3.7 [2.9, 4.6]	62.5 [58.2, 66.7]	37.5 [33.3, 41.8]
Engelmann spruce	31375	97.6 [96.0, 98.6]	2.4 [1.4, 4.0]	65.3 [54.6, 75.5]	34.7 [24.5, 45.4]
Grand fir	187445	98.0 [97.5, 98.5]	2.0 [1.5, 2.5]	61.6 [57.0, 66.2]	38.4 [33.8, 43.0]
Ponderosa pine	286970	96.3 [95.8, 96.8]	3.7 [3.2, 4.2]	54.2 [51.2, 57.2]	45.8 [42.8, 48.8]
Western larch	30708	97.2 [95.5, 98.4]	2.8 [1.6, 4.5]	66.7 [58.4, 74.8]	33.3 [25.2, 41.6]
Overall	636520	96.9 [96.6, 97.3]	3.1 [2.7, 3.4]	57.8 [55.7, 60.0]	42.2 [40.0, 44.3]

Live trees were measured on 3,335 plots surveyed between 2010 and 2018. The estimates and 95% confidence intervals below were derived by resampling bootstrap sampling. Each bootstrap sample ($n = 10^4$) utilized measurements from 25% of inventory plots selected at random.

fir had the lowest percentage of stems ≥21 in DBH (∼2.0%), while ponderosa pine and Douglas-fir had the highest percentage of stems exceeding this threshold (both ∼3.7%). However, large grand fir trees accounted for 38.4% of total species AGC, whereas large Douglas-fir accounted for 37.5% of total species AGC. Western larch had the lowest percentage of total species AGC in trees ≥21 in (∼33.3%), whereas ponderosa pine had the highest percentage (∼45.8%).

Pooling across the five dominant species, large trees accounted for ∼3.1% of the 636,520 trees occurring on the inventory plots, but stored ∼42.2% of the total AGC. Similarly, based on the FIA's CRM method, the five tree species together accounted for 44.9% of total AGC, with species-specific AGC stores ranging from ∼36.5 to ∼49.3% of the total stored by each species (**Supplementary Table 3** and **Supplementary Figure 1**).

A similar examination for trees >30 in DBH (76.2 cm) showed that among the five species, trees larger than 30 in DBH accounted for 0.4–0.9% of stems, but held ∼9.0 to ∼19.0% of each species AGC (**Table 4**). Ponderosa pine had the highest percentage of stems >30 in DBH (∼0.9%) and accounted for the highest percentage of AGC (∼19.4%) among the five species. Douglas-fir had ∼0.6% of stems >30 in DBH, and these stems held ∼12.9% of total species AGC. Engelmann Spruce, grand fir, and western larch each had ∼0.4% stems >30 in DBH, and accounted for ∼10.3, ∼14.0, and ∼9.2% of each species total AGC, respectively. Overall, trees >30 in DBH represent 0.6% of stems on inventory plots, but stored 16.6% of the total AGC.

Snow Basin Case Study: Carbon Consequences of Proposed Large Tree Removal

As per the USFS NEPA documentation, the Snow Basin project preferred alternative would have removed ∼43,447 large trees (DBH ≥ 21 in or 53.3 cm) across 12,371 acres, while retaining ∼53,475 large trees over this area (**Table 2**). We estimate this would translate into removing ∼131.3 Gg AGC stored in large trees, while retaining ∼164.1 Gg AGC in large trees (1 Gg = 10^9 *g*; **Table 5**). Grand fir from cool-moist and warm-dry environments would together comprise ∼67% (∼87.3 Gg C) of large tree AGC

TABLE 4 | Percentage of all tree stems and total aboveground carbon (AGC) occurring in trees above and below the 30 in diameter threshold based on measurements from USFS inventory plots located in the six eastside national forests.

Common name	Number of trees in the population	% of total species stems in trees. . .		% of total species AGC in trees. . .	
		<30 in	>30 in	<30 in	>30 in
Douglas-fir	100021	99.4 [99.2, 99.5]	0.6 [0.5, 0.8]	87.1 [83.7, 90.2]	12.9 [9.8, 16.3]
Engelmann spruce	31375	99.6 [99.2, 99.9]	0.4 [0.1, 0.8]	89.7 [82.7, 95.7]	10.3 [4.3, 17.3]
Grand fir	187445	99.6 [99.5, 99.7]	0.4 [0.3, 0.5]	86.0 [82.3, 89.3]	14.0 [10.7, 17.7]
Ponderosa pine	286970	99.1 [99.0, 99.3]	0.9 [0.7, 1.0]	80.6 [78.3, 82.7]	19.4 [17.3, 21.7]
Western larch	30708	99.6 [99.3, 99.8]	0.4 [0.2, 0.7]	90.8 [86.2, 94.8]	9.2 [5.2, 13.8]
Overall	636520	99.4 [99.3, 99.4]	0.6 [0.6, 0.7]	83.4 [81.8, 85.0]	16.6 [15.0, 18.2]

Tree AGC was derived using the FIA's Component Ratio Method. Live trees were measured on 3,335 plots surveyed between 2010 and 2018. The estimates and 95% confidence intervals below were derived by resampling bootstrap sampling. Each bootstrap sample (n = 10^4) utilized measurements from 25% of inventory plots selected at random.

TABLE 5 | Removal and retention of aboveground carbon (AGC) in large trees (DBH ≥ 21 in) within the proposed Snow Basin project area.

Common name	Env.	Total AGC in large trees (Gg C)...		% of large tree AGC...	
		Removed	Retained	Removed	Retained
Grand fir	Cool moist	13.6 [12.0, 15.3]	24.5 [21.6, 27.5]	35.7 [35.7, 35.7]	64.3 [64.3, 64.3]
Grand fir	Warm dry	73.7 [65.0, 82.5]	73.7 [65.0, 82.5]	50.0 [50.0, 50.0]	50.0 [50.0, 50.0]
Douglas-fir + ponderosa pine + western larch	Warm dry or moist	43.8 [40.5, 47.3]	65.7 [60.8, 71.0]	40.0 [40.0, 40.0]	60.0 [60.0, 60.0]
Overall	–	131.3 [120.8, 141.5]	164.1 [151.8, 176.2]	44.4 [44.2, 44.7]	55.6 [55.3, 55.8]

Estimates of total AGC are given in gigagrams of carbon (1 Gg = 10^9 g). Values in brackets denote 95% confidence intervals derived by resampling (n = 10^4) inventory plots used to determine tree size class distributions.

removed by the project, while ponderosa pine, Douglas-fir, and western larch from warm-dry and warm-moist environments would comprise the remaining ∼33% (∼43.8 Gg C). The project would have the largest relative and absolute impact on grand fir occurring in warm-dry environments, where 50% (∼73.7 Gg C) of large tree AGC would be removed. We obtained similar results albeit with substantially wider confidence intervals using only FIA inventory plots occurring in the Snow Basin project area (**Supplementary Table 4**).

DISCUSSION

Our study reveals the large carbon stocks associated with large-diameter trees in the region, and the potential for significant losses in AGC with large tree logging. The 21-inch rule was initially conceived to protect remaining late successional and old-growth forest and the native species that depend on these unique ecosystems for survival in forests east of the Cascades Crest in Oregon and Washington (Henjum et al., 1994). The carbon storage associated with the 21-inch rule on the six national forests is a significant co-benefit of this protective measure. Large trees (DBH ≥ 21 in or 53.3 cm) constitute ∼3% of the total stems, but store ∼42% (∼45% with CRM; **Supplementary Table 3**) of the AGC across the six eastside forests (**Table 3**). This finding highlights the important role of large trees in storing carbon in eastside forest ecosystems, and is consistent with previous findings on the disproportionately important role of large trees in the forest carbon cycle (Hudiburg et al., 2009; Lutz et al., 2012, 2018; Stephenson et al., 2014). The sharp increase in carbon storage with increasing tree diameter (**Figure 2**) speaks to the importance of preserving mature and old large trees to keep this carbon stored in the forest ecosystem where it remains for centuries (Law et al., 2018; Lutz et al., 2018). Once trees attain large stature, each additional DBH increment results in a significant addition to the tree's total carbon stores, whereas small-diameter trees must effectively ramp up to size before the relationship between DBH and AGC results in significant carbon gains. Harvest of large-diameter trees, even focused on a specific species (e.g., grand fir) can remove upward of 50% of the large tree AGC from these ecosystems (**Table 5**).

There are substantial differences in wood density among the species examined that contributes to the observed differences in AGC at a given DBH. Wood density tends to be higher for ponderosa pine (∼0.45 g cm^3), Douglas-fir (∼0.52 g cm^3), and western larch (∼0.56 g cm^3) than for Engelmann spruce (∼0.37 g cm^3) or grand fir (∼0.40 g cm^3; **Supplementary Table 2**). An evaluation of the relationship between tree height and diameter suggests the observed differences in AGC are not driven by ponderosa pine, Douglas-fir and western larch tending to be taller at a given DBH than Engelmann spruce or grand fir. Although stem decay is common in mature and old grand fir, a synthesis shows no evidence of carbon consequences of heart rot in grand fir (Harmon et al., 2008). While we could not estimate heart rot loss in grand fir due to lack of sufficient data, heart rot respiration has been estimated for another species and it had a scant contribution to ecosystem respiration (Harmon et al., 2004).

Forestry practices exert significant controls on stand structure and forest carbon dynamics, and alterations of harvest practices can substantially alter carbon storage and accumulation (Masek et al., 2011; Turner et al., 2011; Krankina et al., 2012; Kauppi et al., 2015; Law et al., 2018). Generally, there is a negative relationship between harvest intensity and forest carbon stocks whereby as harvest intensity increases, forest carbon stocks decrease while emissions increase (Hudiburg et al., 2009; Mitchell et al., 2009; Simard et al., 2020). It can take centuries to reaccumulate forest carbon stocks reduced by harvest (Birdsey et al., 2006; McKinley et al., 2011). It would take 180 to 310 years to reach maximum biomass in the Blue Mountains and East Cascades, respectively, after harvest of the large trees (Hudiburg et al., 2009), too long to help reach climate mitigation targets in the next few decades. The amount of harvested carbon that remains stored in wood products is insufficient to offset the loss of carbon stored in the forest. If harvested, life cycle assessment shows that 65% of the wood harvested in Oregon over the past 115 years has been emitted to the atmosphere, 16% is in landfills and only 19% remains in wood products (Hudiburg et al., 2019). Thus, harvesting the large trees will increase, not decrease emissions and end centuries of long-term carbon storage in the forests.

The 21-inch rule has preserved the trees that store and accumulate a disproportionately large amount of carbon in these forests (**Figure 3** and **Table 3**). Of the ∼3% of tree stems over 21 in DBH in the study area, about 81% of these are between 21 in and 30 in DBH and account for ∼61% of the AGC in all large trees (**Supplementary Figure 2**). Trees over 30 inches DBH account for ∼19% of the large tree stems and hold ∼39% of AGC in large trees. These findings are similar to those reported by Stephenson et al. (2014) and emphasize the relative importance of the sub-30 in DBH large trees in the study area, and the value in allowing these trees to continue growing and replenish the stock of trees over 30 inches DBH that are rare on the landscape. This proforestation strategy is among the most rapid means for accumulating additional quantities of carbon in forests and out of the atmosphere (Moomaw et al., 2019).

The importance of forest carbon storage is now greatly amplified by a warming climate that must urgently be addressed with reductions in greenhouse gasses and natural climate solutions (IPCC, 2018; Ripple et al., 2020). The preponderance of forests in our study area have medium to high carbon accumulation potential and low future climatic vulnerability (**Figure 1**), which reinforces the value of protecting large trees to help abate our current trajectory toward massive global change (Fargione et al., 2018; Buotte et al., 2020). Rather than holding ecosystems to an idealized conception of the past using historical conditions as management targets, a good understanding of the environmental co-benefits associated with large tree protection is needed to inform management strategies that contribute toward solving humanity's most pressing Earth system challenges (Millar et al., 2007; Rockström et al., 2009; Barnosky et al., 2017; Ripple et al., 2020). Replacing large diameter trees with seedlings will create a major carbon loss to the atmosphere during harvest (Harris et al., 2016) and not achieve storage of comparable atmospheric carbon for the indefinite future.

Large grand fir trees (DBH $\geq$ 21 in or 53.3 cm) accounted for the lowest proportion of tree stems for the five species we evaluated (2%), possibly reflecting the ingrowth of young, small grand fir within portions of our study area (Merschel et al., 2014; Johnston et al., 2016). One of the main premises for the proposed removals of large-diameter grand fir trees is that they have increased over historic levels, especially in drier biophysical environments. However, our data does not indicate an uncharacteristic abundance of large grand fir trees across these forests. Given the recent history of high-grade logging that focused on large and old trees (Henjum et al., 1994; Rainville et al., 2008), historical abundances of large trees were much greater than today (Wales et al., 2007; Hagmann et al., 2013; Kauppi et al., 2015), and thus would have represented a larger fraction of aboveground biomass than currently found on these forests.

Interestingly, with respect to the overall representation of species abundance based on inventory plots (**Table 3**), the population of grand fir with 187,445 stems is a distant second to ponderosa pine with 286,970 stems, followed by Douglas-fir (100,021 stems), Engelmann spruce (31,375 stems), and western larch (30,708 stems). To the extent that current forest stand structure is skewed toward smaller diameter classes, ponderosa pine, grand fir, and Douglas-fir trees are notable for the number of trees on inventory plots.

It is important to note that a diameter limit that emphasized protection of carbon stores would ideally protect trees starting at a lower DBH limit (∼12–15 inches). The 21-inch rule has provided significant leeway for fuels reduction and ecological restoration toward historical baselines to proceed in eastside forests. Ecological restoration treatments generally recommend giving protection to large and old trees, while reducing surface and ladder fuels, and accompanied by understory thinning treatments where appropriate and reintroduction of low-intensity fire at intervals (Allen et al., 2002; Brown et al., 2004; Agee and Skinner, 2005; Noss et al., 2006). From a forest carbon perspective, it would be prudent to restore an appropriate number of the approximately 97% of tree stems <21 inches DBH to replenish the stock of large trees over time (Lutz et al., 2018; Moomaw et al., 2019), while continuing to protect large trees for their carbon stores and the myriad other benefits that they provide. This approach would achieve the benefits of proforestation in the larger, most fire-resistant trees and reduction of fuel loads and stem density in the smaller diameter tree stems.

The Snow Basin project provides a case study for how amending the 21-inch rule to allow logging large trees could change management across the six eastside National Forests. Overall the Snow Basin project would have removed 44% or 131,000 metric tons of carbon stored in large trees. This is equivalent to ∼0.75% of annual Oregon statewide carbon emissions, and this does not include carbon in tree roots or the AGC losses due to the removal of trees <21 in DBH. Removing nearly half of the carbon content from the large trees over 12,000 acres would create a carbon deficit in the live, dead, and soil carbon pools that will persist for many decades to the end of the century. However, left standing, these 43,445 large

trees continue to grow, sequestering more carbon into long-term stores (Stephenson et al., 2014; Law et al., 2018; Domke et al., 2020). Older trees (∼100 years) are the next generation of old growth and already possess qualities associated with large, old trees, such as large canopies, deep root systems, and thick, fire-resistant bark.

Co-Benefits of Carbon, Habitat, Biodiversity, Water Availability, Resilience to Climate Extremes

High carbon conservation-priority forests support important components of biodiversity and are associated with increased water availability (McKinley et al., 2011; Perry and Jones, 2016; Berner et al., 2017; Law et al., 2018; Buotte et al., 2020). Large-diameter snags persist as standing snags for many years, providing valuable wildlife habitat, and account for a relatively high proportion of total snag biomass in temperate forests (Lutz et al., 2012). In PNW forests, large hollow trees, both alive and dead, are the most valuable for denning, shelter, roosting, and hunting by a wide range of animals (Bull et al., 2000; Rose et al., 2001). In the Interior Columbia River Basin, grand fir and western larch form the best hollow trees for wildlife uses (Rose et al., 2001). Downed hollow logs continue to serve as important hiding, denning, and foraging habitat on the forest floor (Bull et al., 1997; Bull et al., 2000). Large decaying wood influences basic ecosystem processes such as soil development and productivity, nutrient immobilization and mineralization, and nitrogen fixation (Harmon et al., 1986). Continuing to protect large trees in eastside forests provides the greatest benefit for carbon, habitat, and biodiversity.

Water availability and microclimatic buffering are also disproportionately affected by large trees and intact forests (Frey et al., 2016; Buotte et al., 2020). Forest canopies of the PNW buffer extremes of maximum temperature and vapor pressure deficit, with biologically beneficial consequences (Davis et al., 2019a). Removal of large trees quickly leads to a large increase in soil and canopy heating, which increases enough to impact photosynthesis (Kim et al., 2016), seedling survival, and regeneration (Kolb and Robberecht, 1996; Davis et al., 2019b). The climatic changes toward warmer and drier conditions expected in the next decades will likely increase forest stress and mortality (Allen et al., 2015). Eastside forests experienced hotter and drier conditions from 2003 to 2012 concentrated in the months of August and September, especially in drier forest type groups (i.e., ponderosa pine, juniper), whereas spring months (April–June) showed trends toward cooler and wetter conditions (Mildrexler et al., 2016). Projections suggest that proportionally, the largest changes in microclimatic buffering capacity will occur in lower elevation or dry forests, which currently have more limited buffering capacity (Davis et al., 2019a). In these drier regions, microclimatic buffering by forest canopies may create important microsites and refugia in a moisture-limited system (Meigs and Krawchuk, 2018). In an old growth ponderosa pine stand in eastern Oregon, ∼35% of the total daily water used from the upper 2 m was replaced by hydraulic redistribution from deep soil by deep-rooted larger trees in summer (Brooks et al., 2002). The bigger trees rarely reach 80% loss of hydraulic conductivity, and both mature pine and mesic Douglas-fir were better buffered from the effects of drought on photosynthesis compared with young pine (∼20-year old) due to full root development and larger stem capacitance in older trees (Kwon et al., 2018). Redistribution of deep soil water can increase seedling survival during summer drought when young trees lack the root development to reach deep soil water (Brooks et al., 2002). While large tree composition may have shifted today relative to European settlement times, these large trees nonetheless continue to perform important functional attributes related to water and climate such as carbon storage, hydraulic redistribution, shielding the understory from direct solar radiation, and providing wildlife habitat. These functional attributes of large trees, irrespective of species, characterize ecosystems through thousands to millions of years (Barnosky et al., 2017), and are not quickly replaced.

In mesic forest environments, microclimatic buffering and transpirational cooling are amplified because sites with higher moisture availability are better able to shift energy to latent as opposed to sensible heat fluxes (Dai et al., 1999; Mildrexler et al., 2011). During midday in full sun the surface temperature of a closed canopy moist forest is warmer than the temperature beneath the canopy which is protected from direct solar radiation (Thomas, 2011). Microclimates in moist forests are strongly linked to their closed-canopy structure (Chen et al., 1999; Aussenac, 2000). Removal of the overstory creates canopy openings that increase solar radiation penetration resulting in increased drying of the understory vegetation and the forest floor, and a thermal response of rising land surface temperatures (Chen et al., 1993, 1999). This alteration in the subcanopy thermal regime changes atmospheric mixing between the ground, subcanopy, and canopy, which in turn modifies the microclimate condition of the affected stand. Microclimate modifications associated with forest harvesting are expected to be greatest in moist forests and may affect resilience to climate change and increase the risk of occurrence and severity of wildfires (Lindenmayer et al., 2009). Maintaining mesic microclimates may give undisturbed moist forests and the species they support some inherent resilience to climate change. Moreover, an evaluation of the effects of water limitations on forest carbon cycling in the eastern Cascade Mountains found that grand fir radial growth was not strongly associated with variability in temperature or water variability (Berner and Law, 2015). A lengthening of the growing season may increase productivity in high-elevation grand fir stands. The microclimatic buffering, current and future potential carbon stores, and intact nature of previously unlogged grand fir and Douglas-fir forest types are co-benefits of protecting large trees that need to be considered in future management decisions.

Potential Solutions

The consequences of reducing protection of large trees are significant reduction in forest carbon stores and their climate mitigation, impacts on habitat for animals including birds, and

resilience to a changing climate for decades to centuries to come. Given the rarity of large trees across the landscape, and their outsized role in *storing carbon removed from the atmosphere*, our findings call into question the value of removing large trees for forest modification in eastside forests.

If the 21-inch rule were retained on these lands, continued protection of the existing carbon stock would prevent large quantities of harvest related biogenic carbon from being released to the atmosphere. It is also essential to let a sufficient number of sub-21 inch trees remain to become additional large, effective carbon stores, and assure that carbon accumulation continues in these forests. Rather than weakening the 21-inch rule, we suggest strengthening this important measure and expanding large tree protections to other western United States public lands that have been adversely affected by a similar history of large-tree logging. Protecting and growing more large trees is the most effective near-term option for accumulating more carbon out of the atmosphere, and will benefit other ecosystem services as well.

Some public lands (local, state, and federal) could become part of a *designated reserve system* that includes intact forest landscapes, and carbon rich forests, that hold most of these large, older trees. This is an appropriate use of public lands because the services they provide including biodiversity, water retention, carbon accumulation and storage, and regional cooling by evapotranspiration serve the public interest, and promote sustainable economies that benefit from land protection and restoration.

The critical need to adapt to more wildfire in the west is congruent with protecting large-trees in fire-prone forests. Older forests experience lower fire-severity compared with younger, intensively managed forests, even during extreme weather conditions (Zald and Dunn, 2018). A shift in policy and management from restoring ecosystems based on historical baselines to adapting to changing fire regimes and from unsustainable defense of the wildland–urban interface to developing fire-adapted communities is needed (Schoennagel et al., 2017). Improved fire and forest management is part of the solution, but the most effective changes in terms of protection of people and property, will be near homes and on private property. Prioritizing federal fuel treatments around communities and creating better mechanisms for reducing fuels on private land can help reduce home loss and better protect communities (Moritz et al., 2014; Schoennagel et al., 2017). Given the natural role of fire in the West, managing more wild and prescribed fires with a range of severities will help reduce future wildfire threats and increase ecological benefits in many systems (Schoennagel et al., 2017).

Eastside forests are surrounded predominantly by rural communities. For production forests, lengthening the forest cycle will keep a larger amount of carbon in trees and soils rather than in the atmosphere (Law et al., 2018). Rather than coupling funding of forest restoration or community payments to logging large trees and disturbing older forests, new policies could be enacted that compensate rural communities for protecting large trees in older forests and some of the younger trees that will become large with their associated carbon stores. To implement such policies, the amount to be paid to a community needs to be marginally greater than the revenue earned from cutting these large trees and the older forests in which they are located. Policies that provide compensation for setting aside reserves and individual trees with microhabitats are already in place in Europe (European Commission, 2015). Because this service benefits society as a whole and is an irreplaceable part of the natural climate solutions framework urgently needed for climate stabilization, the payment funds should come from the treasury since all citizens benefit from carbon accumulation by these trees and forests. With over half of Oregon's forest east of the Cascade Mountains crest, these forests are key to the State's climate mitigation and biodiversity conservation goals.

CONCLUSION

Conducting a quantitative assessment using empirical data has determined the large carbon stock that would be lost and the resulting climate consequences if these large trees are harvested. Research indicates that 2021 begins a pivotal decade for humanity to transition off of fossil-fuels (IPCC, 2018) and move "to achieve ... stabilization of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system." (UNFCCC, 1992, Article 2). To meet net-zero carbon goals by 2050, it is estimated that reductions in net carbon emissions must be 7.6% per year over the decade of the 2020s (UNEP, 2019). This is most readily accomplished by reducing fossil fuel, bioenergy and industrial carbon dioxide emissions while simultaneously accumulating more carbon dioxide by protecting existing older forests that contain the largest share of carbon, and by allowing more forests to continue to accumulate carbon through proforestation (IUCN, 2020). Proforestation allows existing forests to continue growing without harvest or other management practices so that more trees can reach the large tree size that accumulates more carbon in the near and long term than do reforestation and afforestation (Moomaw et al., 2019). No additional land is required as is the case with afforestation, and proforestation is the lowest cost opportunity for reaching the zero net carbon goal by 2050. In fire-prone forests such as in our study area, a diameter limit strikes the balance between protecting the most fire-resistant trees that store the most carbon and allowing fuels reduction with reintroduction of fire in dry biophysical environments. Intact mesic forests are ideal locations for proforestation. Harvesting large trees will add very large amounts of biogenic carbon to the atmosphere (Harris et al., 2016), and make the net zero carbon goal difficult or impossible for Oregon to achieve. The young trees will never be able to recover and accumulate the amount of carbon that is in the growing and older forests during these next critical decades, and will only equal current levels a century or more from now.

Protecting large trees to help stabilize climate is critically important for managing forest ecosystems as social-ecological

systems. Knowledge of the disproportionately large amount of carbon stored in a small fraction of trees creates an opportunity to engage the public, decision makers, and forest managers in their importance as an integral part of the climate solution.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study and are available through the FIA DataMart: https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html.

AUTHOR CONTRIBUTIONS

DM and LB conceived the ideas and designed the study with critical suggestions from BL and RB. DM and LB collected the data. LB processed the data and carried out the modeling. DM and LB analyzed the data and led the writing of the manuscript. BL, RB, and WM assisted with writing, and contributed critically to the drafts. All authors gave final approval for publication.

FUNDING

This research was supported by United States Department of Energy (Grant DE-SC0012194) and Agriculture and Food Research Initiative of the USDA National Institute of Food and Agriculture (Grant numbers 2014-67003-22065 and 2014-35100-22066) for our North American Carbon Program study, "Carbon cycle dynamics within Oregon's urban-suburban-forested-agricultural landscapes." WM received support from Rockefeller Brothers Fund. DM received support from Eastern Oregon Legacy Lands.

ACKNOWLEDGMENTS

Thanks to Dr. Mark Harmon for supporting the initiation of this research.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2020.594274/full#supplementary-material

REFERENCES

Agee, J. K., and Skinner, C. N. (2005). Basic principles of forest fuel reduction treatments. *For. Ecol. Manage.* 211, 83–96. doi: 10.1016/j.foreco.2005.01.034

Allen, C. D., Breshears, D. D., and McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:129. doi: 10.1890/ES15-00203.1

Allen, C. D., Savage, M. S., Falk, D. A., Suckling, K. F., Swetnam, T. W., Schulke, T., et al. (2002). Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol. Appl.* 12, 1418–1433. doi: 10.1890/1051-0761(2002)012[1418:erospp]2.0.co;2

Aussenac, G. (2000). Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Ann. For Sci.* 57, 287–301. doi: 10.1051/forest:2000119

Barnosky, A. D., Hadly, E. A., Gonzalez, P., Head, J., Polly, P. D., Lawing, A. M., et al. (2017). Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* 355:eaah4787. doi: 10.1126/science.aah4787

Beiler, K. J., Simard, S. W., and Durall, D. M. (2015). Topology of *Rhizopogon* spp. mycorrhizal meta-networks in xeric and mesic old-growth interior Douglas-fir forests. *J. Ecol.* 103, 616–628. doi: 10.1111/1365-2745.12387

Berner, L. T., and Law, B. E. (2015). Water limitations on forest carbon cycling and conifer traits along a steep climatic gradient in the Cascade Mountains, Oregon. *Biogeosciences* 12, 6617–6635. doi: 10.5194/bg-12-6617-2015

Berner, L. T., and Law, B. E. (2016). Plant traits, productivity, biomass and soil properties from forest sites in the Pacific Northwest, 1999–2014. *Sci. Data* 3:160002.

Berner, L. T., Law, B. E., and Hudiburg, T. W. (2017). Water availability limits tree productivity, carbon stocks, and carbon residence time in mature forests across the western US. *Biogeosciences* 14, 365–378. doi: 10.5194/bg-14-365-2017

Birdsey, R., Pregitzer, K., and Lucier, A. (2006). Forest carbon management in the United States: 1600-2100. *J. Environ. Qual.* 35, 1461–1469. doi: 10.2134/jeq2005.0162

Birdsey, R. A., Dugan, A. J., Healey, S. P., Dante-Wood, K., Zhang, F., Mo, G., et al. (2019). *Assessment of the Influence of Disturbance, Management Activities, and Environmental Factors on Carbon Stocks of U.S. National Forests. Gen. Tech. Rep. RMRS-GTR-402.* Fort Collins, CO: U.S. Department of Agriculture.

Bivand, R., Keitt, T., and Rowlingson, B. (2019). *rgdal: Bindings for the 'Geospatial' Data Abstraction Library. R package version 1.4-8.* Available online at: https://CRAN.R-project.org/package=rgdal (accessed October 25, 2019).

Bivand, R., and Lewin-Koh, N. (2019). *maptools: Tools for Handling Spatial Objects. R package version 0.9.9.* Available online at: https://CRAN.R-project.org/package=maptools (accessed February 2, 2019).

Brooks, J. R., Meinzer, F. C., Coulombe, R., and Gregg, J. (2002). Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiol.* 22, 1107–1117. doi: 10.1093/treephys/22.15-16.1107

Brown, R. T., Agee, J. K., and Franklin, J. F. (2004). Forest restoration and fire: principles in the context of place. *Conserv. Biol.* 18, 903–912. doi: 10.1111/j.1523-1739.2004.521_1.x

Bull, E. L., Akenson, J. J., and Henjum, M. J. (2000). Characteristics of black bear dens in trees and logs in northeastern Oregon. *Northw. Naturalist* 81, 148–153. doi: 10.2307/3536825

Bull, E. L., Heater, T. W., and Shepherd, J. F. (2005). Habitat selection by the American Marten in Northeastern Oregon. *Northwest Sci.* 79, 36–42.

Bull, E. L., Parks, C. G., and Torgersen, T. R. (1997). *Trees and Logs Important to Wildlife in the Interior Columbia River Basin. Gen. Tech. Rep. PNW-GTR-391.* Portland, OR: U.S. Department of Agriculture.

Buotte, P. C., Law, B. E., Ripple, W. J., and Berner, L. T. (2020). Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States. *Ecol. Appl.* 30:e02039. doi: 10.1002/eap.2039

Chen, J., Franklin, J. F., and Spies, T. A. (1993). Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agric. Forest Meteorol.* 63, 219–237. doi: 10.1016/0168-1923(93)90061-l

Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., et al. (1999). Microclimate in forest ecosystem and landscape ecology. *BioScience* 49, 288–297. doi: 10.2307/1313612

Cochran, P. H. (1985). *Site Index, Height Growth, Normal Yields and Stocking Levels for Larch in Oregon and Washington. Research Paper PNW-RP-424.* Portland, OR: U.S. Department of Agriculture.

Cook-Patton, S. C., Leavitt, S. M., Gibbs, D., Harris, N. L., Lister, K., Anderson-Teixeira, K. J., et al. (2020). Mapping carbon accumulation potential from global natural forest regrowth. *Nature* 585, 545–550. doi: 10.1038/s41586-020-2686-x

Dai, A., Trenberth, K. E., and Karl, T. R. (1999). Effects of clouds, soil moisture, precipitation, and water vapor on diurnal temperature range. *J. Clim.* 12, 2451–2473. doi: 10.1175/1520-0442(1999)012<2451:eocsmp>2.0.co;2

Daly, C., Halbleib, M., Smith, J. I, Gibson, W. P., Dogget, M. K., Taylor, G. H., et al. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int. J. Climatol.* 28, 2031–2064. doi: 10.1002/joc.1688

Davis, K. T., Dobrowski, S. Z., Higuera, P. E., Holden, Z. A., Veblen, T. T., Rother, M. T., et al. (2019b). Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proc. Natl. Acad. Sci. U.S.A.* 116, 6193–6198. doi: 10.1073/pnas.1815107116

Davis, K. T., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E., and Abatzoglou, J. T. (2019a). Microclimatic buffering in forests of the future: the role of local water balance. *Ecography* 42, 1–11. doi: 10.1111/ecog.03836

Dawle, M., and Srinivasan, A. (2019). *data.table: Extension of 'data.frame'. R package version 1.12.8*. Available online at: https://CRAN.R-project.org/package=data.table (accessed October 17, 2019).

Depro, B. M., Murray, B. C., Alig, R. J., and Shanks, A. (2008). Public land, timber harvests, and climate mitigation: quantifying carbon sequestration potential on U.S. public timberlands. *For. Ecol. Manage.* 225, 1122–1134. doi: 10.1016/j.foreco.2007.10.036

Dilling, L., Birdsey, R., and Pan, Y. (2013). "Opportunities and challenges for carbon management on U.S. public lands," in *Land Use and the Carbon Cycle: Advances in Integrated Science, Management and Policy*, eds D. G. Brown, D. T. Robinson, N. H. F. French, and B. C. Reed (Cambridge: Cambridge Press), 455–476. doi: 10.1017/cbo9780511894824.023

Domke, G. M., Oswalt, S. N., Walters, B. F., and Morin, R. S. (2020). Tree planting has the potential to increase carbon sequestration capacity of forests in the United States. *Proc. Natl. Acad. Sci. U.S.A.* 117, 24649–24651. doi: 10.1073/pnas.2010840117

Dugan, A. J., Birdsey, R., Healey, S. P., Pan, Y., Zhang, F., Mo, G., et al. (2017). Forest sector carbon analyses support land management planning and projects: assessing the influence of anthropogenic and natural factors. *Clim. Change* 144, 207–220. doi: 10.1007/s10584-017-2038-5

EPA (2020). *Draft Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990-2018. EPA 430-P-20-001*. Washington, DC: U.S. Environmental Protection Agency, 719.

European Commission (2015). *Natura 2000 and Forests. Part I–II. Technical Report—2015-088*. Brussels: EU Commission Environment.

Fargione, J. E., Bassett, S., Boucher, T., Bridgham, S. D., Conant, R. T., Cook-Patton, S. C., et al. (2018). Natural climate solutions for the United States. *Sci. Adv.* 4:eaat1869. doi: 10.1126/sciadv.aat186

Frey, S. J. K., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., and Betts, M. G. (2016). Spatial models reveal the microclimate buffering capacity of old-growth forests. *Sci. Adv.* 2:e1501392. doi: 10.1126/sciadv.1501392

Friedlingstein, P., Jones, M. W., O'Sullivan, M., Andrew, R. M., Hauck, J., Peter, G. P., et al. (2019). Global carbon budget 2019. *Earth Syst. Sci. Data* 11, 1783–1838. doi: 10.5194/essd-11-1783-2019

Gholz, H. L., Grier, C. C., Campbell, A. G., and Brown, A. T. (1979). *Equations for Estimating Biomass and Leaf Area of Plants in the Pacific Northwest. Res. Pap. 41, Forestry Research Laboratory*. Corvallis: Oregon State University, 38.

Greenwald, D. N., Crocker-Bedford, D. C., Broberg, L., Suckling, K. E., and Tibbitts, T. (2005). A review of Northern Goshawk habitat selection in the home range and implications for forest management in the Western United States. *Wildl. Soc. Bull.* 33, 120–129. doi: 10.2307/3784847

Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., et al. (2017). Natural climate solutions. *Proc. Natl. Acad. Sci. U.S.A.* 114, 11645–11650. doi: 10.1073/pnas.1710465114

Hagmann, R. K., Franklin, J. F., and Johnson, K. N. (2013). Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. *For. Ecol. Manag.* 304, 492–504. doi: 10.1016/j.foreco.2013.04.005

Harmon, M. E., Bible, K., Ryan, M. G., Shaw, D. C., Chen, H., Klopatek, J., et al. (2004). Production, respiration, and overall carbon balance in an old-growth Pseudotsuga-Tsuga forest ecosystem. *Ecosystems* 7, 498–512. doi: 10.1007/s10021-004-0140-9

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., et al. (1986). Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15, 133–302. doi: 10.1016/S0065-2504(03)34002-4

Harmon, M. E., Woodall, C. W., Fasth, B., and Sexton, J. (2008). *Woody Detritus Density and Density Reduction Factors for Tree Species in the United States: A Synthesis. Gen. Tech. Rep. NRS-29*. Newtown Square, PA: U.S. Department of Agriculture, 84.

Harris, N. L., Hagen, S. C., Saatchi, S. S., Pearson, T. R. H., Woodall, C. W., Domke, G. M., et al. (2016). Attribution of net carbon change by disturbance type across forest lands of the conterminous United States. *Carbon Balance Manag.* 11:24. doi: 10.1186/s13021-016-0066-5

Henjum, M. G., Karr, J. R., Bottom, D. L., Perry, D. A., Bednarz, J. C., Wright, S. G., et al. (1994). *Interim Protection for Late Successional Forest, Fisheries and Watersheds: National Forests East of the Cascade Crest, Oregon and Washington*. Bethesda, MD: Wildlife Society.

Hessburg, P. F., Charnley, S., Wendel, K. L., White, E. M., Spies, T. A., Singleton, P. H., et al. (2020). *The 1994 Eastside Screens—Large Tree Harvest Limit: Synthesis of Science Relevant to Forest Planning 25 years Later*. Portland, OR: USDA.

Hijmans, R. J. (2019). *raster: Geographic Analysis and Modeling. R package version 3.0-12*. Available online at: http://CRAN.R-project.org/package=raster (accessed August 22, 2019).

Hudiburg, T., Law, B., Turner, D. P., Campbell, J., Donato, D. C., and Duane, M. (2009). Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. *Ecol. Appl.* 19, 163–180. doi: 10.1890/07-2006.1

Hudiburg, T. W., Law, B. E., Moomaw, W. R., Harmon, M. E., and Stenzel, J. E. (2019). Meeting GHG reduction targets requires accounting for all forest sector emissions. *Environ. Res. Lett.* 14, 095005. doi: 10.1088/1748-9326/ab28bb

Interior Columbia Basin Ecosystem Management Project (2000). *Supplemental Draft Environmental Impact Statement*. Boise: ICBEMP.

IPCC (2018). "Summary for policymakers," in *Global Warming of 1.5oC, An IPCC Special Report*, eds V. Masson Delmotte, P. Zhai, H.-O. P. Rtner, D. Roberts, J. Skea, P. R. Shukla, et al. (Geneva: World Meteorological Organization), 32.

IUCN (2020). *International Union for the Conservation of Nature. Cyril Kormos, Brendan Mackey, Russel Mittermeir, Virginia Young, Primary Forests: A Priority Nature-Based Solution*. Available online at: https://www.iucn.org/crossroads-blog/202003/primary-forests-a-priority-nature-based-solution (accessed August 5, 2020)

Jenkins, J., Chojnacky, D., Heath, L., and Birdsey, R. (2004). *Comprehensive Database of Diameter-Based Biomass Regressions for North American Tree Species. Gen Tech Rep NE-319*. Newtown Square, PA: U.S. Department of Agriculture.

Johnson, C. G., and Clausnitzer, R. R. (1992). *Plant Associations of the Blue and Ochoco Mountains. R6-ERW-T-036-92*. Portland, OR: USDA Forest Service Pacific Northwest Region.

Johnston, J. D., Bailey, J. D., and Dunn, C. J. (2016). Influence of fire disturbance and biophysical heterogeneity on pre-settlement ponderosa pine and mixed conifer forests. *Ecosphere* 7:e01581. doi: 10.1002/ecs2.1581

Johnston, J. D., Dunn, C. J., Vernon, M. J., Bailey, J. D., Morrissette, B. A., and Morici, K. E. (2018). Restoring historical forest conditions in a diverse inland Pacific Northwest landscape. *Ecosphere* 9:e02400. doi: 10.1002/ecs2.2400

Kauppi, P. E., Birdsey, R. A., Pan, Y., Ihalainen, P., Nöjd, P., and Lehtonen, A. (2015). Effects of land management on large trees and carbon stocks. *Biogeosciences* 12, 855–886. doi: 10.5194/bg-12-855-2015

Kerns, B. K., Powell, D. C., Mellmann-Brown, S., Carnwath, G., and Kim, J. B. (2017). Effects of projected climate change on vegetation in the Blue Mountains ecoregion, USA. *Clim. Serv.* 10, 33–43. doi: 10.1016/j.cliser.2017.07.002

Kim, Y., Still, C. J., Hanson, C. V., Kwon, H., Greer, B. T., and Law, B. E. (2016). Canopy skin temperature variations in relation to climate, soil temperature, and carbon flux at a ponderosa pine forest in central Oregon. *Agr. Forest Meteorol.* 226, 161–173. doi: 10.1016/j.agrformet.2016.06.001

Kolb, P. F., and Robberecht, R. (1996). High temperature and drought stress effects on survival of Pinus ponderosa seedlings. *Tree Physiol.* 16, 665–672. doi: 10.1093/treephys/16.8.665

Krankina, O. N., Harmon, M. E., Schnekenburger, F. S., and Sierra, C. A. (2012). Carbon balance on federal forest lands of Western Oregon and Washington: the impact of the Northwest Forest Plan. *For. Ecol. Manage.* 286, 171–182. doi: 10.1016/j.foreco.2012.08.028

Kwon, H., Law, B. E., Thomas, C. K., and Johnson, B. G. (2018). The influence of hydrological variability on inherent water use efficiency in forests

of contrasting composition, age, and precipitation regimes in the Pacific Northwest. *Agric. For. Meteorol.* 249, 488–500. doi: 10.1016/j.agrformet.2017.08.006

Lamlom, S., and Savidge, R. (2003). A reassessment of carbon content in wood: variation within and between 41 North American species. *Biomass Bioenergy* 25, 381–388. doi: 10.1016/S0961-9534(03)00033-3

Law, B. E., Hudiburg, T. W., Berner, L. T., Kent, J. J., Buotte, P. C., and Harmon, M. (2018). Land use strategies to mitigate climate change in carbon dense temperate forests. *Proc. Nat. Acad. Sci. U.S.A.* 115, 3663–3668. doi: 10.1073/pnas.1720064115

Lindenmayer, D. B., Hunter, M. L., Burton, P. J., and Gibbons, P. (2009). Effects of logging on fire regimes in moist forests. *Conserv. Lett.* 2, 271–277. doi: 10.1111/j.1755-263x.2009.00080.x

Lindenmayer, D. B., and Laurance, W. F. (2017). The ecology, distribution, conservation and management of large old trees. *Biol. Rev.* 92, 1434–1458. doi: 10.1111/brv.12290

Lindenmayer, D. B., Laurance, W. F., Franklin, J. F., Likens, G. E., Banks, S. C., Blanchard, W., et al. (2014). New policies for old trees: averting a global crisis in a keystone ecological structure. *Conserv. Lett.* 7, 61–69. doi: 10.1111/conl.12013

Lutz, J. A., Furniss, T. J., Johnson, D. J., Davies, S. J., Allen, D., Alonso, A., et al. (2018). Global importance of large-diameter trees. *Glob. Ecol. Biogeogr.* 27, 849–864. doi: 10.1111/geb.12747

Lutz, J. A., Larson, A. J., Swanson, M. E., and Freund, J. A. (2012). Ecological importance of large-diameter trees in a temperate mixed-conifer forest. *PLoS One* 7:e36131. doi: 10.1371/journal.pone.0036131

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B. E., et al. (2008). Old-growth forests as global carbon sinks. *Nature* 455, 213–215. doi: 10.1038/nature07276

Masek, J. G., Cohen, W. B., Leckie, D., Wulder, M. A., Vargas, R., de Jong, B., et al. (2011). Recent Rates of Forest Harvest and Conversion in North America. *J. Geophy. Res.* 116:G00K03. doi: 10.1029/2010JG001471

McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T., and Theobald, D. M. (2016). Achieving climate connectivity in a fragmented landscape. *Proc. Natl. Acad. Sci. U.S.A.* 113, 7195–7200. doi: 10.1073/pnas.1602817113

McKinley, D. C., Ryan, M. G., Birdsey, R. A., Giardina, C. P., Harmon, M. E., Heath, L. S., et al. (2011). A synthesis of current knowledge on forests and carbon storage in the United States. *Ecol. Appl.* 21, 1902–1924. doi: 10.1890/10-0697.1

Means, J. E., Hansen, H. A., Koerper, G. J., Alaback, P. B., and Klopsch, M. W. (1994). *Software for Computing Plant Biomass–BIOPAK Users Guide*. Portland, OR: U.S. Department of Agriculture.

Meigs, G. W., and Krawchuk, M. A. (2018). Composition and structure of forest fire refugia: what are the ecosystem legacies across burned landscapes? *Forests* 9:243. doi: 10.3390/f9050243

Merschel, A., Vora, R. S., and Spies, T. (2019). Conserving dry old-growth forest in Central Oregon, USA. *J. For.* 117, 128–135. doi: 10.1093/jofore/fvy085

Merschel, A. G., Spies, T. A., and Heyerdahl, E. K. (2014). Mixed−conifer forests of central Oregon: effects of logging and fire exclusion vary with environment. *Ecol. Appl.* 24, 1670–1688. doi: 10.1890/13-1585.1

Mildrexler, D. J., Yang, Z., and Cohen, W. B. (2016). A forest vulnerability index based on drought and high temperatures. *Rem. Sens. Environ.* 173, 314–325. doi: 10.1016/j.rse.2015.11.024

Mildrexler, D. J., Zhao, M., and Running, S. W. (2011). A global comparison between station air temperatures and MODIS land surface temperatures reveals the cooling role of forests. *J. Geophys. Res.* 116:G03025. doi: 10.1029/2010JG001486

Millar, C. I., Stephenson, N. L., and Stephens, S. L. (2007). Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* 17, 2145–2151. doi: 10.1890/06-1715.1

Mitchell, S. R., Harmon, M. E., and O'Connell, K. E. B. (2009). Forest fuel reduction alters fire severity and long-term carbon storage in three Pacific Northwest ecosystems. *Ecol. Appl.* 19, 643–655. doi: 10.1890/08-0501.1

Moomaw, W. R., Masino, S. A., and Faison, E. K. (2019). Intact forests in the United States: proforestation mitigates climate change and serves the greatest good. *Front. For. Glob. Change* 2:27. doi: 10.3389/ffgc.2019.00027

Moritz, M. A., Batllori, E., Bradstock, R. A., Gill, A. M., Handmer, J., Hessburg, P. F., et al. (2014). Learning to coexist with wildfire. *Nature* 515, 58–66. doi: 10.1038/nature13946

Noss, R. F., Franklin, J. F., Baker, W. L., Schoennagel, T., and Moyle, P. B. (2006). Managing fire-prone forests in the western United States. *Front. Ecol. Environ.* 4:481–487. doi: 10.1890/1540-929520064[481:MFFITW]2.0.CO;2

O'Connell, B. M., Conkling, B. L., Wilson, A. M., Burrill, E. A., Turner, J. A., Pugh, S. A., et al. (2017). *The Forest Inventory and Analysis Database: Database Description and User Guide Version 7.0 for Phase 2*. Washington, DC: U.S. Department of Agriculture, 830.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., et al. (2011). A large and persistent carbon sink in the World's forests. *Science* 333, 988–993. doi: 10.1126/science.1201609

Perry, T. D., and Jones, J. A. (2016). Summer streamflow deficits from regenerating Douglas-fir forests in the Pacific Northwest, USA. *Ecohydrology* 10:e1790. doi: 10.1002/eco.1790

Peterson, D. L., and Waring, R. H. (1994). Overview of the Oregon transect ecosystem research project. *Ecol. Appl.* 4, 211–225. doi: 10.2307/1941928

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rainville, R., White, R., and Barbour, J. (2008). *Assessment of Timber Availability from Forest Restoration within the Blue Mountains of Oregon. Gen. Tech. Rep. PNW-GTR-752*. Portland, OR: USDA, 65.

Ripple, W. J., Wolf, C., Newsome, T. M., Barnard, P., and Moomaw, W. B. (2020). World scientists' warning of a climate emergency. *BioScience* 70, 8–12. doi: 10.1093/biosci/biz088

Rockström, J., Steffen, W., Noone, K., Persson, A., Chapin, F. S. III, Lambin, E., et al. (2009). Planetary boundaries: exploring the safe operating space for humanity. *Nature* 461, 472–475.

Rose, C. L., Marcot, B. G., Mellen, T. K., Ohmann, J. L., Waddell, K. L., Lindely, D. L., et al. (2001). ""Decaying wood in Pacific Northwest forests: concepts and tools for habitat management" Pages," in *Wildlife–Habitat Relationships in Oregon and Washington*, eds D. H. Johnson and T. A. O'Neil (Corvallis, OR: Oregon State University Press), 580–623.

Ross, R. J. (2010). *Wood Handbook: Wood as an Engineering Material. USDA Forest Service, Forest Products Laboratory, General Technical Report FPL-GTR-190, 2010: 509 p. 1 v. 190*. Madison: United States Department of Agriculture Forest Service.

Ruefenacht, B., Finco, M. V., Nelson, M. D., Czaplewski, R., Helmer, E. H., Blackard, J. A., et al. (2008). Conterminous U.S. and alaska forest type mapping using forest inventory and analysis data. *Photogramm. Eng. Rem. Sens.* 74, 1379–1388. doi: 10.14358/pers.74.11.1379

Schoennagel, T., Balch, J. K., Brenkert-Smith, H., Dennison, P. E., Harvey, B. J., Krawchuk, M. A. K., et al. (2017). Adapt to more wildfire in western North American forests as climate changes. *Proc. Natl Acad. Sci. U.S.A.* 114, 4582–4590. doi: 10.1073/pnas.1617464114

Sheil, D. (2018). Forests, atmospheric water and an uncertain future: the new biology of the global water cycle. *For. Ecosyst.* 5:19.

Simard, S. W., Roach, W. J., Defrenne, C. E., Pickles, B. J., Snyder, E. N., Robinson, A., et al. (2020). Harvest intensity effects on carbon stocks and biodiversity are dependent on regional climate in Douglas-fir forests of British Columbia. *Front. For. Glob. Change* 3:88. doi: 10.3389/ffgc.2020.00088

Stephenson, N. L., Das, A. J., Condit, R., Russo, S. E., Baker, P. J., Beckman, N. J., et al. (2014). Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507, 90–93.

Thomas, C. K. (2011). Variability of subcanopy flow, temperature, and horizontal advection in moderately complex terrain. *Boundarawry Layer Meteorol.* 139, 61–81. doi: 10.1007/s10546-010-9578-9

Turner, D. P., Ritts, W. D., Yang, Z., Kennedy, R. E., Cohen, W. B., Duane, M. V., et al. (2011). Decadal trends in net ecosystem production and net ecosystem carbon balance for a regional socioecological system. *For. Ecol. Manag.* 262, 1318–1325. doi: 10.1016/j.foreco.2011.06.034

UNEP (2019). *UN Environment Programme Emissions Gap Report*. Available online at: https://www.unenvironment.org/resources/emissions-gap-report-2019 (accessed August 4, 2020)

UNFCCC (1992). *Un Framework Convention on Climate Change Article 2*. Available online at: unfccc.int/resource/docs/convkp/conveng.pdf (accessed August 4, 2020).

USDA Forest Service (1995). *Appendix N, Eastside Screens. In: Appendix B–Revised Interim management direction establishing riparian, ecosystem, and wildlife standards for timber sales. Regional Forester's Forest Plan Amendment #2.* Portland, OR: U.S. Department of Agriculture Forest Service.

Van Tuyl, S., Law, B. E., Turner, D. P., and Giterman, A. I. (2005). Variability in net primary production and carbon storage in biomass across Oregon forests – an assessment integrating data from forest inventories, intensive sites, and remote sensing. *For. Ecol. Manage.* 209, 273–291. doi: 10.1016/j.foreco.2005.02.002

Wales, B. C., Suring, L. H., and Hemstrom, M. A. (2007). Modeling potential outcomes of fire and fuel management scenarios on the structure of forested habitats in northeast Oregon, USA. *Landscape Urban Plan.* 80, 223–236. doi: 10.1016/j.landurbplan.2006.10.006

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York, NY: Springer-Verlang.

Wisdom, M. J., Holthausen, R. S., Wales, B. C., Hargis, C. D., Saab, V. A., Lee, D. C., et al. (2000). *Source Habitats for Terrestrial Vertebrates of Focus in the Interior Columbia Basin: Broad-Scale Trends and Management Implications, 3 vols. Gen. Tech. Rep. PNW-GTR-485*. Portland, OR: U.S. Department of Agriculture Forest Service.

Zald, H. S. J., and Dunn, C. J. (2018). Severe fire weather and intensive forest management increase fire severity in a multi-ownership landscape. *Ecol. Appl.* 28, 1068–1080. doi: 10.1002/eap.1710

Conflict of Interest: LB was employed by EcoSpatial Services L.L.C.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Copyright © 2020 Mildrexler, Berner, Law, Birdsey and Moomaw. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

Check for updates

Received: 12 September 2022 | Revised: 8 February 2023 | Accepted: 10 April 2023

DOI: 10.1111/csp2.12944

Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access
WILEY

PERSPECTIVE

Protect large trees for climate mitigation, biodiversity, and forest resilience

David J. Mildrexler[1] | **Logan T. Berner**[2] | **Beverly E. Law**[3] | **Richard A. Birdsey**[4] | **William R. Moomaw**[4,5]

[1]Eastern Oregon Legacy Lands, Joseph, Oregon, USA

[2]EcoSpatial Services L.L.C, Juneau, Alaska, USA

[3]Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA

[4]Woodwell Climate Research Center, Falmouth, Massachusetts, USA

[5]Center for International Environment and Resource Policy, Fletcher School, Tufts University, Medford, Massachusetts, USA

Correspondence
David J. Mildrexler, Eastern Oregon Legacy Lands, PO Box 666, Joseph, OR 97846, USA.
Email: davidm@eorlegacylands.org

Funding information
Eastern Oregon Legacy Lands; OSU Agricultural Research Foundation; Rockefeller Brothers Fund; Woodwell Climate Research Center

Abstract

Protecting the climate system requires urgently reducing carbon emissions to the atmosphere and increasing cumulative carbon stocks in natural systems. Recent studies confirm that large trees accumulate and store a disproportionate share of aboveground forest carbon. In the temperate forests of the western United States, a century of intensive logging drastically reduced large-trees and older forest, but some large trees remain. However, recent changes to large tree management policy on National Forest lands east of the Cascade Mountains crest in Oregon and southeastern Washington allows increased harvesting of large-diameter trees (≥53 cm or 21 inches) that account for just 3% of all stems, but hold 42% of total aboveground carbon. In this article, we describe synergies with protecting large trees for climate mitigation, biodiversity, and forest resilience goals to shift species composition, reduce fuel loads and stem density, and adapt to climatically driven increases in fire activity in eastern Oregon.

KEYWORDS

aboveground forest carbon, biodiversity, climate change, eastern Oregon, large trees

1 | INTRODUCTION

Society has a narrow window of opportunity left to avert catastrophic consequences from the intertwined climate and biodiversity crises (IPCC, 2022), and forests offer major solutions at the intersection of these urgent imperatives. Forests account for 92% of all terrestrial biomass globally (Pan et al., 2013), store about 45% of the total organic carbon on land in their biomass and soils (Bonan, 2008), and removed the equivalent of about 30% of fossil fuel emissions annually from 2009 to 2018, of which 44% was by temperate forests (Friedlingstein et al., 2019). Moreover, forests provide critical habitats to more than half of all known plant and animal species on Earth (Gibson et al., 2011; Vié et al., 2009). As climate change increases and accelerates amplifying feedbacks, preserving species- and carbon-rich forests becomes ever more important, alongside a rapid transition to net-zero fossil fuel CO_2 emissions (Matthews et al., 2022).

Forests of the western US contain large stocks of carbon and remove significant quantities of CO_2 from the atmosphere to help protect climate, biodiversity, and water security (Buotte et al., 2020; Law et al., 2021). But how we manage these forests will play a large role in determining future outcomes (Fargione et al., 2018; Hudiburg et al., 2009; Law et al., 2018). Oregon stands

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2023 The Authors. *Conservation Science and Practice* published by Wiley Periodicals LLC on behalf of Society for Conservation Biology.

out with the most forested area in the western USA, yet the lowest proportion of its forests protected (Law et al., 2021), and significant opportunities to create strategic forest reserves (Law, Berner, et al., 2022). About 80% of tree mortality in Oregon and Washington is attributed to harvest (Berner et al., 2017). In this article we provide insights from a recent study that quantified large tree carbon stocks in diverse forests of eastern Oregon (Mildrexler et al., 2020), and describe synergies with protecting disproportionately valuable large trees for biodiversity and climate mitigation, and forest resilience goals.

2 | LARGE TREES DOMINATE ABOVEGROUND CARBON STORAGE

Trees capture and store massive amounts of carbon, thus forests are an essential component of limiting global warming to 1.5–2°C (IPCC, 2018). However, trees are not all equal in their capacity to slow climate change in the coming critical decades. Large trees play an inordinately large role in removing carbon from the atmosphere and storing it in long-lived tissues (Figure 1; Lutz et al., 2012; Leverett et al., 2021). Globally, studies have found that about half the aboveground carbon is concentrated in a small proportion of large trees (1%–5% of total stems) (Lutz et al., 2018; McNicol et al., 2018). Because most global forests are well below their potential carbon stocks due to past and current land management practices, they could store twice the carbon than now (Erb et al., 2018). As large trees grow larger, small increases in diameter add a relatively large amount of volume and biomass (Mildrexler et al., 2020; Stephenson et al., 2014). Protecting existing forests with large trees and letting more forests mature and develop additional large trees is crucial for preventing carbon emissions and for continued accumulation of carbon from the atmosphere in the coming decades (Birdsey et al., 2023; Law, Moomaw, et al., 2022; Moomaw et al., 2019).

2.1 | The 21-inch rule and carbon stocks

Forests in eastern Oregon and southeastern Washington are recovering from a century of intensive logging that eliminated much of the region's large trees by selective harvest of the largest, most robust trees including clear-cutting older forests. Nevertheless, the United States Forest Service (USFS) recently weakened protection for trees 21 inches diameter at breast height (DBH) and larger ("21-inch rule") across six national forests in this region. The 21-inch rule specifically applied to large-diameter trees on millions of acres of federal public lands. To assess the consequences of the loss of these trees it is essential to quantify large tree carbon stocks prior to changes in management actions. Mildrexler et al. (2020) evaluated carbon storage in large-diameter trees across the six national forests located east of the Cascade Crest in Oregon and Washington ("eastside forests") (Figure 2). Specifically, we quantified the relative contribution of large trees (≥21 inches DBH) to aboveground carbon (AGC) storage based on analysis of 636,520 trees on 3335 USFS Forest Inventory & Analysis (FIA) plots, and also assessed the carbon implications of relaxing the 21-inch rule. In these forests, large trees compose a small fraction of total stems (2.0% to 3.7% of all stems among five dominant tree species) yet hold 33% to 46% of total AGC stored by each species (Figure 3). The very largest trees, >30 inches DBH, held an even greater proportion of carbon (16.6%) relative to their small numbers (0.6%) demonstrating the importance of letting large trees grow larger and accumulate more carbon. Our research contributes to growing recognition that forests with large trees play a



FIGURE 1 Large-diameter grand fir (*Abies grandis*) in a mesic, mixed-conifer forest of northeast Oregon. These carbon-rich forests have a large cooling effect on maximum temperatures, provide thermal refugia for biodiversity including sensitive species, and are a high priority for protection. Large grand fir form the best hollow trees for wildlife (Rose et al., 2001).

25784854, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/csp2.12944, Wiley Online Library on [25/04/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

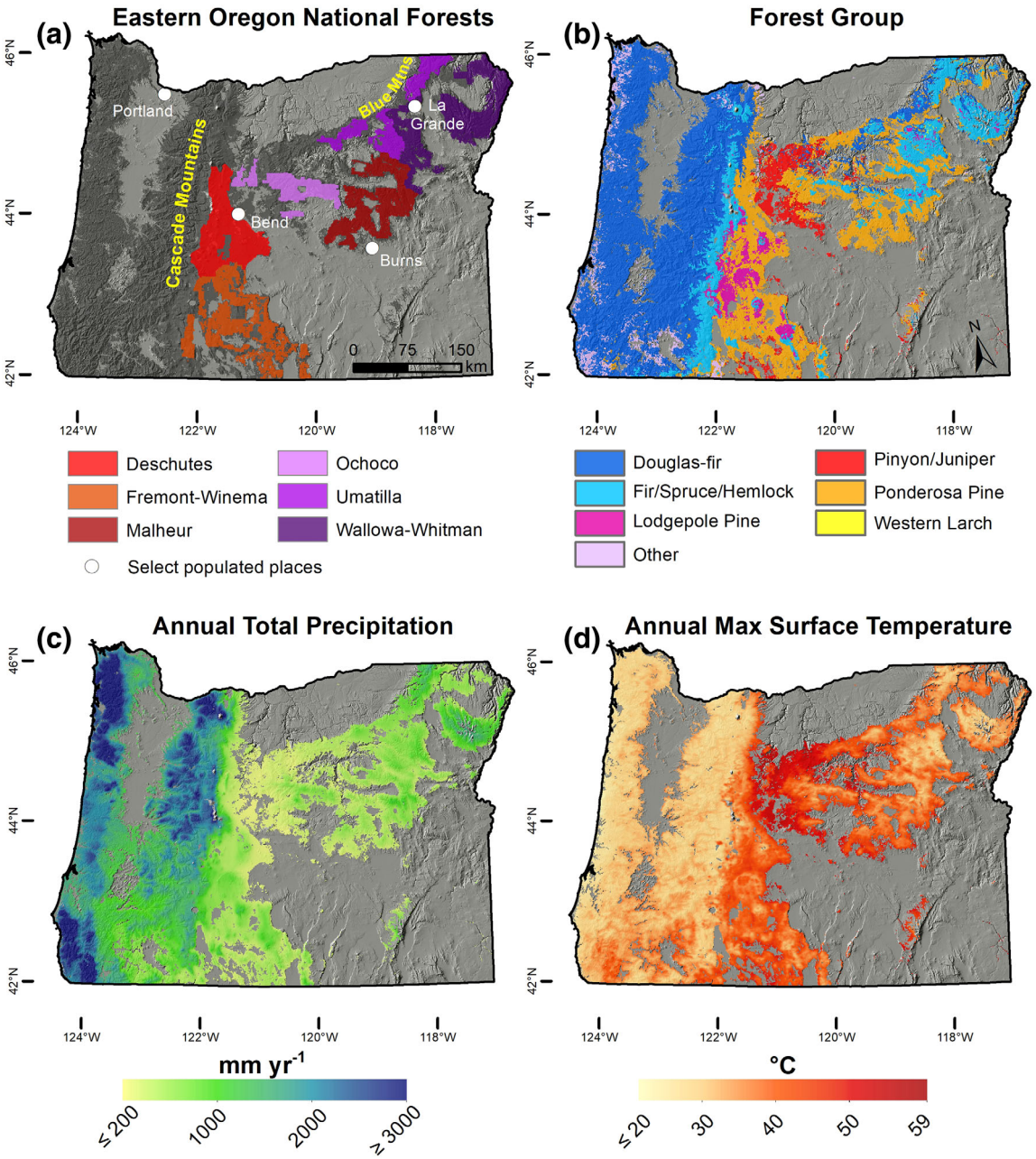


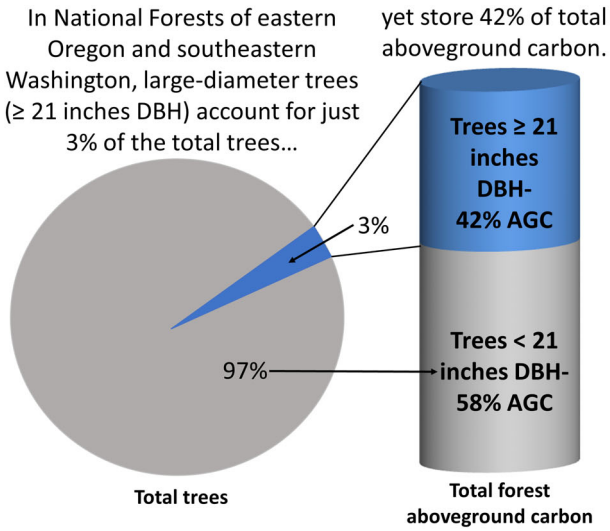
FIGURE 2 Forest and climatic diversity across the state of Oregon. (a) Extent of National Forests in Eastern Oregon. (Note a small portion of southeastern Washington included in our original study is not shown in this figure). (b) Distribution of forest groups. (c) Mean annual total precipitation from 1981 to 2010. (d) Mean annual maximum land surface temperature [LSTmax] from 2003 to 2020. Data sources include forest groups from Ruefenacht et al. (2008), precipitation climatology from Daly et al. (2008), and annual LSTmax derived using MODIS Aqua satellite data from Wan (2014).

very important role in climate mitigation now and in the near future (Lutz et al., 2018; Stephenson et al., 2014).

2.2 | A wildlife protection measure with a crucial carbon co-benefit

The 21-inch rule was implemented in the early 1990s as a habitat and species protection measure to recover large tree structure and to protect remaining late successional and old-growth forest and associated species (e.g., American Marten, Northern Goshawk) (Bull et al., 2005; Bull & Hohmann, 1994; Henjum et al., 1994), similar to the Northwest Forest Plan (NWFP) that was implemented to ensure persistence of old-growth forest species and their habitat in the western portion of the region (FEMAT, 1993). The NWFP resulted in a strong carbon benefit for climate mitigation, in addition to protecting sensitive species and riparian

25784854, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/csp2.12944, Wiley Online Library on [25/04/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License



Species common name	% of total species trees ≥ 21 inches	% of total species AGC in trees ≥ 21 inches
Douglas-fir	3.7	37.5
Engelmann spruce	2.4	34.7
Grand fir	2.0	38.4
Ponderosa pine	3.7	45.8
Western larch	2.8	33.3
Overall	**3.1**	**42.2**

FIGURE 3 Percentage of all tree stems above and below the 21-inch DBH threshold and their total aboveground carbon (AGC) stores overall, and for five dominant tree species, evaluated based on measurements from USFS inventory plots located in the six eastside national forests.

systems (Turner et al., 2011). Mildrexler et al. (2020) showed that carbon storage associated with the 21-inch rule on the six eastside national forests is a significant co-benefit of this protective measure (Pörtner et al., 2021).

Detailed analysis of stand structure and carbon impacts is essential for science-based decision-making about large-tree forest management policies because such policies affect many different values and services provided by forests (Davis et al., 2019; Teich et al., 2022), including consequences on greenhouse gas emissions and for increasing atmospheric carbon removal and accumulation in forests (Fargione et al., 2018; Griscom et al., 2017). Moreover, large live trees eventually create large-diameter snags and downed wood that continue to store carbon for decades and contribute directly to biodiversity by providing unique specialized habitats such as hollow trees and logs, and microenvironments (Lutz et al., 2021; Rose et al., 2001). However, the USFS General Technical Report on the 21-inch rule did not assess large tree carbon stocks (Hessburg et al., 2020), even though storage and accumulation of carbon in forests is an increasing priority in National Forests (Depro et al., 2008; Dilling et al., 2013; Dugan et al., 2017). Consequently, quantitative assessments of management effects on both forest carbon and biodiversity are important, including assessment of the effects of long-standing rules before they are eliminated or weakened (Mildrexler et al., 2020).

The 21-inch rule has since been amended. Grand fir (DBH ≥53 cm and <150 years) has lost protections in stands not designated as Late and Old Structure, and protections for all tree species have been significantly weakened from a standard to a guideline (USDA, 2021). This represents a major shift in management of large trees across the region, highlighting escalating tradeoffs between goals for carbon sequestration to mitigate climate change, and efforts to increase the pace, scale, and intensity of cutting across national forest lands. The potential impacts of removal of large grand fir on wildfire are unclear, although a trait-based approach to assess fire resistance found that the grand fir forest type had the second highest fire resistance score, and one of the lowest fire severity values among forest types of the Inland Northwest USA (Moris et al., 2022).

3 | ARE LARGE GRAND FIR OUTCOMPETING LARGE PONDEROSA PINE AND LARCH?

The key rationale for amending the 21-inch rule is that increased cutting of large-diameter fir trees (≥53 cm DBH and <150 years) is needed to facilitate the conservation and recruitment of early-seral, shade-intolerant old ponderosa pine (*Pinus ponderosa*) and western larch (*Larix occidentalis*) by reducing competition from shade-tolerant large grand fir (*Abies grandis*) (USDA, 2021). Previous studies have looked at tree age-size relationships (Merschel et al., 2019; Perry et al., 2004), large tree numbers, and changes in basal area (Hessburg et al., 2022), but there has been no spatial analysis of close-range co-mingling of large-diameter tree species across the six national forests covered by the 21-inch rule. This is an important consideration because the competitive interaction among large-diameter trees, and their protection under the 21-inch rule, should not be conflated with small tree dynamics and common dry forest restoration strategies to reduce small tree density and favor retention of early-seral species.

We therefore examined how often large trees (≥53 cm DBH) of these species co-mingle on USFS FIA plots (~1 acre) across the same six eastside national forests where we previously examined carbon storage by large trees (Mildrexler et al., 2020). Drawing on the same USFS FIA measurements as our prior study, we found that large ponderosa pine, grand fir, and western larch were present

25784854, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/csp2.12944, Wiley Online Library on [25/04/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Coverage, mean annual precipitation from 1981 to 2010, and mean annual maximum land surface temperature from 2003 to 2020 for the major FTG's within the six national forests, standard deviations in parenthesis (excludes lands in Washington and Idaho).

		Mean annual precipitation		Mean annual maximum LST	
Forest type group	**Area (km^2)**	**mm**	**in**	**°C**	**°F**
Douglas-fir	2372	679.9 (187.3)	26.8 (7.4)	37.8 (3.5)	100.1 (6.3)
Fir/Spruce/Hemlock	12,224	974.3 (369.5)	38.4 (14.5)	33.2 (2.8)	91.8 (5.0)
Lodgepole pine	3573	822.0 (274.6)	32.4 (10.8)	37.2 (3.8)	99.0 (6.8)
Pinyon/Juniper	634	329.5 (96.0)	13.0 (3.8)	50.4 (3.7)	122.7 (6.6)
Ponderosa pine	18,514	548.3 (139.2)	21.6 (5.5)	39.8 (3.5)	103.6 (6.3)
Western larch	47	746.9 (78.9)	29.4 (3.1)	31.5 (2.4)	88.7 (4.3)

on 56%, 18%, and 7% of all plots ($n = 3335$). Large ponderosa pine co-mingle with large grand fir about 14% of the time (259 plots), leaving 86% of plots with large ponderosa pine without large grand fir (1616 plots). Similarly, large western larch co-mingle with large grand fir about 56% of the time. Large ponderosa pine and grand fir are found together on only 8% of all plots in the region, while large larch and grand fir are found together on only 4% of all plots in the region. In other words, large ponderosa pine are by far the most common tree species found in these six National Forests and infrequently co-mingle with large grand fir at the FIA plot scale, whereas large western larch are far less common and co-mingle with large grand fir about half the time, which is expected since these species occupy similar environmental settings that receive more moisture (Table 1, Johnson & Clausnitzer, 1992).

The relative prevalence of large ponderosa pine in eastside forests is good for climate resilience given that large-diameter pines are exceptionally drought and fire-resistant trees (Irvine et al., 2004; Irvine et al., 2007). In the drought-prone region of central Oregon, mature and old ponderosa pine forests had 60% to 85% higher seasonal gross photosynthesis than a young forest (Irvine et al., 2004). Large ponderosa pine trees experienced only 34% mortality in moderate severity fire, and accounted for 91% of post-fire stemwood production, while small trees experienced 82% mortality (Irvine et al., 2007).

Across the entirety of all six national forests large grand fir represent 2% of the total species population, a proportion slightly lower, but roughly on par with other dominant species (Figure 3, Mildrexler et al., 2020). It is not uncommon for grand fir to reach 250 to 300 years of age (Howard & Aleksoff, 2000). Thus, large grand fir ≥53 cm DBH and <150 years of age can continue growing and play an important role in storing and accumulating carbon from the atmosphere to help abate the climate crisis.

Synergy: Enhancing forest resilience does not necessitate widespread cutting of any large-diameter tree species. Favoring early-seral species can be achieved with a focus on smaller trees and restoring surface fire, while retaining the existing large tree population.

4 | LARGE TREES, VULNERABILITY, STAND DYNAMICS, AND THE CARBON COST OF THINNING

As eastside forests recover from a century of intensive logging, it is important to distinguish between the shift of AGC stocks into small-diameter, fire-sensitive trees and the retention of a small fraction of the largest more fire-resistant trees that store disproportionately massive amounts of carbon. Small tree carbon stores are relatively unstable and at risk of loss to fire and drought, whereas large tree carbon stores are relatively stable and resistant (Hurteau et al., 2019). Physiological-based studies in ponderosa pine forests of Oregon have found that small trees are most vulnerable during drought relative to mature trees that have reached full root, bark and canopy development and respond to climate variability better than smaller trees (Domec et al., 2004; Irvine et al., 2004; Vickers et al., 2012). Buotte et al. (2019, 2020) identified forests in the western U.S. with high potential carbon accumulation and low vulnerability to future drought and fire using the Community Land Model and two climate models with high CO_2 emissions (RCP8.5), and species-specific traits capturing sensitivity of different species to water limitations and to drought and fire. The Eastern Cascades and Blue Mountains contain substantial area with opportunity to enhance forest carbon in large trees (Buotte et al., 2020; Law et al., 2018).

In dry forests historically maintained by a frequent, low-severity fire regime, the priority ought to be restoring the process of periodic surface fire. Prescribed fires create landscape heterogeneity, reduce surface and ladder fuels, lower stand density, and confer drought resistance to surviving trees (Knapp & Keeley, 2006; van Mantgem et al., 2016). In

25784854, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/csp2.12944, Wiley Online Library on [25/04/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

these forests prescribed fire can modulate future fire activity (Schoennagel et al., 2017), and favor early-seral species such as ponderosa pine, western larch and Douglas-fir. Large trees of these species and grand fir are resilient to prescribed fire because they have attained the thick bark that provides resistance to low- and moderate-severity fire (Howard & Aleksoff, 2000; Pellegrini et al., 2017).

Thinning also has an inherent carbon cost that increases as larger trees are harvested, thereby putting thinning of larger trees in conflict with carbon goals because it takes so long to replace the harvested biomass (James et al., 2018; Law & Harmon, 2011). The underlying principle for these losses is the negative relationship between harvest intensity and forest carbon stocks whereby as harvest intensity increases, forest carbon stocks decrease and emissions increase (Hudiburg et al., 2009; Mitchell et al., 2009; Simard et al., 2020). Claims that carbon stores will be "stabilized" by increasing harvest of large-diameter trees that store and accumulate the most carbon (Johnston et al., 2021) are inconsistent with basic science on thinning (Zhou et al., 2013) and the carbon cycle (Campbell et al., 2012; Law et al., 2018). These claims ignore the large amounts of CO_2 rapidly released to the atmosphere following harvest (Hudiburg et al., 2019), and that large trees cannot be replaced in short timeframes. It can take centuries to reaccumulate forest carbon stocks reduced by harvest of large trees (Birdsey et al., 2006).

Even thinning smaller trees involves substantial carbon tradeoffs in the short term, a 30%–40% reduction in live tree carbon stores in some forests (Krofcheck et al., 2017; North et al., 2009). To minimize reductions in carbon stocks and emissions, focus on removing smaller-sized trees, restoring surface fire, and managed wildfire in favorable weather conditions (Mitchell et al., 2009; Stenzel et al., 2021).

Synergy: Small trees are more relevant to drought and fire vulnerability and store less carbon, whereas large trees are more resilient to fire and drought and are the highest priority for keeping carbon in the forest.

5 | DIVERSE CLIMATE REGIMES AND FOREST TYPES REDUCE CLIMATIC EXTREMES

It is critical to accurately represent the diversity of climatic regimes and forest types in decisions affecting large tree management because large trees play unique roles in ecosystem water and energy cycles, and these biophysical effects can promote local climate stability by reducing extreme temperatures in all seasons and times of day (Lawrence et al., 2022). Forest modulation of summer maximum temperature is especially powerful (Mildrexler et al., 2018) and can partly offset the projected increases in temperature due to anthropogenic climate change (de Frenne et al., 2019). With heatwave frequency and severity projected to increase, the capacity of forests to buffer against temperature extremes and provide refugia is increasingly recognized as important to sustaining biodiversity in a warming world (Davis et al., 2019; de Frenne et al., 2019).

The six eastside national forests affected by the 21-inch rule cover a region of pronounced geographic and climatic variation and associated forest types (Figure 2; Johnson & Clausnitzer, 1992; Wyatt, 2017). Mean annual precipitation varied from 484 to 571 mm per year on the Ochoco and Malheur National Forests, to ~800 mm per year on the Deschutes, Umatilla and Wallowa Whitman National Forests (Mildrexler et al., 2020). We further examined the climatic regimes of the major forest types across the six national forests using satellite-based annual maximum land surface temperature (LST_{max}) and mean annual precipitation datasets (Figure 2D, Table 1). Our analysis shows that ponderosa pine and fir/spruce/hemlock types cover the largest area on the six national forests. The fir/spruce/hemlock type received the most total precipitation (~974 mm yr^{-1}) and had the second lowest annual LST_{max} (33.2°C). Average LST_{max} for the fir/spruce/hemlock type was 6.6°C (~12 °F) cooler than ponderosa pine (39.8°C), and 4.6°C (~8 °F) cooler than Douglas-fir (37.8°C). The pinyon juniper type had the lowest total precipitation (329 mm yr^{-1}) and highest annual LST_{max} (50.4°C) due to low canopy cover and heating of the dry surface during summer. These results show the region's pronounced variability in hydrologic and forest thermal regimes and highlight the thermal offsetting capacity of closed-canopied mesic forest systems. These valuable ecosystem services can be severely degraded by industrial logging (Lindenmayer et al., 2009).

Synergy: Mature and old mesic forests are a high priority for protection, provide crucial biophysical benefits on climate, including a large cooling effect on maximum temperatures regulating climate extremes and protecting biodiversity. Large grand fir is essential to this ecology.

6 | CONCLUSIONS

The 21-inch rule is an excellent example of a policy initiated for wildlife and habitat protection that has also provided significant climate mitigation values across extensive forests of the PNW Region. The rule resulted in a valuable resource of large-diameter trees in a landscape that remains below historical levels for large live trees and large snags due to historical logging (Bell et al., 2021). We have described synergies between protecting these disproportionately valuable large trees and forest resilience goals, providing common potential solutions for these urgent challenges.

25784854, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/csp2.12944, Wiley Online Library on [25/04/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Inland PNW forests can make a significant contribution to climate mitigation goals by protecting and enhancing carbon stores in large trees that accumulate and store the most carbon and are much more resistant to fire and drought than small trees, even when the current status of ecosystems has changed from historical baselines. Climate science makes clear that we do not have time to wait for regrowth after logging to accomplish these important ecosystem services (IPCC, 2022).

AUTHOR CONTRIBUTIONS

David J. Mildrexler led the writing. David J. Mildrexler and Logan T. Berner performed data analysis, investigation, and visualization. All authors commented on drafts, and assisted with writing, review and editing. All authors gave final approval for publication.

ACKNOWLEDGMENT

We thank two anonymous reviewers for their helpful comments.

FUNDING INFORMATION

David J. Mildrexler was supported by Eastern Oregon Legacy Lands. Beverly E. Law was funded by OSU Agricultural Research Foundation. William R. Moomaw was supported from Rockefeller Brothers Fund. Richard A. Birdsey received support from the Woodwell Climate Research Center.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

This study relied on data from prior studies that are publicly available: Forest Inventory Data from the United States Forest Service (https://apps.fs.usda.gov/fia/datamart/datamart.html), MODIS Land Surface Temperature data from the Land Processes Distributed Active Archive Center accessed through Google Earth Engine, and gridded precipitation climatologies from Oregon State University PRISM Climate Group (https://prism.oregonstate.edu/normals/).

ORCID

David J. Mildrexler https://orcid.org/0000-0001-8370-8714

REFERENCES

Bell, D. M., Acker, S. A., Gregory, M. J., Davis, R. J., & Garcia, B. A. (2021). Quantifying regional trends in large live tree and snag availability in support of forest management. *Forest Ecology and Management*, *479*, 118554. https://doi.org/10.1016/j.foreco.2020.118554

Berner, L. T., Law, B. E., & Hudiburg, T. W. (2017). Water availability limits tree productivity, carbon stocks, and carbon residence time in mature forests across the western US. *Biogeosciences*, *14*, 365–378. https://doi.org/10.5194/bg-14-365-2017

Birdsey, R., Pregitzer, K., & Lucier, A. (2006). Forest carbon management in the United States: 1600-2100. *Journal of Environmental Quality*, *35*, 1461–1469.

Birdsey, R. A., DellaSala, D. A., Walker, W. S., Gorelik, S. R., Rose, G., & Ramírez, C. E. (2023). Assessing carbon stocks and accumulation potential of mature forests and larger trees in U.S. federal lands. *Frontiers in Forests and Global Change*, *5*, 1074508. https://doi.org/10.3389/ffgc.2022.1074508

Bonan, G. B. (2008). Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, *320*, 1444–1449. https://doi.org/10.1126/science.1155121

Bull, E. L., Heater, T. W., & Shepherd, J. F. (2005). Habitat selection by the American Marten in northeastern Oregon. *Northwest Science*, *79*, 36–42.

Bull, E. L., & Hohmann, J. H. (1994). Breeding biology of northern goshawks in northeastern Oregon. *Studies in Avian Biology*, *16*, 103–105.

Buotte, P. C., Law, B. E., Ripple, W. J., & Berner, L. T. (2020). Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States. *Ecological Applications*, *30*, e02039. https://doi.org/10.1002/eap.2039

Buotte, P. C., Levis, S., Law, B. E., Hudiburg, T. W., Rupp, D. E., & Kent, J. J. (2019). Near-future vulnerability to drought and fire varies across the western United States. *Global Change Biology*, *25*, 290–303. https://doi.org/10.1111/gcb.14490

Campbell, J., Harmon, M. E., & Mitchell, S. R. (2012). Can fuel-reduction treatments really increase forest carbon storage in the western US by reducing future fire emissions? *Frontiers in Ecology and the Environment*, *10*(2), 83–90. https://doi.org/10.1890/110057

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J., & Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, *28*, 2031–2064.

Davis, K. T., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E., & Abatzoglou, J. T. (2019). Microclimatic buffering in forests of the future: The role of local water balance. *Ecography*, *42*, 1–11. https://doi.org/10.1111/ecog.03836

de Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, *3*, 744–749. https://doi.org/10.1038/s41559-019-0842-1

Depro, B. M., Murray, B. C., Alig, R. J., & Shanks, A. (2008). Public land, timber harvests, and climate mitigation: Quantifying carbon sequestration potential on U.S. public timberlands. *Forest Ecology and Management*, *225*, 1122–1134.

Dilling, L., Birdsey, R., & Pan, Y. (2013). in land use and the carbon cycle: Advances in integrated science, management and policy. In D. G. Brown, D. T. Robinson, N. H. F. French, & B. C. Reed (Eds.), *Opportunities and challenges for carbon management on U.S. public lands* (pp. 455–476). Cambridge Press.

Domec, J. C., Warren, J. M., Meinzer, F. C., Brooks, J. R., & Coulombe, R. (2004). Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: Mitigation

25784854, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/csp2.12944, Wiley Online Library on [25/04/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

by hydraulic redistribution. *Oecologia*, *141*, 7–16. https://doi.org/10.1007/s00442-004-1621-4

Dugan, A. J., Birdsey, R., Healey, S. P., Pan, Y., Zhang, F., Mo, G., Chen, J., Woodall, C. W., Hernandez, A. J., McCullough, K., McCarter, J. B., Raymond, C. L., & Dante-Wood, K. (2017). Forest sector carbon analyses support land management planning and projects: Assessing the influence of anthropogenic and natural factors. *Climatic Change*, *144*, 207–220. https://doi.org/10.1007/s10584-017-2038-5

Erb, K. H., Kastner, T., Plutzar, C., Bais, A. L. S., Carvalhais, N., Fetzel, T., Gingrich, S., Haberl, H., Lauk, C., Niedertscheider, M., Pongratz, J., Thurner, M., & Luyssaert, S. (2018). Unexpectedly large impact of forest management and grazing on global vegetation biomass. *Nature*, *553*, 73–76. https://doi.org/10.1038/nature25138

Fargione, J. E., Bassett, S., Boucher, T., Bridgham, S. D., Conant, R. T., Cook-Patton, S. C., Ellis, P. W., Falcucci, A., Fourqurean, J. W., Gopalakrishna, T., Gu, H., Henderson, B., Hurteau, M. D., Kroeger, K. D., Kroeger, T., Lark, T. J., Leavitt, S. M., Lomax, G., Mcdonald, R. T. I., … Griscom, B. W. (2018). Natural climate solutions for the United States. *Science Advances*, *4*, eaat1869. https://doi.org/10.1126/sciadv.aat186

Forest Ecosystem Management Assessment Team (FEMAT). (1993). *Forest ecosystem management: An ecological, economic and social assessment*. U.S. Forest Service and Collaborating Agencies.

Friedlingstein, P., Jones, M. W., O'Sullivan, M., Andrew, R. M., Hauck, J., Peters, G. P., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., Bakker, D. C. E., Canadell, J. G., Ciais, P., Jackson, R. B., Anthoni, P., Barbero, L., Bastos, A., Bastrikov, V., Becker, M., … Zaehle, S. (2019). Global Carbon Budget 2019. *Earth System Science Data*, *11*, 1783–1838. https://doi.org/10.5194/essd-11-1783-2019

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, *478*, 378–381. https://doi.org/10.1038/nature10425

Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R. T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M. R., … Fargione, J. (2017). Natural climate solutions. *Proceedings of the National Academy of Sciences*, *114*, 11645–11650. https://doi.org/10.1073/pnas.1710465114

Henjum, M. G., Karr, J. R., Bottom, D. L., Perry, D. A., Bednarz, J. C., Wright, S. G., Beckwitt, S. A., & Beckwitt, E. (1994). *Interim protection for late successional forest, fisheries and watersheds: National forests east of the cascade crest*. Wildlife Society, Bethesda, MD.

Hessburg, P. F., Charnley, S., Gray, A. N., Spies, T. A., Peterson, D. W., Flitcroft, R. L., Wendel, K. L., Halofsky, J. E., White, E. M., & Marshall, J. (2022). Climate and wildfire adaptation of inland northwest US forests. *Frontiers in Ecology and the Environment*, *20*(1), 40–48. https://doi.org/10.1002/fee.2408

Hessburg, P. F., Charnley, S., Wendel, K. L., White, E. M., Spies, T. A., Singleton, P. H., … White, R. (2020). The 1994 eastside screens: Large tree harvest limit: Review of science relevant to Forest planning 25 years later. Pages 114. General Technical Report PNW-GTR-990. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Howard, J. L., & Aleksoff, K. C. (2000). Abies grandis. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). https://www.fs.fed.us/database/feis/plants/tree/abigra/all.html

Hudiburg, T., Law, B., Turner, D. P., Campbell, J., Donato, D. C., & Duane, M. (2009). Carbon dynamics of Oregon and northern California forests and potential land-based carbon storage. *Ecological Applications*, *19*, 163–180. https://doi.org/10.1890/07-2006.1

Hudiburg, T. W., Law, B. E., Moomaw, W. R., Harmon, M. E., & Stenzel, J. E. (2019). Meeting GHG reduction targets requires accounting for all forest sector emissions. *Environmental Research Letters*, *14*, 095005. https://doi.org/10.1088/1748-9326/ab28bb

Hurteau, M. D., North, M. P., Koch, G. W., & Hungate, B. A. (2019). Opinion: Managing for disturbance stabilizes forest carbon. *Proceedings of the National Academy of Sciences*, *116*, 10193–10195. https://doi.org/10.1073/pnas.1905146116

IPCC (2018). "*Summary for policymakers*," in Global warming of 1.5°C, an IPCC special report, eds V. M. Delmotte, P. Zhai, H. O. P. Pörtner, D. Roberts, J. Skea, P. R. Shukla, et al. World Meteorological Organization, 32.

IPCC. (2022). Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change. In H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Climate change 2022: Impacts, adaptation, and vulnerability*. Cambridge University Press.

Irvine, J., Law, B. E., & Hibbard, K. (2007). Post-fire carbon pools and fluxes in semi-arid ponderosa pine in Central Oregon. *Global Change Biology*, *13*, 1748–1760.

Irvine, J., Law, B. E., Kurpius, M., Anthoni, P. M., Moore, D., & Schwarz, P. (2004). Age related changes in ecosystem structure and function and the effects on carbon and water exchange in ponderosa pine. *Tree Physiology*, *24*, 753–763.

James, J. N., Kates, N., Kuhn, C. D., Littlefield, C. E., Miller, C. W., Bakker, J. D., Butman, D. E., & Haugo, R. D. (2018). The effects of forest restoration on ecosystem carbon in western North America: A systematic review. *Forest Ecology Management*, *429*, 625–641.

Johnson, C. J., & Clausnitzer, R. R. (1992). Plant associations of the blue and Ochoco Mountains. Tech. Pub. R6 ERW TP 036 92. *USDA Forest Service, Pacific Northwest Region, Wallowa-Whitman National Forest*, 164 p.

Johnston, J. D., Hagmann, R. K., Seager, T., Merschel, A., Franklin, J. F., & Johnson, K. N. (2021). General commentary: Large trees dominate carbon storage east of the Cascade crest in the U.S. Pacific northwest. *Frontiers in Forests and Global Change*, *4*, 653774. https://doi.org/10.3389/ffgc.2021.653774

Knapp, E. E., & Keeley, J. E. (2006). Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest. *International Journal of Wildland Fire*, *15*, 37–45. https://doi.org/10.1071/wf04068

25784854, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/csp2.12944, Wiley Online Library on [25/04/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Krofcheck, D. J., Hurteau, M. D., Scheller, R. M., & Loudermilk, E. L. (2017). Restoring surface fire stabilizes forest carbon under extreme fire weather in the Sierra Nevada. *Ecosphere*, *8*(1), e01663. https://doi.org/10.1002/ecs2.1663

Law, B. E., Berner, L. T., Buotte, P. C., Mildrexler, D. J., & Ripple, W. J. (2021). Strategic Forest reserves can protect biodiversity in the western United States and mitigate climate change. *Communications Earth and Environment*, *2*, 254. https://doi.org/10.1038/s43247-021-00326-0

Law, B. E., Berner, L. T., Mildrexler, D. J., Bloemers, R. O., & Ripple, W. J. (2022). Strategic reserves in Oregon's forests for biodiversity, water, and carbon to mitigate and adapt to climate change. *Frontiers in Forests and Global Change*, *5*, 1028401. https://doi.org/10.3389/ffgc.2022.1028401

Law, B. E., & Harmon, M. (2011). Forest sector carbon management, measurement and verification, and discussion of policy related to climate change. *Carbon Management*, *2*(1), 73–84.

Law, B. E., Hudiburg, T. W., Berner, L. T., Kent, J. J., Buotte, P. C., & Harmon, M. (2018). Land use strategies to mitigate climate change in carbon dense temperate forests. *Proceedings of the National Academy of Sciences*, *115*, 3663–3668. https://doi.org/10.1073/pnas.1720064115

Law, B. E., Moomaw, W. R., Hudiburg, T. W., Schlesinger, W. H., Sterman, J. D., & Woodwell, G. M. (2022). Creating strategic reserves to protect Forest carbon and reduce biodiversity losses in the United States. *Land*, *11*, 721. https://doi.org/10.3390/land11050721

Lawrence, D., Coe, M., Walker, W., Verchot, L., & Vandecar, K. (2022). The unseen effects of deforestation: Biophysical effects on climate. *Frontiers in Forests and Global Change*, *5*, 756115. https://doi.org/10.3389/ffgc.2022.756115

Leverett, R. T., Masino, S. A., & Moomaw, W. R. (2021). Older eastern White pine trees and stands accumulate carbon for many decades and maximize cumulative carbon. *Frontiers in Forests and Global Change*, *4*, 620450. https://doi.org/10.3389/ffgc.2021.620450

Lindenmayer, D. B., Hunter, M. L., Burton, P. J., & Gibbons, P. (2009). Effects of logging on fire regimes in moist forests. *Conservation Letters*, *2*, 271–277.

Lutz, J. A., Furniss, T. J., Johnson, D. J., Davies, S. J., Allen, D., Alonso, A., Anderson-Teixeira, K. J., Andrade, A., Baltzer, J., Becker, K. M. L., Blomdahl, E. M., Bourg, N. A., Bunyavejchewin, S., Burslem, D. F. R. P., Cansler, C. A., Cao, K., Cao, M., Cárdenas, D., Chang, L.-W., ... Zimmerman, J. K. (2018). Global importance of large-diameter trees. *Global Ecology and Biogeography*, *27*, 849–864. https://doi.org/10.1111/geb.12747

Lutz, J. A., Larson, A. J., Swanson, M. E., & Freund, J. A. (2012). Ecological importance of large-diameter trees in a temperate mixed-conifer forest. *PLoS One*, *7*, e36131. https://doi.org/10.1371/journal.pone.0036131

Lutz, J. A., Struckman, S., Germain, S. J., & Furniss, T. J. (2021). The importance of large-diameter trees to the creation of snag and deadwood biomass. *Ecological Processes*, *10*, 28. https://doi.org/10.1186/s13717-021-00299-0

Matthews, H. D., Zickfeld, K., Dickau, M., MacIsaac, A. J., Mathesius, S., Nzotungicimpaye, C.-M., & Luers, A. (2022). Temporary nature-based carbon removal can lower peak warming in a well-below 2 °C scenario. *Communications Earth & Environment*, *3*, 65. https://doi.org/10.1038/s43247-022-00391-z

McNicol, I. M., Ryan, C. M., Dexter, K. G., Ball, S. M. G., & Williams, M. (2018). Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in south-eastern Tanzania. *Ecosystems*, *21*, 740–754. https://doi.org/10.1007/s10021-017-0180-6

Merschel, A., Vora, R. S., & Spies, T. (2019). Conserving dry old-growth forest in Central Oregon, USA. *Journal of Forestry*, *117*(2), 128–135. https://doi.org/10.1093/jofore/fvy085

Mildrexler, D. J., Berner, L. T., Law, B. E., Birdsey, R. A., & Moomaw, W. R. (2020). Large trees dominate carbon storage in forests east of the Cascade crest in the United States Pacific northwest. *Frontiers in Forests and Global Change*, *3*, 594274. https://doi.org/10.3389/ffgc.2020.594274

Mildrexler, D. J., Zhao, M., Cohen, W. B., Running, S. W., Song, X., & Jones, M. O. (2018). Thermal anomalies detect critical global land surface changes. *Journal of Applied Meteorology and Climatology*, *57*, 391–397. https://doi.org/10.1175/JAMC-D-17-0093.1

Mitchell, S. R., Harmon, M., & O'Connell, K. E. B. (2009). Forest fuel reduction alters fire severity and long-term carbon storage in three Pacific northwest ecosystems. *Ecological Applications*, *19*(3), 643–655. https://doi.org/10.1890/08-0501.1

Moomaw, W. R., Masino, S. A., & Faison, E. K. (2019). Intact forests in the United States: Proforestation mitigates climate change and serves the greatest good. *Frontiers in Forests and Global Change*, *2*, 1–27. https://doi.org/10.3389/ffgc.2019.00027

Moris, J. V., Reilly, M. J., Yang, Z., Cohen, W. B., Motta, R., & Ascoli, D. (2022). Using a trait-based approach to asses fire resistance in forest landscapes of the inland northwest, USA. *Landscape Ecology*, *37*, 2149–2164. https://doi.org/10.1007/s10980-022-01478-w

North, M., Hurteau, M., & Innes, J. (2009). Fire suppression and fuels treatment effects on mixed conifer carbon stocks and emissions. *Ecological Applications*, *9*, 1385–1396.

Pan, Y., Birdsey, R. A., Phillips, O. L., & Jackson, R. B. (2013). The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 593–622.

Pellegrini, A. F. A., Anderegg, W. R. L., Paine, C. E. T., Hoffmann, W. A., Kartzinel, T., Rabin, S. S., Sheil, D., Franco, A. C., & Pacala, S. W. (2017). Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. *Ecology Letters*, *20*, 307–316. https://doi.org/10.1111/ele.12725

Perry, D. A., Jing, H., Youngblood, A., & Oetter, D. R. (2004). Forest structure and fire susceptibility in volcanic landscapes of the eastern high cascades, Oregon. *Conservation Biology*, *18*, 913–926.

Pörtner, H. O., Scholes, R. J., Agard, J., Archer, E., Arneth, A., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W. L., Diamond, S., Donatti, C., Duarte, C., Eisenhauer, N., Foden, W., Gasalla, M. A., Handa, C., Hickler, T., Hoegh-Guldberg, O., ... Ngo, H. T. (2021). IPBES-IPCC co-sponsored workshop report on biodiversity and climate change. *IPBES and IPCC*. https://doi.org/10.5281/zenodo.4782538

25784854, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/csp2.12944, Wiley Online Library on [25/04/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Rose, C. L., Marcot, B. G., Mellen, T. K., Ohmann, J. L., Waddell, K. L., Lindely, D. L., & Schreiber, B. (2001). Wildlife–habitat relationships in Oregon and Washington. In D. H. Johnson & T. A. O'Neil (Eds.), *Decaying wood in Pacific northwest forests: Concepts and tools for habitat management* (pp. 580–623). Oregon State University Press.

Ruefenacht, B., Finco, M., Nelson, M., Czaplewski, R., Helmer, E., Blackard, J., Holden, G. R., Lister, A. J., Salajanu, D., Weyermann, D., & Winterberger, K. (2008). Conterminous US and Alaska forest type mapping using forest inventory and analysis data. *Photogrammetric Engineering & Remote Sensing*, *74*, 1379–1388. https://doi.org/10.14358/PERS.74.11.1379

Schoennagel, T., Balch, J. K., Brenkert-Smith, H., Dennison, P. E., Harvey, B. J., Krawchuk, M. A., Mietkiewicz, N., Morgan, P., Moritz, M. A., Rasker, R., Turner, M. G., & Whitlock, C. (2017). Adapt to more wildfire in western North American forests as climate changes. *Proceedings of the National Academy of Sciences*, *114*, 4582–4590. https://doi.org/10.1073/pnas.1617464114

Simard, S. W., Roach, W. J., Defrenne, C. E., Pickles, B. J., Snyder, E. N., Robinson, A., & Lavkulich, L. M. (2020). Harvest intensity effects on carbon stocks and biodiversity are dependent on regional climate in Douglas-fir forests of British Columbia. *Frontiers in Forests and Global Change*, *3*, 88. https://doi.org/10.3389/ffgc.2020.00088

Stenzel, J. E., Berardi, D. B., & Hudiburg, T. W. (2021). Restoration thinning in a drought-prone Idaho forest creates a persistent carbon deficit. *Journal of Geophysical Research*, *126*, e2020JG005815. https://doi.org/10.1029/2020JG005815

Stephenson, N. L., Das, A. J., Condit, R., Russo, S. E., Baker, P. J., Beckman, N. J., Beckman, N. G., Coomes, D. A., Lines, E. R., Morris, W. K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S. J., Duque, Á., Ewango, C. N., Flores, O., ... Zaval, M. A. (2014). Rate of tree carbon accumulation increases continuously with tree size. *Nature*, *507*, 90–93.

Teich, M., Becker, K. M. L., Raleigh, M. S., & Lutz, J. A. (2022). Large-diameter trees affect snow duration in post-fire old-growth forests. *Ecohydrology*, *15*(3), e2414. https://doi.org/10.1002/eco.2414

Turner, D. P., Ritts, W. D., Yang, Z., Kennedy, R. E., Cohen, W. B., Duane, M. V., Thornton, P., & Law, B. E. (2011). Decadal trends in net ecosystem production and net ecosystem carbon balance for a regional socioecological system. *Forest Ecology and Management*, *262*, 1318–1325. https://doi.org/10.1016/j.foreco.2011.06.034

United States Department of Agriculture (USDA) Forest Service. (2021). Forest Plans Amendment. Forest Management Direction for Large Diameter Trees in Eastern Oregon and Southeastern Washington. Environmental Assessment. USDA, Forest Service, Pacific Northwest Region. Portland, OR, 174. https://www.fs.usda.gov/nfs/11558/www/nepa/113601_FSPLT3_5575542.pdf

van Mantgem, P. J., Caprio, A. C., Stephenson, N. L., & Das, A. J. (2016). Does prescribed fire promote resistance to drought in low elevation forests of the Sierra Nevada, California, USA? *Fire Ecology*, *12*, 13–25. https://doi.org/10.4996/fireecology.1201013

Vickers, D., Thomas, C. K., Pettijohn, C., Martin, J. G., & Law, B. E. (2012). Five years of carbon fluxes and inherent water-use efficiency at two semi-arid pine forests with different disturbance histories. *Tellus B*, *64*, 17159. https://doi.org/10.3402/tellusb.v64i0.17159

Vié, J.-C., Hilton-Taylor, C., & Stuart, S. N. (Eds.). (2009). *Wildlife in a changing world: An analysis of the 2008 IUCN red list of threatened species* (p. 180). IUCN.

Wan, Z. (2014). New refinements and validation of the collection-6 MODIS land-surface temperature/emissivity product. *Remote Sensing of Environment*, *140*, 36–45.

Wyatt, C. H. (2017). Chapter 2: Ecological, biogeographical, and historical context of the Blue Mountains. In J. E. Halofsky & D. L. Peterson (Eds.), *Climate change vulnerability and adaptation in the Blue Mountains region. Gen. Tech. Rep. PNW-GTR-939* (p. 331). U.S. Forest Service, Pacific Northwest Research Station.

Zhou, D., Liu, S., Zhao, S., & Oeding, J. (2013). A meta-analysis on the impacts of partial cut on forest structure and carbon storage. *Biogeosciences*, *10*, 3691–3703. https://doi.org/10.5194/bg-10-3691-2013

How to cite this article: Mildrexler, D. J., Berner, L. T., Law, B. E., Birdsey, R. A., & Moomaw, W. R. (2023). Protect large trees for climate mitigation, biodiversity, and forest resilience. *Conservation Science and Practice*, e12944. https://doi.org/10.1111/csp2.12944

25784854, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/csp2.12944, Wiley Online Library on [25/04/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Author's personal copy

Ecological Indicators 10 (2010) 311–319

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

The effects of land use on environmental features and functional organization of macroinvertebrate communities in Patagonian low order streams

M. Laura Miserendino [a,*], Carolina I. Masi [b]

[a] Laboratorio de Investigaciones en Ecología y Sistemática Animal (LIESA), Universidad Nacional de la Patagonia, Sede Esquel, Sarmiento 849, 9200 Esquel, Chubut, Argentina
[b] IADIZA - Instituto Argentino de Investigaciones de las Zonas Àridas, CRICYT, Mendoza, Argentina

ARTICLE INFO

Article history:
Received 13 August 2008
Received in revised form 12 February 2009
Accepted 8 June 2009

Keywords:
Forestry practices
Pastures
Benthos
Functional feeding groups
Water quality
Mountain streams

ABSTRACT

Benthic invertebrates, water quality variables, chlorophyll *a* and particulate organic matter (POM) were studied in 18 sites of mountain streams in Patagonia (Argentina) subjected to six different land uses: native forest, pine plantation, pasture, harvest forest, urban and reference urban. Three streams of each land use were studied in March 2006. Macroinvertebrates were sampled in three riffles and three pools ($n = 108$) and biomass of detrital fractions of POM were quantified. Overall benthic POM biomass was higher at native and harvest forest than pastures, whereas fine fraction (FPOM) was higher in harvest forest than in pastures. Regarding to autotrophic subsidies bryophytes were the only that changed consistently among uses. These differences in energy resources were correlated with changes in community attributes. Shredder richness was clearly higher at native and harvest forest than exotic pine plantations, collector gatherers density was consistently high at harvest sites, and total density was significantly higher at urban and harvest forest. Multidimensional scaling ordination based on macroinvertebrate density data showed a clear separation of forested (either native or exotic species) from riparian modified areas (pasture, urban and harvest sites). Environmental variables having explanation power on macroinvertebrate assemblages were mostly related with: detritus availability (wood and leaves biomass) and impairment (total phosphorous and % sand). These results confirm that macroinvertebrate assemblage structure in Patagonian low order streams can be altered by land use practices. Among guild structure measures, those indicators based on benthic community functional attributes, shredders richness and collectors density, resulted good candidates to assess land use impacts. On account of riparian corridor management may be critical to the distribution of benthic taxa, the maintenance of good conditions of vegetation adjacent to rivers will enhance water quality and the environment for highly endemic headwater communities of Patagonian streams.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Land use changes have resulted in profound modifications of running waters in mountain streams of temperate areas (Allan et al., 1997). In developed basins the conversion of riparian margins from forest to grassland has been one of the most widespread phenomena. Moreover, shifts in land use practices (agriculture to silviculture) have also determined the replacement of native by exotic vegetation as for example pine plantations, sometimes affecting riparian corridors (Baillie and Davies, 2002; Albariño and Balseiro, 2002). Changes in the adjacent vegetation can alter the complex biotic and abiotic processes that govern the function and attributes of aquatic communities including benthic macroinvertebrates (Roy et al., 2003; Thompson and Towsend, 2004; Utz et al., 2009). Early works revealed the consequences that the loss of riparian vegetation can have on physical properties of streams (Newbold et al., 1980). The extirpation of riparian corridors can alter the light and temperature regimes and lead to increases in nutrients and augment primary production (Scarsbrook and Halliday, 1999; Kratzer et al., 2006). The establishment of pastures for agricultural grazing can significantly reduce the amount of allochthonous leaf material entering the river, which consecutively produces a significant effect on trophic structure (Abelho and Graça, 1998; Miserendino, 2005). Scrimgeour and Kendall (2003) found that shredder biomass was significantly lower in Canadian streams under intense pasture development than in those without pastoral use. Loss of insect species (Collier et al., 2001) and higher invertebrate densities have been documented in New Zealand streams in which forest was converted to pasture (Quinn et al., 1997). Thompson and Towsend (2004) observed significant differences between shredders and collector filterer biomass in basins under different land uses such as pasture conversion, native, or exotic vegetation. In a recent

* Corresponding author. Tel.: +54 2945451165; fax: +54 2945452271.
E-mail addresses: lmiserendino@liesa.org.ar (M.L. Miserendino), cmasi@lab.cricyt.edu.ar (C.I. Masi).

1470-160X/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecolind.2009.06.008

Author's personal copy

study of 60 sites in streams subjected to different land uses Kratzer et al. (2006) found that macroinvertebrate communities responded considerably to land use and most species variation was accounted by variables related to watershed and riparian conditions. Similarly, Compin and Céréghino (2007) detected significant responses of functional feeding groups to landscape alterations. They recognized macroinvertebrate trophic measurements useful for assessing river health with development along riparian zones with collector gatherers showing higher percentages in urban landscapes and scrapers and predators increasing in agricultural landscapes.

The functional structure along streams in Patagonian mountains seems to correspond well with the predictions of the RCC (River Continuum Concept, Vannote et al., 1980) with biomass of shredders decreasing and collector's biomass increasing downstream from the headwaters (Miserendino and Pizzolón, 2003; Miserendino, 2007). Some differences in the functional attributes of benthic communities between rivers bordered by the native *Nothofagus* forest and those dominated by *Salix* spp. have been observed, the former showed higher biomass of shredders while *Salix* bordered rivers had dominance of collector and filterers (Miserendino and Pizzolón, 2003, 2004). In recent experimental studies, Albariño and Balseiro (2002) suggested that the litter processing mechanisms would be affected as a consequence of the substitution of native *Nothofagus* forest by exotic pine plantations.

Streams in Patagonian mountains are subjected to different land use practices; the most common are pasture conversion, exotic plantations, and wood collection/deforestation. The consequences that these activities are having on functional structure of the local, highly endemic biota are not explicitly known. A better understanding of these relationships may contribute to the development of improved land use management practices and to purpose mitigation plans on freshwater ecosystems (Morley and James, 2002; Danger and Robson, 2004).

The aim of this study was to assess the impacts of different land use practices (native forest, exotic, pasture, wood collection, reference urban and urbanizations) on physicochemical characteristics and macroinvertebrate community, and also to evaluate

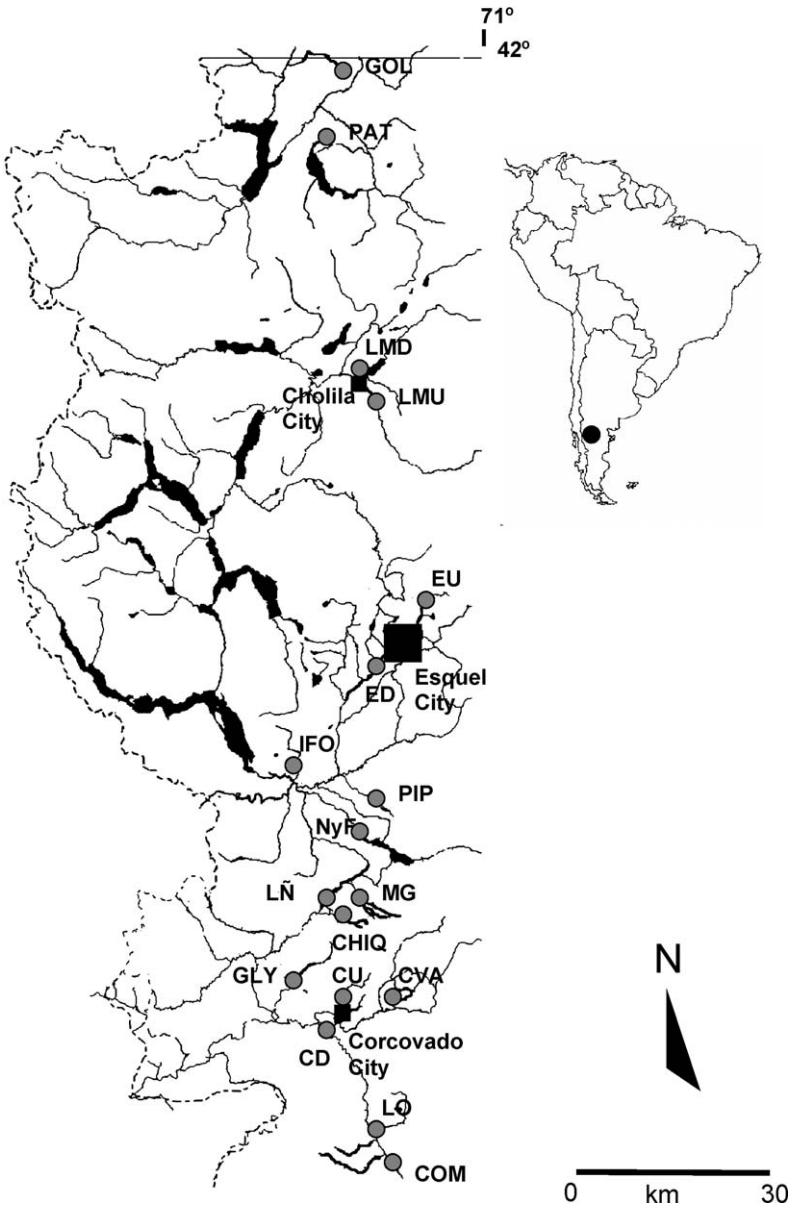


Fig. 1. Map of study area with locations of sampling points, Chubut, Argentina. Site codes are shown in Table 1.

Author's personal copy

the usefulness of guild structure indicators in mountain streams of northwest Patagonia (Argentina).

2. Materials and methods

2.1. Study area and site selection

The study area is located in the Northwest of Chubut Province (Fig. 1) in the ecotone between the Subantarctic forest and the Patagonian steppe, and exhibits a marked altitudinal gradient. Perennial (*Austrocedrus chilensis*, *Nothofagus dombeyi* and *Maitenus boaria*) and deciduous tree species (*Nothofagus pumilio*, *Nothofagus anctarctica*) constitute the Subantarctic forests. The shrub and herbaceous strata are characterized mainly by *Chusquea culeou*, *Berberis buxifolia*, and *Fuchsia magellanica*. The valleys are dominated by the herbaceous, shrub-like steppe vegetation (Tell et al., 1997). Exotic vegetation is composed mainly by the implanted forest of *Pseudotsuga menziesii*, *Pinus ponderosa*, *Pinus radiata* and *Pinus lambertiana*, in many cases species are included in the riparian corridor and replacing most of the native species.

The survey was conducted on March 2006 on 18 sites in 15 rivers. We choose this month because most streams have stable flow conditions (Coronato and del Valle, 1988). Three sampling sites were placed on non-impacted native *Nothofagus* forest (Chiquito, Comisario, and Loro), these sites were considered as reference sites to test for impacts: pasture, pine plantation and wood collection.

Three sites on streams with native *N. antarctica* and *N. pumilio* forest with wood collection or extraction (Glyn, Cabeza de vaca, Pipo) were selected. At these sites the harvest was achieved during previous spring (3 months before the survey). The logging operations imply a selective cut of trees, which should exclude specimens from the river corridor. Operators also have to keep free the streams of debris and branches once the tree is logged. However during the survey we observed some river corridors having logged trees, and some watercourses obstructed with debris.

For pasture sites we selected three sites that had been cleared from the native *Nothofagus* forest and had been grazed intensively (Nant y Fall, Manguera and Los Ñires). At the present pasture sites sustain cattle livestock mainly cow and sheep. The pine plantations sites corresponded to streams running (950–1200 m) through plantations of *Pseudotsuga menziesii*, *Pinus ponderosa*, *P. radiata* and *P. lambertiana* (Golondrinas, Patriada and Ifona). Three urban rivers (Las Minas, Carbón and Esquel) plus their respective reference sites (Las Minas ref, Carbón ref and Esquel ref) were also included in the survey (Fig. 1).

In order to know basin features, vegetation types and coverage, a LandSat image was analyzed and processed in the Dirección General de Bosques y Parques. Per each surveyed site we obtained sub-basin area, % of native vegetation coverage, % of exotic vegetation coverage, % pasture and % of urban areas. We included percentage of the basin corresponding to lakes and areas above the timberline.

2.2. Environmental characterization and macroinvertebrate analysis

Percentages of boulder, cobble, gravel, pebble, and sand in the reach were estimated at each site using a 1-m^2 grid. Current speed was measured in mid-channel on three occasions by timing a float (average of three trials) as it moved over a distance of 10 m (Gordon et al., 1994). Average depth was estimated from five measurements along one transversal profile across the channel with a calibrated stick. Discharge was obtained by combining depth, wet width and current velocity as in Gordon et al. (1994). At each site, air and water temperature were measured with a mercury thermometer.

Specific conductance ($\mu S\,cm^{-1}$), pH, dissolved oxygen (DO, $mg\,O_2\,l^{-1}$) were measured with a Horiba U2-probe. For nutrient analyses water samples were collected below the water surface and kept at 4 °C prior to analysis and transported to the laboratory. Total suspended solids (TSS), total nitrogen (TN), total phosphorus (TP), nitrate plus nitrite nitrogen ($NO_3 + NO_2$), ammonia (NH_4), and soluble reactive phosphate (SRP) were analyzed following standard methods (APHA, 1994).

Quantitative macroinvertebrate samples were taken with a Surber sampler (0.09 m^2; 250 μm mesh size). On each reach, three samples were taken from riffles and three from pools ($n = 6$). Samples were fixed *in situ* with 4% formaldehyde, and sorted in the laboratory under at least 5× magnification. Macroinvertebrate species were identified using available keys (Fernández and Domínguez, 2001). Functional feeding groups (FFGs) were assigned using available references, knowledge of feeding modes (mouthpart morphology and behaviour), and analysis of gut contents (Merritt and Cummins, 1996; Albariño and Balseiro, 2002).

Macroinvertebrate total density (TD), total richness of taxa (TR), diversity (H: Shannon Weaver diversity index) and dominance (BPD; Berger–Parker dominance index) were calculated per site. Species richness, percentage and total density of shredders (S), grazer/scrapers (SG), collector filterers (CF), collector gatherers (CG) and predators (P) were also obtained (Ludwig and Reynolds, 1988).

2.3. Particulate organic matter and chlorophyll analysis

Detritus from benthic samples was divided into fine (250–1000 μm) and coarse (>1000 μm) particulate fractions (FPOM and CPOM, respectively). CPOM was separated into wood, leaves (mainly entire leaves), macrophytes, bryophytes and others (fragments of leaves, grass, seeds, roots, buds, etc.) (Miserendino, 2007). All fractions were dried (105° C for 4 h) and weighed on an electronic balance (Scout Pro) to ±0.003 g. Total benthic particulate organic material (BPOM) was obtained by adding FPOM and CPOM.

Algal biomass (as chlorophyll *a*) was determined by scraping algae from five randomly selected rocks (length range: 5–16 cm) collected within a 20 m run/riffle reach at each site. Scrapings were brought back to the laboratory and drawn on to GF/FF filters. Chlorophyll *a* was extracted from pulverized filters in 90% acetone and the extract was measured, spectrophotometrically as described by Wetzel and Likens (1991).

2.4. Statistical analyses

Land use differences in physicochemical parameters and functional groups attributes were tested using one-factor analysis of variance, or where assumption of normality was violated, Kruskal–Wallis tests. Location of significant differences was tested using Tukey's post hoc test for ANOVA and Duncan test for Kruskal–Wallis (Sokal and Rohlf, 1995). Variability within and among groups of selected streams was assessed by means of a similitude matrix based on taxa percentage composition (Bray Curtis matrix) (Ludwig and Reynolds, 1988), this was performed using the program Bio Diversity Pro. A Pearson correlation matrix based on quantitative macroinvertebrate data was performed, this matrix was employed to produce a non-linear ordination using the Multidimensional Scaling method. This is an alternative to the factorial method and the objective is to display significant distances among investigated objects (Ludwig and Reynolds, 1988). The associations between the MDS ordination scores and environmental variables were tested by mean Spearman rank correlations.

Author's personal copy

3. Results

3.1. Environmental features

Stream shade was lower at Pas and Ur than at forested sites, as a consequence lower water temperatures were recorded in canopied sites (Table 1) thus NF sites had significantly lower water temperature than Pas and Ur sites (ANOVA, Tukey test $p < 0.01$). Both wet (range 0.9–21 m) and channel width (range 1.8–31.5 m) varied considerably between sites, having Pas and Ur the most expanded channels, however differences were only significant when comparing pasture dry width with all types of forested channels (ANOVA, Tukey test $p < 0.01$). At most sites the substrate particle size was mainly boulder, cobble and pebble. However, a higher proportion of sand was observed in some particular sites (LÑ, PAT, PIP) having sedimentation symptoms (Table 1). Current velocity was comprised between 0.1 and 3 m seg^{-1} but did not vary in a systematic manner among different uses.

There were also evident differences in physico-chemistry, with dissolved oxygen contents higher ($F_{(5,12)} = 4.0$, $p < 0.02$) and conductivity lower (Kruskal–Wallis, $p < 0.02$) at NF sites than the rest. Most chemical variables including SRP, TP, NO_3 and NH_4 showed higher mean values at Ur use than at the rest, including R-ur sites. However, values were highly variable, possibly explained by extreme values at ED urban site. A comparison of the same variables, excluding Ur sites from the analyses, highlighted that SRP was slightly lower at Pn sites, TP increased at Pas sites, NO_3–NO_2, TN and NH_4 values were higher at HF, but none of these results was statistically significant ($p > 0.05$). Nonetheless, the trend was that lowest values of NH_4, TN, and TP were recorded at reference native forest sites (Table 1).

The land coverage with exotic (pine) plantation at selected sites ranged between 3.1 and 7.3% and land coverage with pastures primarily dedicated to sustain livestock varied between <1% and 25%. Urbanization affected between 0.4% and 9% of the basins however, rural/agricultural areas affected near of 18.7% of some basins as was the case of ED.

3.2. Particulate organic matter and chlorophyll a

Differences in energy availability with land uses were also evident particularly in the POM fractions: wood, leaves, CPOM, BPOM, and FPOM (Fig. 2). HF streams contain significantly higher leaves than Ur sites (Mann–Whitney U test, $p < 0.04$) and NF showed more wood than Pas and Ur sites (Kruskal–Wallis, $p < 0.04$). As expected, BPOM biomass was higher at NF and HN than Pas (Mann–Whitney U test, $p < 0.05$). Although FPOM did not varied in a consistent manner among land uses (ANOVA, $p = 0.30$), HF sites had higher FPOM biomass than Pas sites (Mann–Whitney, $p < 0.04$, $n = 6$, Fig. 2).

Regarding to autotrophic subsidies differences observed in chlorophyll a (range 2.3 and 17.9 mg m^{-2}) and macrophytes biomass (0 and 15.56 g m^{-2}) were not significant among land uses ($p = 0.84$, 0.77, respectively). However, bryophytes biomass was significantly higher at native forest sites than at Pn, Ur, Pas and R-ur sites (Kruskal–Wallis, $p < 0.01$, Fig. 2).

3.3. Functional metrics and land use

A total of 112 taxa were identified in the survey, being 22 shredders, 27 collector gatherers, 13 collector filterers, 23 scrapers/grazers and 27 predators. Taxa richness ranged between 20 and 48 taxa, and as expected the lowest value (20 taxa) corresponded to ED an urban site (Table 2).

Significant differences in shredder richness were observed among land uses with more shredders species found in HF and NF

Table 1
Environmental features of 18 sampled sites of streams in Patagonia (Argentina) during March 2006. Land use codes—Pas: pasture, R-ur: reference for urban site, Ur: urban site, Pn: pine plantation, HF: harvest forest, NF: native forest reference site.

Site	Site code	Land use	Elevation (m.a.s.l.)	% Native forest	% Pasture wetlands	% Exotic forest	% Urban areas	% Timberline and lakes	Water temperature (°C)	Wet and dry width (m)	Depth (cm)	W. velocity (m seg^{-1})	% Sand	Conductivity (μS cm^{-1})	DO (mg l^{-1})	TSS (mg l^{-1})	SRP (μg l^{-1})	TP (μg l^{-1})	NO_3 (μg l^{-1})	TN (μg l^{-1})	NH_4 (μg l^{-1})	Chlorophyll a (mg m^{-2})
Nant y Fall	NyF	Pas	690	56.3	25.9	0.2	0	14.6	13.6	21–31.5	19	1.5	15	113	7.7	1.7	0.4	8	0.0	410	0.7	2.3
E. Los ñires	LÑ	Pas	667	81.0	7.9	0	0	11.0	9.4	4.3–22.5	20.6	0.9	40	98	9.8	1.1	0.5	18	0.1	<10	0.5	5.4
Manguera	MG	Pas	699	76	<1	0	0	23	8.8	5.9–14.2	13.2	1.5	5	87	10.2	1.3	0.7	13	0.0	<10	0.4	10.4
Esquel	EU	R-ur	721	11.3	0	0.7	0	88.0	13.1	2.8–10.8	13.1	3	10	105	7.8	0.1	0.4	4	0.0	467	0.5	4.5
Las Minas	LMU	R-ur	573	93.1	1.3	0	0	5.6	10.2	3.25–5	17.9	0.9	10	164	9.2	0.8	0.4	2	nd	228	0.8	3.5
Carbón	CU	R-ur	384	97.0	1.4	1.4	0.2	0	9.3	7.57–10.5	18.9	1.7	10	93	9.8	1.7	0.7	14	0.1	319	0.5	9.3
Esquel	ED	Ur	491	11.0	18.7	5.6	9.0	55.7	11.9	9.8–10.5	23.1	1.9	20	366	8.3	4.1	21.0	816	69.0	5464	271.5	3.7
Las Minas	LMD	Ur	555	92.3	1.3	0	0.7	5.7	12.4	4.3–9	10.5	3	5	72	8.3	1.1	0.3	6	0.1	55	0.6	4.2
Carbón	CD	Ur	403	96.6	1.5	1.1	0.4	0.4	10.1	15.8–23.5	27.6	1.3	10	84	9.3	0.7	0.4	13	0.3	45	0.6	5.6
Golondrinas	GOL	Pn	361	57.1	1.3	4.7	0	38.2	8.7	1.6–4.2	20.5	2.6	30	126	10.1	1.5	0.2	12	0.1	<10	0.4	5.7
Patriada	PAT	Pn	495	79.1	0	7.3	0	13.6	8.4	1.2–1.8	7.8	0.3	35	76	10.3	0.5	0.6	8	0.5	354	0.6	4.1
Ifona	IFO	Pn	368	69.5	0	3.1	0	27.4	10.5	8.8–10.5	33.2	1.3	5	38	9.1	4.1	0.2	7	0.0	<10	1.6	15.5
Cab. De vaca	CVA	HF	699	90.4	2.8	0	0	6.8	9.4	4.6–6.9	21.6	1.1	15	63	9.7	0.7	0.7	13	0.2	10	0.6	3.7
Pipo	PIP	HF	728	99.0	0	0	0	1.0	10.6	0.9–2.3	7.7	0.1	35	84	8.9	0.6	0.9	13	0.2	280	4.0	15.5
Glyn	GLY	HF	615	98.8	0	0	0	1.2	8	3.5–5.7	15.6	1.5	15	69	10.6	0.7	0.2	2	0.4	524	0.5	3.7
Comisario	COM	NF	770	60.8	0	0	0	37.2	7.4	8.7–9	24.1	0.8	5	29	11.0	0.7	0.2	4	0.0	<10	0.5	5.0
Loro	LO	NF	820	43.7	0	0	0	56.3	6.1	3.4–4	22.1	1.1	5	26	11.9	4	0.2	3	nd	153	0.5	4.7
Chiquito	CHI	NF	670	97.1	0	0	0	2.9	6.8	2.4–3.5	10.4	3	10	9	11.3	5.2	0.9	26	0.2	<10	0.5	17.9

Author's personal copy

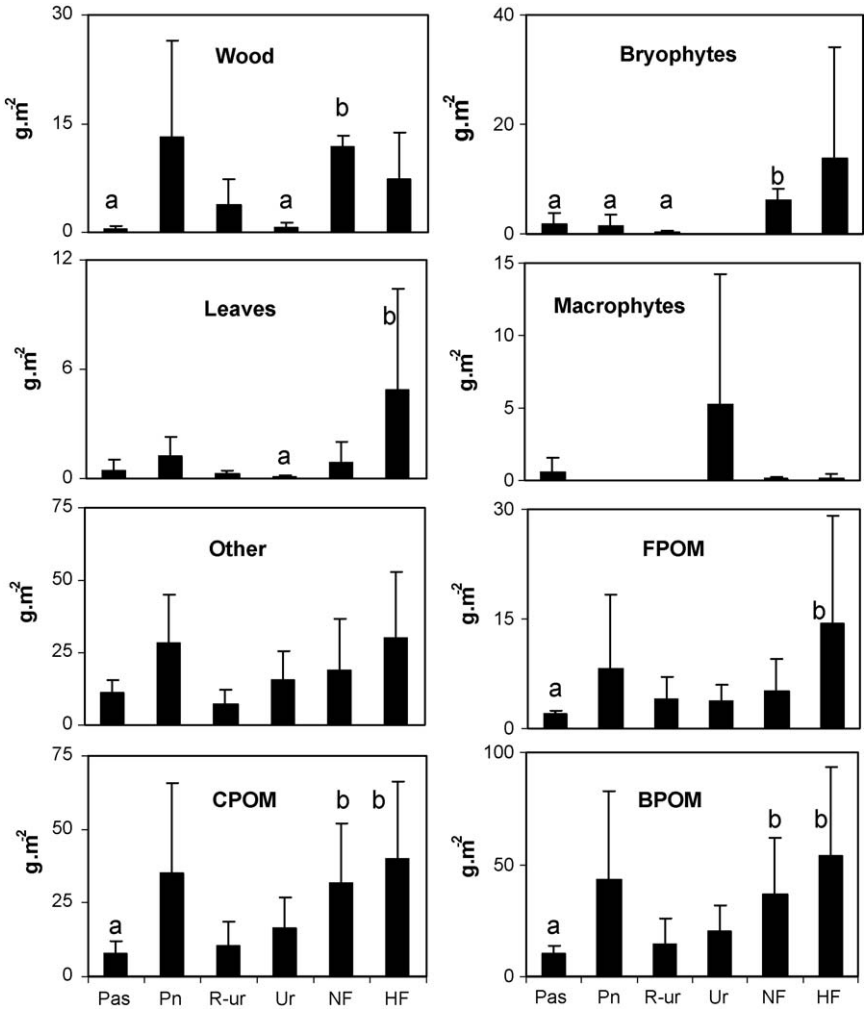


Fig. 2. Mean dry biomass of different energy supplies across different land uses at 18 sampling sites, Chubut, Argentina. Items: wood, entire leaves, other (mainly fragments), macrophytes, bryophytes, fine particulate organic matter (FPOM), total coarse benthic organic matter (CPOM) and total benthic organic matter (BPOM) (±SD, g m^{-2}). Superscript letters show significant differences among sites ($p < 0.05$) as indicated by Kruskal–Wallis test.

Table 2
TR: total richness, TD: total density (ind. 0.09 m^{-2}), D: density (S: shredders, CG: collector gatherers, CF: collector filterers SG: scrapers/grazers and P: predators), H: Shannon Weaver diversity index, BPD: Berger–Parker dominance (%) ($n = 6$). Data from 18 sampled streams in Patagonia Argentina (March 2006).

	Site (land use)																	
	NyF (Pas)	LÑ (Pas)	MG (Pas)	EU (R-ur)	LMU (R-ur)	CU (R-ur)	ED (Ur)	LMD (Ur)	CD (Ur)	GOL (Pn)	PAT (Pn)	IFO (Pn)	CVA (HF)	PIP (HF)	GLY (HF)	COM (NF)	LO (NF)	CHI (NF)
TR	32	37	28	31	31	36	20	31	42	38	27	31.5	39	32	48	33	34	45
S	3	6	5	5	4	4	1	7	6	4	5	5	7	6	7	6	9	8
CG	9	11	4	7	8	9	9	6	12	8	6	6	11	7	13	10	9	13
CF	5	2	3	5	4	2	1	3	5	2	1	3	4	1	2	2	2	1
SG	9	9	10	9	8	11	7	7	11	10	6	8	9	7	13	7	4	10
P	6	9	6	5	7	10	2	8	8	14	9	9.5	8	11	13	8	10	13
% S	48.3	12.8	42.1	15.2	23.2	12.2	0.1	20.7	17.2	9	35.1	13.5	11.1	17.5	62.6	26.4	42.8	21.1
%CG	18.5	16.2	21	18.1	36.8	34.8	93.1	42.4	26.8	8.3	9.9	24.4	39.8	43.6	16.1	28.4	14	20.3
%CF	16.5	42.1	5.9	7.7	8	5.8	0.1	16.6	14.3	36.8	14.9	5	25.4	0.2	3.5	2.8	2.7	35.7
% SG	15.5	25.6	27.9	54.7	26.1	40.3	0.2	14.5	37.6	37.6	33.5	52.9	17.9	16.3	14.6	37.4	26.1	19.6
% P	1.2	3.2	3.1	4.3	5.9	6.9	6.5	5.8	3.9	8.2	6.7	4.2	5.8	22.4	3.2	5	14.4	3.2
TD	1119	548.5	629.6	273	229.8	494.5	3497	2126	1051	457.6	141.8	83.9	1192.2	1488.5	1866.8	206.8	108.9	614.3
DS	540.8	70.2	265.5	41.5	53.3	60.3	1	440.8	181.1	41	49.6	11.3	132.2	260	1168.5	55.2	46.6	129.8
D CG	207.6	89	132	49.3	84.5	172.1	3254.6	901	282.2	38	14	20.5	474	649	299	58.6	15.2	124.6
D CF	184.6	231	37.2	21.2	18.3	28.5	5.3	353.2	150.8	168.6	21.2	4.2	302.3	3.7	66.3	5.8	3	219.5
D SG	172.8	140.5	175.5	149.3	60	199.5	8.7	308.2	395.5	172.3	47.5	44.4	213.8	242.6	272.8	77.3	28.3	120.6
D P	13	17.8	19.5	11.6	13.6	34	227.3	122.8	41.3	37.6	9.5	3.5	69.8	333.2	60.2	9.8	15.7	19.6
H	2.33	2.04	2.12	2.51	2.58	2.81	1.89	2.07	2.93	2.34	2.11	2.28	2.75	2.26	1.86	2.7	2.89	2.42
BPD	27.4	41.9	36.7	22.5	20.8	17.4	39.3	20.9	13.2	33.1	31.1	30.2	14.9	32.3	60.5	20.5	13.6	35.7

Author's personal copy

Table 3
Results of Kruskal–Wallis (H, $n = 6$) or Mann–Whitney U test (pair site comparison) for effects of land use on macroinvertebrates functional attributes.

	$H_{(5,18)}$	p	Post hoc test	Mann–Whitney U test ($p < 0.05$)
Total richness	4.58	0.46		
Richness				
Shredders	9.7	**0.026**	HF, NF > Pn, R-ur	
Collector gatherers	5.89	0.32		
Collector filterers	4.48	0.48		
Scraper/grazers	2.56	0.76		
Predators	8.02	0.15		
Relative abundance				
% Shredders	4.32	0.50		
% Collector gatherers	7.90	0.16		
% Collector filterers	2.77	0.73		
% Scraper/grazer	9.98	0.07		Pn > HF
% Predator	6.49	0.26		
Density				
Total density	13.8	**0.016**	Ur, HF > Pn, NF, R-ur	
Shredders	9.6	0.08		HF, Pas > Pn
Collector gatherers	14.5	**0.012**	HF > Pas, NF, R-ur > Pn	
Collector filterers	3.30	0.65		
Scraper/grazer	7.61	0.18		HF > Pn, NF, Pas
Predator	11.7	**0.04**	Ur > Pas, NF	

Significant differences are in bold. Significant post hoc comparisons (Duncan, Kruskal–Wallis). Land use codes—Pas: pasture; R-ur: reference for urban site; Ur: urban site; Pn: pine plantation; NH: native harvest; NF: native forest reference site.

than Pn and R-ur sites (Kruskal–Wallis, $p < 0.026$, Table 3, Fig. 3). Collector gatherers richness was highly variable (range: 4–13 taxa) and collector filterers (range: 1–5 taxa) were poorly represented mostly at Pas, Pin and NF sites.

As expected total density of macroinvertebrates was significantly higher at Ur and HF than at Pn, NF and R-ur sites (Kruskal–Wallis, $p < 0.016$). Collector's gatherers were significantly more abundant at HF sites than at the rest of uses, moreover, Pas, NF and R-ur had higher density of collector's gatherers than Pn (Kruskal–Wallis, $p < 0.012$). Abundance of shredders was significantly lower at Pn sites than at Pas and HF. Density of scrapers/grazer was higher at HF compared to Pn, Pas and NF (Mann–Whitney U test, $p < 0.05$) (Table 3, Fig. 3). More predators were recorded at Ur sites than at Pas and NF sites.

Diversity values ranges between 1.86 and 2.93 and lowest values were found at Pas and Pn sites. Dominance values were high at HF, Pn and Pas uses. However, some particular sites showed extreme values as GLY by recruitment of the stonefly *Antarctoperla michaelseni* (Gripopterygidae) and ED by high density of *Hyalella araucana*, *Limnodrilus* spp. and Orthocladiinae species.

Regarding to species composition, similarity percentages showed that sites in Pas overlapped more with Ur, R-ur, and HF (Table 4), than with Pn and NF. Similarities between sites within land uses were relatively high, although Ur sites were more variable probably reflecting differences in degrees of impairment. NF selected sites showed a reasonable similitude among each other (55.8%), the same as HF sites (57%). However, the within similarity of land cover types ranged 36.9–64.3%. This might show a fairly

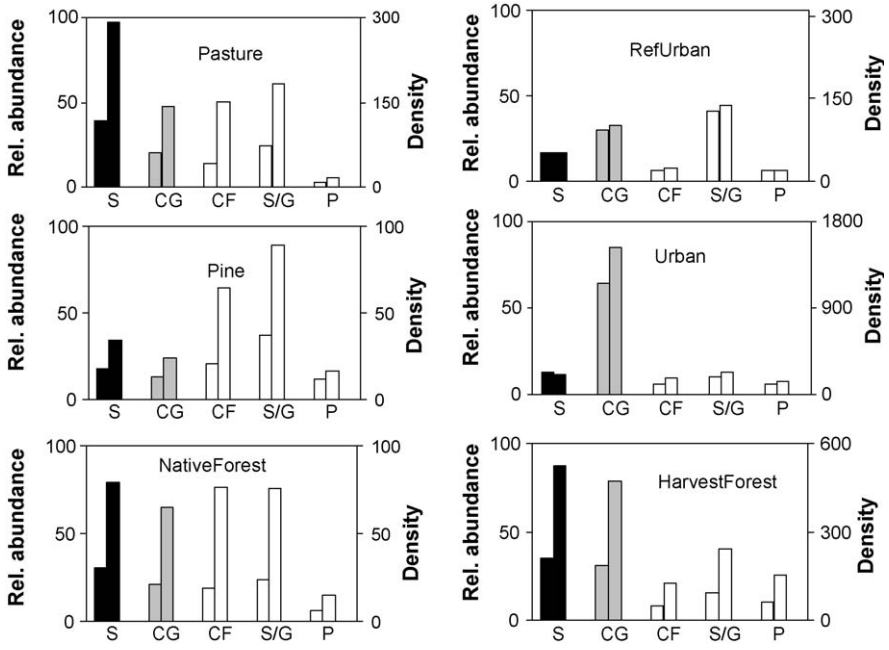


Fig. 3. Relative abundance (left bar) and total density (right bar, ind. m^{-2}) of functional feeding groups at 18 sampling sites subjected to different land uses, Chubut, Argentina. Functional feeding groups are—S: shredders, CG: collector gatherers, CF; collector filterers, S/G: scrapers/grazers and P: predators.

Author's personal copy

Table 4
Similarity percentages (Bray Curtis matrix) showing similarity in species composition within and between land uses types.

	Pasture	Ref urban	Urban	Pine	Native forest	Harvest forest
Pasture	53.4					
Ref urban	58.9	64.3				
Urban	50.3	49.6	36.9			
Pine	39.8	50.6	37.4	40.7		
Native forest	41.5	51.3	38.1	47.3	55.8	
Harvest forest	53.1	55.6	46.7	47.7	51.6	57

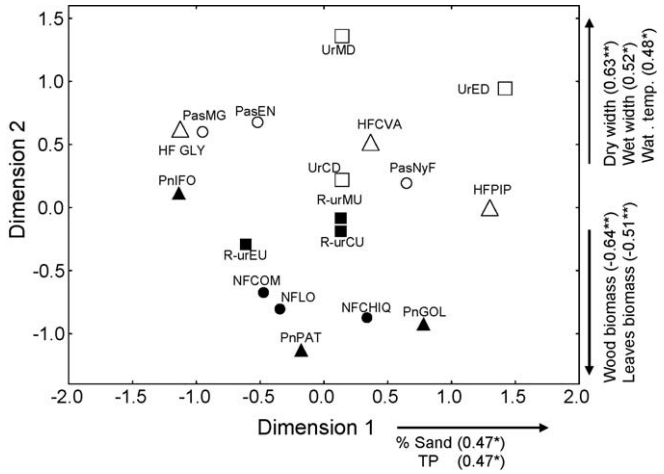


Fig. 4. Results of the multidimensional ordination of macroinvertebrate community data collected from 18 sampling sites subjected to different land uses (Chubut, Argentina). Symbols are: (□) urban sites; (△) harvest forest; (○) pasture; (■) reference urban sites; (●) reference native forest and (▲) pine plantations. Significant correlation coefficients (Spearman rank) with dimension 1 and 2 are given ($^{*}p < 0.05$, $^{**}p < 0.005$).

high within-type variability, which was largest in Ur and Pn forest sites.

3.4. Environmental relationships

The separation of forested either with native or exotic species, plus reference sites (dark symbols) from pasture, urban and harvest sites (open symbols) was clearly evident in the site ordination using density data of macroinvertebrate species (dimension 2, Fig. 4). Thus, NF, R-ur and Pn sites were grouped to the negative end of dimension 2, whereas Pas, HF and Ur were positioned to the positive end of dimension 2. When identifying variables associated with dimension 2, wood and leaf biomass which were negatively correlated, resulted as significant variables explaining sites ordination (Fig. 4). Other significant variables were water temperature and dry and wet width, which were positively correlated with dimension 2. On the other hand, dimension 1 highlighted a water quality impairment gradient or sedimentation; variables that were positively correlated with dimension 1 were TP and sand percentage (Fig. 4).

4. Discussion

Our results suggest that distribution of detritus and trophic structure were different among land uses, this is in agreement with what has been reported for streams draining in developed catchments (Delong and Brusven, 1993; Riley et al., 2003; Thompson and Towsend, 2004; Danger and Robson, 2004). Changes in physical attributes of streams produced by some land use practices were also documented in this study. The buffering effect of the riparian corridors on water temperature (Collier et al., 2000; Scrimgeour and Kendall, 2003; Leunda et al., 2009) was evident at native forested sites. Similarly the percentage of fine sediment on the streambed varied among uses and explained some differences in benthic assemblages. Agricultural land use and pasture development often results in an increased supply of fine sediments (Scarsbrook and Halliday, 1999; Brisbois et al., 2008). Niyogi et al. (2007) found that fine sediment covered 33% of the stream bottom at agricultural streams in New Zealand. We observed that LÑ showed a high percentage of sand as consequence of the constant supply from the severely eroded banks while post-harvest sedimentation effects were evident at Pipo (HF). At this site several trees from the riparian zone were cut and the channel was obstructed by debris (branches and leaves) after the harvest. Logging operations can produce increases of sand and silt in the streambed and this is more significant in small streams (Death et al., 2003). Some groups favored by the presence of fine sediments such as the collector gatherers *Lumbriculus variegatus* and *Pseudochironomus* sp. were abundant at these sites.

We expected higher values of chlorophyll *a* at pasture sites as a consequence of higher temperatures or nutrients levels. On the contrary, chlorophyll *a* pattern was highly variable as were nutrients, which is consistent with observations of Scrimgeour and Kendall (2003) and Scarsbrook and Halliday (1999). They did not report any significant difference in chlorophyll patterns and land uses, although values increased with distance to forested areas. In our study, even though nutrients did not show any significant differences among land use practices, lower values of NH_4, TN, and TP were recorded at reference native forest sites. Likely we were unable to separate cattle effects from other effects in our sampling design, thus cattle is an all-pervading land use in the area. Then some of the patterns observed at harvest sites could result of the combined effect of wood collection and pasturing.

A noteworthy feature in our study was that bryophyte biomass was significantly higher at native forest than at other land uses. Similarly, Riley et al. (2003) found lower moss coverage of streambeds at developed pasture streams than at undeveloped or lightly grazed native grassland catchments. They concluded that the presence of moss can be influenced by substrate stability (bedrock, boulder vs. gravel, sand), trampling by stock and nutrient concentrations.

As reported in other studies (Delong and Brusven, 1993; Benfield, 1997), forested sites showed consistently more allochthonous material than pastures, thus BPOM was significantly higher at NF and HF than at Pas. However, BPOM varied in a non-systematic manner among Pn sites. Scarsbrook et al. (2001) found more detritus material in pine plantations than in pasture sites and Thompson and Towsend (2004) reported a decreasing gradient of detritus biomass from pine, native forest to pasture grasslands. Likely differences observed in the attributes of the riparian corridors (composition, coverage and age) at our Pn sites, were the cause of high variation in detritus biomass.

The contribution of shredders to benthic community at pasture sites was higher than expected (12.8–48%). Most selected pasture sites have remnant forest upstream and this probably had some positive effects on detritus supply. From all of our pasture sites, the most extreme situation was Los Ñires with benthos community basically dominated by filterers (Hydropsychidae: *Smicridea annulicornis*). Predominance of filtering and gathering collectors in rural and agricultural landscapes has been well documented (Shieh et al., 2003, Ometto et al., 2004; Utz et al., 2009) and as suggested by Strand and Merritt (1999) a high proportion of filterers reflect the relative amount of fine particulate organic matter in transport in the water column. In addition, in our study collectors dominated or co-dominated at all urban sites (Compin and Céréghino, 2007) but also at most harvest forest sites. Thus, the

Author's personal copy

relative proportion of collectors was higher at HF sites than forest reference sites suggesting a compositional shift from CPOM feeders to FPOM feeders. McCord et al. (2007) observed that increases of collector's relative abundance was a significant response indicating detrimental effects of silviculture operations when comparing harvest from reference sites. As we mentioned the accumulation of logging slash due to the incorrect treatment of debris was evident at least in one site (Pipo).

Whiles and Wallace (1997) stated that conversion of forest to pine monoculture can influence benthic taxonomic composition. In our study, when assessing the possible effects of exotic plantation on functional feeding groups, the most marked finding was that shredder richness was consistently higher at HF and NF than Pn sites. Besides, total density of shredders was significantly lower at Pn than at Pas and HF. Valdovinos (2001) found more density and biomass of shredders in leaf packs of *N. pumilio* (native) than *Pinus radiata* in experimental trials in Chilean streams. In other experiments, Albariño and Balseiro (2002) noticed that large shredders (*Klapopteryx kuscheli* and *Parasericostoma cristatum*) fed only on *N. pumilio* and not on *Pinus ponderosa* leaf packs in Patagonian streams. The most dramatic situation in our study was the site PAT, in which the riparian corridor is completely replaced by *Pseudotsuga menziesii* and the stream runs through 1200 m of the exotic forest. Paradoxically, the shredder *Myotricha murina* was well represented at this site and constitutes almost 35% of the benthic community. However, other common shredders such as *Senzilloides panguipulli*, *Antarctoperla michaelseni*, and *Udamocercia arumifera* that were well represented at HF and HF sites were practically absent at Pn sites.

As was showed in the ordination analysis, pasture sites were clearly separated from forested sites (either native or exotic) in agreement with reports from similar studies (Hall et al., 2001; Death et al., 2003; Thompson and Towsend, 2004; Compin and Céréghino, 2007). Moreover, in our study harvest forest sites were also clearly separated from undisturbed native forest suggesting changes in composition and structure of benthic community. Detritus biomass, sedimentation processes and habitat impoverishment, factors associated with the removal of the forest canopy and harvesting procedure, appear as important variables determining those assemblages. As we tested here there is also a potential usefulness of functional metrics in particular shredders richness and collectors density to indicate the impact of land use change on macroinvertebrates.

This study reinforces the idea that riparian corridor management may be critical to the distribution of benthic taxa as well functional organization in headwater Patagonian streams. For this reason maintenance of good conditions of vegetation adjacent to rivers will enhance water quality and the environment for stream communities.

Acknowledgments

This study was supported by CONICET (PIP 5733) and Project A.W.A.R.E. Foundation (P-001036). We thank Dr. M. Archangelsky for helpful comments on the English style and Dr. Adriana Kutschker, Cecilia Brand and Cecilia Di Prinzio for fieldtrip assistance. Thanks to anonymous reviewers for valuable comments that greatly improved the manuscript. This is Scientific Contribution no. 36 from LIESA.

References

Abelho, M., Graça, M.A.S., 1998. Litter in first-order stream of a temperate deciduous forest (Margaraça Forest, central Portugal). Hydrobiologia 386, 147–152.
Albariño, R.J., Balseiro, E., 2002. Leaf litter breakdown in Patagonian streams: native versus exotic trees and the effect of invertebrate size. Aquat. Conserv. 12, 181–192.
Allan, J.D., Erickson, D.L., Fay, J., 1997. The influence on catchment land use on stream integrity across multiple spatial scales. Freshw. Biol. 37, 149–161.
APHA, 1994. Standard Methods for the Examination of Water and Wastewater. American Public Health Association, Hanover, MD, USA.
Baillie, B.R., Davies, T.R., 2002. Influence of large woody debris on channel morphology in native forest and pine plantation in the Nelson region, New Zealand. N. Zeal. J. Mar. Fresh. 36, 763–774.
Benfield, E.F., 1997. Comparison of litter fall input to streams. J. N. Am. Benthol. Soc. 16, 104–108.
Brisbois, Mc.G., Jamieson, R., Gordon, R., Stratton, G., Madani, A., 2008. Assessing ecosystem health in rural mixed land use watersheds. In: 21st Century Watershed Technology: Improving Water Quality and Environment Conference Proceedings, Concepcion, Chile, 29 March–3 April.
Collier, K.J., Rutherford, J.C., Quinn, J.M., Davies-Colley, R.J., 2001. Forecasting rehabilitation outcomes for degraded New Zealand pastoral streams. Water Sci. Technol. 43, 175–184.
Collier, K.J., Smith, B.J., Quinn, J.M., Scarsbrook, M.R., Halliday, N.J., Crocker, G.F., Parkyn, S.M., 2000. Biodiversity of stream invertebrate faunas in a Waikato hill-country catchment in relation to land use. N. Zeal. Entomol. 23, 9–22.
Compin, A., Céréghino, R., 2007. Spatial pattenrs of macroinvertebrate functional feeding groups in streams in relation to physical variables and land-cover in Southwestern France. Landsc. Ecol. 22, 1215–1225.
Coronato, F.R., del Valle, H.F., 1988. Caracterización hídrica de las cuencas hidrográficas de la provincia del Chubut, Publicación Técnica. Cenpat-Conicet, Puerto Madryn, Chubut, Argentina.
Danger, A.R., Robson, B.J., 2004. The effects of land use on leaf-litter processing by macroinvertebrates in an Australian temperate coastal stream. Aquat. Sci. 66, 1–09.
Death, R.G., Baillie, B., Fransen, P., 2003. Effect of *Pinus radiata* logging on stream invertebrate communities in Hawke's Bay, New Zealand. N. Zeal. J. Mar. Fresh. 37, 50–520.
Delong, M., Brusven, M.A., 1993. Macroinvertebrate community structure along the longitudinal gradient of an agriculturally impacted stream. Environ. Manage. 22, 77–88.
Fernández, H.R., Domínguez, E., 2001. Guía para la determinación de los Artrópodos bentónicos sudamericanos. EUDET, Tucumán, Argentina.
Gordon, N.D., McMahon, T.A., Finlayson, B.L., 1994. Stream hydrology, an introduction for ecologists. Wiley and Sons, New York.
Hall, M.J., Closs, P., Riley, R.H., 2001. Relationships between land use and stream invertebrate community structure in South Island, New Zealand, coastal stream catchment. N. Zeal. J. Mar. Fresh. 35, 591–603.
Kratzer, E.B., Jackson, J.K., Arscott, D.B., Aufdenkampe, A.K., Dow, C.L., Kaplan, L.A., Newbold, J.D., Sweeney, B.W., 2006. Macroinvertebrate distribution in relation to land use and water chemistry in New York City drinking-water-supply watersheds. J. N. Am. Benthol. Soc. 25, 954–976.
Leunda, P.M., Oscoz, J., Miranda, R., Ariño, A.H., 2009. Longitudinal and seasonal variation of the benthic macroinvertebrate community and biotic indices in an undisturbed Pyrenean River. Ecol. Indic. 9, 52–63.
Ludwig, J.A., Reynolds, J.F., 1988. Statistical Ecology. Wiley-Interscience, New York.
McCord, S.B., Grippo, R., Eagle, D., 2007. Effects of silviculture using best management practices on stream macroinvertebrate communities in three ecoregions of Arkansas, USA. Water Air Soil Poll. 184, 299–311.
Merritt, R.W., Cummins, K.W., 1996. An introduction to the aquatic insects of North America. Kendall-Hunt, Dubuque.
Miserendino, M.L., 2005. Interacciones bosque río implicaciones para los ecosistemas acuáticos. Patagonia Forest. XI (4), 14–17.
Miserendino, M.L., 2007. Macroinvertebrate functional organization and water quality in a large arid river from Patagonia (Argentina). Ann. Limnol. 43 (3), 133–145.
Miserendino, M.L., Pizzolón, L.A., 2003. Distribution of macroinvertebrates assemblages in the Azul-Quemquemtreu river basin, Patagonia, Argentina. N. Zeal. J. Mar. Fresh. 37, 525–539.
Miserendino, M.L., Pizzolón, L.A., 2004. Interactive effects of basin features and land use change on macroinvertebrate communities of headwater streams in the Patagonian Andes. River Res. Appl. 20, 967–983.
Morley, S.A., James, R.K., 2002. Assessing and restoring the health of urban streams in the Puget Sound Basin. Conserv. Biol. 16 (6), 1498–1509.
Newbold, J.D., Erman, D.C., Roby, K.B., 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Can. J. Fish. Aquat. Sci. 37, 1076–1085.
Niyogi, D.K., Koren, M., Arbuckle, C.J., Townsend, C.R., 2007. Longitudinal changes in biota along four New Zealand streams: declines and improvements in stream health related to land use. N. Zeal. J. Mar. Fresh. 41, 63–75.
Ometto, J.P., Gessner, A., Martinelli, L.A., Bernardes, M.C., Krusche, A.W., Camargo, P.B., 2004. Macroinvertebrate community as indicator of land use changes in tropical watersheds, southern Brazil. Int. J. Ecohydrol. Hydrobiol. 4, 35–47.
Quinn, J.M., Cooper, A.B., Davies-Collier, R.J., Rutherford, J.C., Williamson, R.B., 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. N. Zeal. J. Mar. Fresh. 31, 579–597.
Riley, R., Towsend, C.R., Niyogi, D.K., Arbuckle, C.A., Peacock, K.A., 2003. Headwater stream response to grassland agricultural development in New Zealand. N. Zeal. J. Mar. Fresh. 37, 389–403.
Roy, A.H., Rosemond, A.D., Paul, M.J., Leigh, D.S., Wallace, J.B., 2003. Stream macroinvertebrate response to catchment urbanization (Georgia, U.S.A.). Freshw. Biol. 48, 329–346.

Author's personal copy

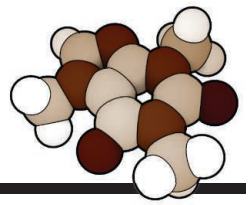
Scarsbrook, M.R., Halliday, J., 1999. Transition from pasture to native forest land-use along stream continua: effects on stream ecosystems and implications for restoration. N. Zeal. J. Mar. Fresh. 33, 293–310.
Scarsbrook, M.R., Quinn, J., Halliday, J.M., Morse, R., 2001. Factors controlling litter input dynamics in streams draining pasture, pine, and native forest catchments. N. Zeal. J. Mar. Fresh. 35, 751–762.
Scrimgeour, G.J., Kendall, S., 2003. Effects of livestock grazing on benthic invertebrates from a native grassland ecosystem. Freshw. Biol. 48, 347–362.
Shieh, S.H., Ward, J.V., Kondratieff, B.C., 2003. Longitudinal changes in macroinvertebrate production in a stream affected by urban and agricultural activities. Arch. Hydrobiol. 157, 483–503.
Sokal, R.R., Rohlf, F.J., 1995. Biometry, 3rd edition. W.H. Freeman and Company, New York.
Strand, Mc.D., Merritt, R.W., 1999. Impacts of livestock grazing activities on stream insect communities and the riverine environment. Am. Entomol. 45, 13–29.
Tell, G., Izaguirre, I., Quintana, R., 1997. Flora y Fauna Patagónicas. Ediciones Caleuche, Argentina.
Thompson, R.M., Towsend, C.R., 2004. Land use influences on New Zealand stream communities effects on species composition, functional organization, and food-web structure. N. Zeal. J. Mar. Fresh. 38, 595–608.
Utz, R.M., Hilderbrand, H., Boward, D.M., 2009. Identifying regional differences in threshold responses of aquatic invertebrates to land cover gradients. Ecol. Indic. 9, 556–567.
Valdovinos, C., 2001. Procesamiento de detritus ripariano por macroinvertebrados bentónicos en un estero boscoso de Chile central. Rev. Chil. Hist. Nat. 74, 445–453.
Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37, 130–137.
Wetzel, R.G., Likens, G.E., 1991. Limnological Analysis, 2nd edition. Springer-Verlag, New York.
Whiles, M.R., Wallace, J.B., 1997. Leaf litter decomposition and macroinvertebrate communities in headwater streams draining pine and hardwood catchments. Hydrobiologia 353, 107–119.

View publication stats

INSIGHTS

On the renaissance of coal *p. 1286*

How caffeine disturbs sleep *p. 1289* ▸



PERSPECTIVES



ENVIRONMENTAL SCIENCE

Reform forest fire management

Agency incentives undermine policy effectiveness

By **M. P. North,[1,2]* S. L. Stephens,[3] B. M. Collins,[1,3] J. K. Agee,[4] G. Aplet,[5] J. F. Franklin,[4], P. Z. Fulé[6]**

Globally, wildfire size, severity, and frequency have been increasing, as have related fatalities and taxpayer-funded firefighting costs (*1*). In most accessible forests, wildfire response prioritizes suppression because fires are easier and cheaper to contain when small (*2*). In the United States, for example, 98% of wildfires are suppressed before reaching 120 ha in size (*3*). But the 2% of wildfires that escape containment often burn under extreme weather conditions in fuel-loaded forests and account for 97% of fire-fighting costs and total area burned (*3*). Changing climate and decades of fuel accumulation make efforts to suppress every fire dangerous, expensive, and ill advised (*4*). These trends are attracting congressional scrutiny for a new approach to wildfire management (*5*). The recent release of the National Cohesive Wildland Fire Management Strategy (NCWFMS) (*6*) and the U.S. Forest Service's (USFS's) current effort to revise national forest (NF) plans provide openings to incentivize change. Although we largely focus on the USFS, which incurs 70% of national firefighting costs (*7*), similar wildfire policies and needed management reforms are relevant throughout the United States and fire-prone areas worldwide.

POLICY

Accumulated fuels in dry forests need to be reduced so that when fire occurs, rather than "crowning out" and killing most trees, it is more likely to burn along the surface at low-moderate intensity, consuming many small trees and restoring forest resilience to future drought and fire. Mechanical thinning can reduce tree density and some fuels but is often limited by legal (wilderness and park areas), operational (steep or remote ground), and cost constraints (*8*). Fire can also be used to reduce fuels either intentionally (prescribed burning) or opportunistically (letting a natural ignition burn as "managed wildfire") under moderate weather conditions. Although these burns are much less precise than mechanical thinning, in remote locations, fire is usually more efficient, cost-effective, and ecologically beneficial than mechanical treatments (*9*).

Many severe wildfires are due to past fire suppression. Firefighters during the Rim Fire near Yosemite National Park, California, 25 August 2013.

PHOTO: © JAE C. HONG/AP/CORBIS

ENTRENCHED DISINCENTIVES. Management reform in the United States has failed, not because of policy, but owing to lack of coordinated pressure sufficient to overcome entrenched agency disincentives to working with fire. Responding to established research, official agency policy now supports a more flexible response to fire than ever before (*6*). Actual wildfire response, however, has changed little because of substantial management impediments. Suppression generally begets larger, more intense wildfires, which in turn intensifies agencies' suppression response (*10*). The alternative, working with fire, is rarely used because of liability and casualty risks and little tolerance for management errors.

Downloaded fro www.sciencemag.org on September 18, 2015

Published by AAAS

For example, during the most recent decade when data were collected (ending in 2008), only 0.4% of ignitions were allowed to burn as managed wildfires (*7*). For individual NFs, there is little economic incentive to change because fire suppression is steadfastly financed through dedicated congressional appropriations, which are augmented with emergency funding, whereas fuels reduction and prescribed burning costs come out of a limited budget allotted to each NF and is often borrowed to cover wildfire suppression costs. With these deterrents, "battling" fire and "only you can prevent wildfire" campaigns have more traction than recognizing that many severe fires result from accrued management decisions. This skewing of agency motivation also distorts economic, insurance, and local regulatory incentives that influence development in fire-prone regions (*11*).

Although agencies are slow to reform internally, they may more rapidly respond to local stakeholder pressure. The core problem has been the lack of a public constituency that advocates for reform of fire-use practices (*11*). The benefits of greater fire use have been a difficult sell because of public objections to smoke and a negative perception of forest fires. This has begun to change as communities increasingly threatened by large fires are urging land-management agencies to accelerate fuel reduction efforts, including the use of managed fire (e.g., yosemitestanislaussolutions.com and 4FRI.org). Timber companies would also benefit from more fire-resilient landscapes in which their private lands are embedded. There is growing awareness that large, severe fires are inevitable in many dry forests, especially in a warming climate. Smoke, safety threats, fire intensity, and human health risks can be better managed for public benefit with proactive fire use under favorable weather and wind dispersal conditions (*12*).

EFFECTING CHANGE. Public support for expanded fire use could thus be directed toward revision of each NF plan, which provides standards and guidelines for daily management decisions. Plans can divide the landscape into zones for different fire management strategies, an approach used by Parks Canada. U.S. forest plans could zone areas close to homes (wildland-urban interface) as an area where most fuels reduction relies on mechanical thinning and fires are suppressed. Beyond this could be an intermediate area where prescribed fire and mechanical treatment are used to optimize fuels reduction. More remote forests could be intentionally burned with prescribed fire, or lightning ignitions allowed to burn as managed wildfires under moderate weather conditions.

Three of the first eight NFs to develop new plans have proposed that more than half of their area in the southern Sierra Nevada be zoned for prescribed and managed fire use. Over the next decade, most of the 155 NFs will begin writing new plans and holding public forums. Engaged local stakeholders will need to look beyond short-term impacts of fire use (e.g., smoke, limited access, and risk of escape) to support managers working with fire and challenge suppression in remote forest zones.

Public support of NCWFMS may help overcome reform disincentives by stressing national interagency collaboration. In response to decades of problem wildfires, the U.S. Congress passed the FLAME Act in 2009 requesting development of NCWFMS, a coordinated strategy to support landscape restoration and fire-adapted communities. Coordination is essential as large, intense wildfires often cross ownership boundaries. For example, in California's 2013 Rim Fire, large patches of old-growth trees in Yosemite National Park were killed when fuel-loaded forests on nearby NF land generated extreme fire behavior that crossed into the park (*13*). NCWFMS can exert peer pressure between agencies and provide support for tough decisions. To accomplish these changes, some policy and resource-deployment decisions supporting fire use could be made at the national level. In the United States, federal land agencies each fund their own fire crews but the National Interagency Fire Center (NIFC) coordinates resource deployment between agencies and nationally across geographic areas. Dedicated crews could be hired and trained for managed fire use, and NIFC could be charged with deploying them for beneficial burning (*14*). Some local and regional agencies have briefly created such crews, but they were often pulled into fire suppression when wildfire activity increased. By giving NIFC deployment authority, it could ensure that these crews are only used for working with fire and are available to burn when weather conditions are favorable. Optimal weather and smoke dispersal conditions occur even in heavily populated and regulated areas such as California, but many burn windows are missed because crews are at or being held for wildfire deployment (*9*). Air-quality regulations limit prescribed fires, although they have much lower emissions than the inevitable wildfire. The Environmental Protection Agency could consider treating prescribed fire smoke like wildfire, as an unregulated "exceptional event."

National government also has an incentive to reduce wildfire expenses and forest agencies' emergency fire borrowing. In many years, suppression costs consume 50% of agency annual budgets, which, after operating expenses, leaves little money for proactive fuels treatment or forest restoration (*11*). Costs and injuries, however, are much lower on managed fires than on escaped wildfires (*7*, *15*). The estimated cost savings for using managed fire compared with wildfire suppression over the same area (*15*) could be reported to Congress to highlight the economy of using proactive restoration rather than reactive triage.

Increased fire use will necessitate management changes (*16*). Mechanical fuels reduction could also be used not only for fire containment but also to establish safe-zone anchors to facilitate greater fire reintroduction (*8*). Large prescribed burns commonly used in Western Australia are possible because a network of these anchors allows 6 to 8% of the forest to be burned annually (*16*). Australian foresters make substantial efforts to educate the public about the inevitability of fire and its ecological benefits and to build support for fire use and smoke tolerance.

We will not eliminate wildfire, but public support for proactive use of managed fires can help restore millions of hectares of forest ecosystems. ■

[1]*USFS Pacific Southwest Research Station, Davis, CA 95618, USA.* [2]*University of California, Davis, CA 95616, USA.* [3]*University of California, Berkeley, CA 94720, USA.* [4]*University of Washington, Seattle, WA 98195, USA.* [5]*The Wilderness Society, Denver, CO 80202, USA.* [6]*Northern Arizona University, Flagstaff, AZ 86011, USA.* **Corresponding author. E-mail: mpnorth@ucdavis.edu*

REFERENCES

1. S. L. Stephens *et al.*, *Front. Ecol. Environ.* **12**, 115 (2014).
2. M. A. Finney, *For. Ecol. Manage.* **211**, 97 (2005).
3. D. E. Calkin *et al.*, *J. For.* **103**, 179 (2005).
4. M. A. Moritz *et al.*, *Nature* **515**, 58 (2014).
5. Staff of Sen. M. Cantwell, "The Wildfire Management Act of 2015: A white paper" (Office of Sen. M. Cantwell, Washington, DC, 2015); http://1.usa.gov/1hDuJ2D.
6. Forests and Rangelands, National Cohesive Wildland Fire Management Strategy, (2014); http://1.usa.gov/1EDCyQL.
7. National Interagency Fire Center, Statistics (NIFC, Boise, ID, 2015); http://1.usa.gov/1NZBOZ4.
8. M. North *et al.*, *J. For.* **113**, 40 (2015).
9. L. N. Quinn-Davidson, J. M. Varner, *Int. J. Wildland Fire* **21**, 210 (2012).
10. D. E. Calkin *et al.*, *For. Ecosyst.* **2**, 9 (2015).
11. K. Bradshaw, D. Lueck, *Wildfire Policy: Law and Economics Perspectives* (Routledge, London, 2012).
12. D. Schweizer, R. Cisneros, *J. Environ. Manage.* **144**, 265 (2014).
13. J. M. Lydersen, M. P. North, B. M. Collins, *For. Ecol. Manage.* **328**, 326 (2014).
14. M. P. Dombeck, J. E. Williams, C. A. Wood, *Conserv. Biol.* **18**, 883 (2004).
15. G. Snider, P. J. Daugherty, D. Wood, *J. For.* **104**, 431 (2006).
16. R. J. Sneeuwjagt *et al.*, *Fire Ecol.* **9**, 14 (2013).

ACKNOWLEDGMENTS

The content is solely the responsibility of the authors and does not necessarily represent the official views of the USFS.

10.1126/science.aab2356

Published by AAAS

Managing fire-prone forests in the western United States

Reed F Noss[1], Jerry F Franklin[2], William L Baker[3], Tania Schoennagel[4], and Peter B Moyle[5]

The management of fire-prone forests is one of the most controversial natural resource issues in the US today, particularly in the west of the country. Although vegetation and wildlife in these forests are adapted to fire, the historical range of fire frequency and severity was huge. When fire regimes are altered by human activity, major effects on biodiversity and ecosystem function are unavoidable. We review the ecological science relevant to developing and implementing fire and fuel management policies for forests before, during, and after wildfires. Fire exclusion led to major deviations from historical variability in many dry, low-elevation forests, but not in other forests, such as those characterized by high severity fires recurring at intervals longer than the period of active fire exclusion. Restoration and management of fire-prone forests should be precautionary, allow or mimic natural fire regimes as much as possible, and generally avoid intensive practices such as post-fire logging and planting.

Front Ecol Environ 2006; 4(9): 481–487

The management of fire-prone forests, especially within the national forests of the west, is one of the most contentious natural resource issues in the US today. One recent response to the controversy is the Healthy Forests Restoration Act (HFRA) of 2003 (Public Law 108-V148). This law has potentially profound consequences for forests and their biodiversity and must therefore be implemented on the basis of the best scientific information and guidance. Towards this end, the North American Section of the Society for Conservation Biology convened a scientific panel to review issues related to the ecology and management of fire-prone forests of the western US. This article is adapted from the unpublished report of that panel (Noss *et al.* 2006a).

The vegetation of North America has been shaped by recurring fires over millions of years. Fossils of pines (*Pinus* spp), which are closely associated with fire, date from the Cretaceous Period, more than 100 million years ago (Millar 1998). Fire remains the primary natural disturbance influencing plant and animal communities across much of the continent today (Habeck and Mutch 1973; Agee 1993). Many forests, however, have been degraded over the past century by misguided fire management, as well as other impacts such as logging and livestock grazing. Uncharacteristic fuel loads contribute to altered fire regimes in some forest types (Covington and Moore 1994; Schoennagel *et al.* 2004). Key structural elements (eg old "veteran" trees), terrestrial and aquatic biodiversity, and habitats of many threatened and endangered species are already greatly diminished and at continuing risk of loss. Increased human habitation of wildlands has intensified problems of managing fire, especially at the wildland–urban interface (Dombeck *et al.* 2004).

For this paper we evaluated the scientific literature that is relevant to conservation, restoration, and management of forests in the western US (excluding Alaska). Our review addresses ecological science relevant to developing and implementing fire and fuel management policies, including activities conducted before, during, and after wildfires. Our focus is primarily on wildlands, rather than the wildland–urban interface, where ecological values may be secondary to fire-risk mitigation to protect people and homes (DellaSala *et al.* 2004). In wildlands especially, sustainable forest management must be based on well-grounded ecological principles.

In a nutshell:

- The complexity created by variability in fire regimes defies a one-size-fits-all management prescription
- Restoration is warranted where fire exclusion has led to substantial alterations in ecosystem qualities
- Post-fire logging usually has no ecological benefits and many negative impacts; the same is often true for post-fire seeding
- Although many forests will require continued management, a common sense conservation goal is to achieve forests that are low maintenance and require minimal repeated treatment

[1]*Department of Biology, University of Central Florida, Orlando, FL 32816 (rnoss@mail.ucf.edu);* [2]*College of Forest Resources, University of Washington, Seattle, WA 98195;* [3]*Ecology Program and Department of Geography, University of Wyoming, Laramie, WY 82071;* [4]*Department of Geography, University of Colorado, Boulder, CO 80309;* [5]*Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616*

Fire in western forests

Fire provides fundamental services, including recycling nutrients, regulating the density and composition of

© The Ecological Society of America



Courtesy of D Stepnisky

Figure 1. *A juvenile northern hawk owl (*Surnia ulula*) in a recently burned boreal forest. This species and a number of other North American birds are closely associated with post-fire forests and are typically absent from unburned or salvage-logged forests.*

young trees, creating and shaping wildlife and fish habitat, structuring the spatial pattern of landscapes, and influencing water and sediment delivery across watersheds. Many plant and animal species are adapted to post-fire conditions, and populations of some (eg many bird species; Figure 1) decline after fire exclusion or post-fire logging (Hutto 1995). Different species benefit from different fire severities and intervals between fires.

Given fuel, lightning, and dry weather, wildfire is inevitable. Nevertheless, the characteristic fire regime, especially the extent and severity of fire and how often it recurs, varies over a surprisingly large spectrum. Fires recur in western forests from once a decade or less in some dry ponderosa pine (*Pinus ponderosa*) forests to a cycle of 250–400 years or more in coastal forests (Hemstrom and Franklin 1982; Covington *et al.* 1997; Agee 1998). Even within a forest type, fire frequency may vary by two orders of magnitude across sites, for example, from 6 to 600 years in redwood (*Sequoia sempervirens*) forests (Noss 2000). Frequent fires are typically lower in intensity (energy output) and severity (impact on vegetation) than infrequent fires, such as those that occurred in and around Yellowstone National Park in 1988 (Turner *et al.* 2003).

Characteristic fire regimes (Panel 1) result from a combination of forest type, fuels, topography, climate, and ignition sources (Schoennagel *et al.* 2004). Forests subject to high severity fire typically support high tree densities. When dense fuels dry out and an ignition source is present, the resulting fires can spread rapidly and are almost impossible to suppress. High severity fires kill most or all trees in substantial portions of the burn, although fire pattern is often a mosaic that includes areas of unburned or less severely burned forest (Figure 2). This is true in such diverse forests as productive coastal Douglas-fir (*Pseudotsuga menziesii*; Agee 1993) and low productivity, high elevation lodgepole pine (*Pinus contorta*) in the Rocky Mountains (Wallace 2004). Many large, high severity fires are associated with infrequent, severe droughts (Westerling *et al.* 2003), often related to broad-scale climatic anomalies (Gedalof *et al.* 2005). Fire exclusion has had minimal effect on most forests characterized by high severity fire – a fact that is especially relevant to fire policy. High severity fires are infrequent (from one to many centuries; Romme and Despain 1989; Agee 1993; Kipfmueller and Baker 2000), whereas the period of active fire exclusion in North America is 50 years at most. Furthermore, many of these forests are remote and occur at high elevations, making access for fire fighting difficult.

In contrast, dry, less productive forests may have annual droughts that promote frequent fires. As a consequence of lower productivity and higher fire frequencies, fuel accumulations and fire intensities are characteristically lower in such forests than in coastal or subalpine forests. Low-severity fire regimes characterized many pine and mixed-conifer forests at warm, dry sites prior to European settlement (Table 1). Fires in ponderosa pine and dry, mixed-conifer forests historically burned fine fuels (eg grasses and litter on the forest floor) at regular intervals (Veblen *et al.* 2000; Heyerdahl *et al.* 2001; Stephens and Collins 2004). These surface fires rarely killed large, fire-

Panel 1. What are "characteristic" and "uncharacteristic" fire regimes?

"Characteristic" is a controversial concept among ecologists. We use this term in reference to the dominant natural disturbance regime and associated structural characteristics for a particular forest type or site historically, before major disruption by Euro-Americans. Conversely, the term "uncharacteristic" refers to disturbances, forest structure, or fuel loads of a scale or type outside the historical range of variability, based on site-specific vegetation reconstructions using tree rings, fire scars, pollen, charcoal, or early historical records. Characteristic does not imply uniformity, because substantial variability occurs within as well as among forest types in fire regime and structure. A forest type that was "historically characterized" by low severity fire may, on many sites, experience high or moderate severity fire (Ehle and Baker 2003). What is characteristic also changes over time, sometimes radically, for example with changing climate (Pierce *et al.* 2004). Despite difficulties with the concept, some idea of the characteristic fire regime for a given forest is needed, to give management strategies proper direction.

© The Ecological Society of America

resistant trees, but did kill smaller trees of all species, thereby helping to maintain sparse, open stands. Human activities following European settlement – including fire exclusion, grazing, logging, and tree planting – dramatically modified the fuel structure in these forests. Grazing reduced the fine fuels that carry surface fires and facilitated dense tree reproduction by reducing or eliminating herbaceous competition (Rummell 1951; Savage and Swetnam 1990; Belsky and Blumenthal 1997). Logging also promoted higher stand densities in many dry ponderosa pine forests by stimulating dense natural regeneration (Agee 1993; Kaufmann *et al.* 2000). These forests therefore changed from relatively open stands with low fuel loadings to dense stands that can carry crown fires (Skinner 1995). Restoration of such forests (ie guiding their composition, structure, and function to a condition within the historical range of variability) is often desirable (Figure 3) and can involve active techniques such as thinning of small trees and prescribed burning or passive management such as allowing natural fires to burn and removing livestock (Allen *et al.* 2002; Brown *et al.* 2004; Schoennagel *et al.* 2004). Large wildland landscapes are especially well-suited to passive restoration (Noss *et al.* 2006b).


Courtesy of J Peaco

Figure 2. *A mosaic fire pattern in Madison Canyon, Yellowstone National Park, approximately one year after the major 1988 fires.*

Fire is variable in severity in certain mid- and low-elevation forests of moderate to high productivity. In addition to the effects of shifts in the weather during a fire, variable fire severity can result from spatial heterogeneity in topography (which affects microclimate), the relative abundance of fuels, and the legacies of past episodes of fire and other disturbances. Topographically complex mountain landscapes may be especially prone to mixed severity fire, because drier, south-facing slopes with lower fuel loads may burn at low severity while adjacent, moister, north-facing slopes that support higher tree densities experience high severity fire (Taylor and Skinner 2003; Spies *et al.* 2006) or escape fire due to wetter conditions. Evidence of mixed severity fire in moist ponderosa pine forests and mixed evergreen–conifer forests is accumulating (Shinneman and Baker 1997; Brown *et al.* 1999; Odion *et al.* 2004). The inherent variability of mixed-severity fire regimes precludes easy analysis of fire-exclusion effects, because high tree density or an abundance of shade-tolerant trees is not necessarily the result of fire exclusion.

The complexity created by variability in fire regimes defies a simple, one-size-fits-all prescription for restoration. Fortunately, plant association groups, which have predictable relationships to fire regimes (Table 1), provide a classification of this diversity that is useful for managers, albeit plant association–fire relationships can be expected to change as climate changes (McKenzie *et al.* 2004; Pierce *et al.* 2004).

Forest management prior to wildfire

How can forests be managed to ensure that fire will play its characteristic role in maintaining composition, structure, and function of forest ecosystems? Management will vary greatly with the type of forest and its dominant fire regime (Table 1). Developing a management and restoration program requires that the effects of past land uses be identified so that they can be remedied. In forests characterized by low-severity fire regimes, restoration varies along a continuum from restoring structure (eg reducing densities of small trees and increasing the density of large trees) to restoring the processes (eg low severity fire, competition between grasses and tree seedlings) that create and maintain that structure (Figure 4). The continuum also represents a gradient from symptoms (eg uncharacteristically high tree densities) to causes (eg exclusion of fire). The following are some of our key findings that relate to decisions about fire management. (1) Fire exclusion and other human activities led to significant deviations from historical variability in some, but not all, forests. Restoration treatments are warranted, sometimes urgently, only where such activities have resulted in major alterations in ecosystem structure, function, or composition. (2) Fire exclusion has had little effect on fuels or forest structure in forests characterized by high severity (stand-replacement) fire. High severity fires are relatively infrequent, occurring at intervals of one to many centuries,

© The Ecological Society of America

Table 1. Fire regimes of major western forests and some examples of plant association groups in each type

Dominant fire type(s)	*General forest type*	*Common plant association groups*
High severity	Coastal temperate forests	Sitka spruce, western hemlock, western red cedar, Douglas-fir
	Coastal subalpine forests	Mountain hemlock, Pacific silver fir
	Pinyon pine–juniper woodlands	Colorado pinyon, singleleaf pinyon, Utah juniper, western juniper
	Interior Northwest montane forests	White pine, western red cedar, western hemlock
	Interior subalpine forests	Engelmann spruce–subalpine fir, lodgepole pine, bristlecone pine, limber pine, whitebark pine, quaking aspen
Mixed severity	Coastal oak woodlands	
	Rocky Mountain ponderosa pine–Douglas-fir forests	Ponderosa pine, Douglas-fir, western larch
	Interior mesic mixed conifer forests	Douglas-fir, white fir, aspen
	Klamath–Siskiyou mixed evergreen forests	
	Sierra Nevada red fir forests	Shasta red fir
	Sierra Nevada giant sequoia forests	Giant sequoia
Low severity	Dry ponderosa pine forests	Ponderosa pine, Jeffrey pine
	Dry mixed conifer forests	Ponderosa pine, Douglas-fir, dry grand fir

Sources: Agee 1993, 1998; Arno 2000

whereas active fire exclusion, especially in remote forests, began only decades ago. Because fuel structures or tree densities are usually within the historical range of variability, active restoration is ecologically inappropriate in these forests. (3) Restoration of dry ponderosa pine and dry mixed-conifer forests – where low severity fires were historically most common – is ecologically appropriate on many sites. Active (eg mechanical thinning of small stems, prescribed fire) or passive (eg wildland fire use, livestock removal) management can restore stand densities to the levels that existed prior to fire exclusion, livestock grazing, logging, and plantation establishment. Retention of old live trees, large snags, and large logs in restoration treatments is critical. Also, restoring other key components of these ecosystems, such as native understory plants, is essential for full recovery of natural conditions, including the characteristic fire regime. (4) Scientific understanding of mixed severity fire regimes is limited, making it difficult to provide defensible guidelines for restoration. These are often complex landscape mosaics; it is therefore necessary to plan and conduct activities at large spatial scales. Where sufficient ecological and fire-history information is available, a combination of thinning and prescribed fire may be useful in restoration. Nevertheless, only portions of these landscapes may warrant treatment. (5) Restoration plans should systematically incorporate fire to maintain restored forests. Forests are dynamic; therefore, any restoration program must provide for sustained fire management to maintain the desired condition. Low-maintenance forests, which can often be achieved through managed natural fire, are an appropriate restoration goal in many cases; where this is not possible, prescribed fire should mimic the characteristic fire regime as closely as possible. Because fire regimes vary tremendously on a regional scale, managers should allow for a range of fire severities. (6) Species closely associated with late- or early-successional conditions in fire-prone landscapes need special management consideration. For example, managed forests are often fragmented by periodic logging and road-building, or consist only of stands of trees too small or too open to meet the needs of late-successional dependent species, such as the spotted owl (*Strix occidentalis*).

Forest management during wildfire

Fire management policies focus on responses to wildfire, including such basic decisions as whether to suppress it. A generalized policy of fire suppression is inappropriate given the documented negative ecological impacts of fire suppression during the 20th century. Responses to fire must take into consideration many ecological and social factors, beginning with the nature of the forest type and societal goals.

Our findings indicate that allowing fires to serve their natural role is ecologically beneficial. Although fire must be managed when close to human infrastructure, in many wilderness areas, national parks, and large areas of public land there is opportunity to increase the use of wildland fire. Such management benefits species that require the shifting mosaics of post-fire habitats found in natural landscapes (Smucker *et al.* 2005). Furthermore, fire suppression may be ecologically warranted in some cases, particularly where special values are at risk. For example, it may be appropriate where habitat of critically imperiled species could be lost, where uncharacteristic fuel accumu-

© The Ecological Society of America

lations have created the potential for a fire outside the historical range of variability, or where high severity fires are not now viewed as ecologically desirable (eg old-growth forests in the Pacific Northwest). Finally, ecologists should be included on fire management teams to ensure that decisions consider the ecological costs and benefits of management actions.



Figure 3. *A restored ponderosa pine stand, Grand Canyon National Park (North Rim).*

Forest management after wildfire

Forest landscapes that have been affected by a major natural disturbance, such as a severe wildfire or wind storm, are commonly viewed as devastated. Such perspectives are usually far from ecological reality. Overall species diversity, measured as number of species – at least of higher plants and vertebrates – is often highest following a natural stand-replacement disturbance and before redevelopment of closed-canopy forest (Lindenmayer and Franklin 2002). Important reasons for this include an abundance of biological legacies, such as living organisms and dead tree structures, the migration and establishment of additional organisms adapted to the disturbed, early-successional environment, availability of nutrients, and temporary release of other plants from dominance by trees. Currently, early-successional forests (naturally disturbed areas with a full array of legacies, ie not subject to post-fire logging) and forests experiencing natural regeneration (ie not seeded or planted), are among the most scarce habitat conditions in many regions.

Our key findings on post-fire management are as follows. First, post-burn landscapes have substantial capacity for natural recovery. Re-establishment of forest following stand-replacement fire occurs at widely varying rates; this allows ecologically critical, early-successional habitat to persist for various periods of time. Second, post-fire (salvage) logging does not contribute to ecological recovery; rather, it negatively affects recovery processes, with the intensity of impacts depending upon the nature of the logging activity (Lindenmayer *et al.* 2004). Post-fire logging in naturally disturbed forest landscapes generally has no direct ecological benefits and many potential negative impacts (Beschta *et al.* 2004; Donato *et al.* 2006; Lindenmayer and Noss 2006). Trees that survive fire for even a short time are critical as seed sources and as habitat that sustains biodiversity both above- and belowground. Dead wood, including large snags and logs, rivals live trees in ecological importance. Removal of structural legacies, both living and dead, is inconsistent with scientific understanding of natural disturbance regimes and short- and long-term regeneration processes. Third, in forests subjected to severe fire and post-fire logging, streams and other aquatic ecosystems will take longer to return to historical conditions or may switch to a different (and often less desirable) state altogether (Karr *et al.* 2004). Following a severe fire, the biggest impacts on aquatic ecosystems are often excessive sedimentation, caused by runoff from roads, which may continue for years. Fourth, post-fire seeding of non-native plants is often ineffective at reducing soil erosion and generally damages natural ecological values, for example by reducing tree regeneration and the recovery of native plant cover and biodiversity (Beyers 2004). Non-native plants typically compete

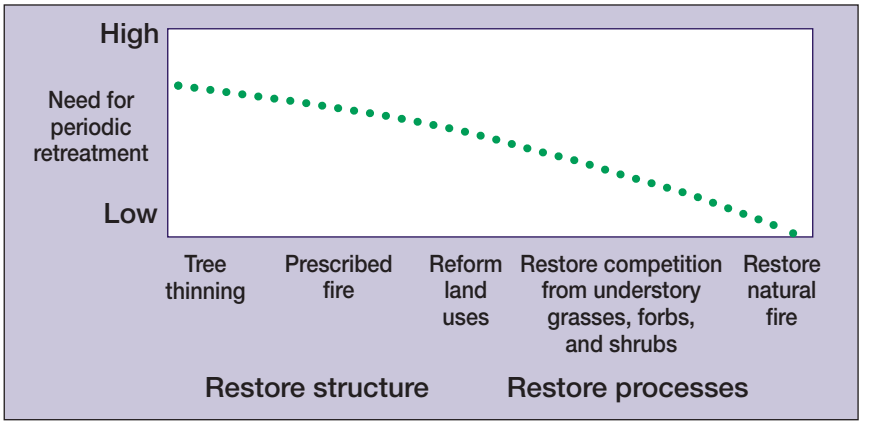


Figure 4. *Forest restoration varies along a continuum from restoring structure (which requires periodic retreatment) to restoring potentially self-sustaining processes.*

© The Ecological Society of America

with native species, reducing both native plant diversity and cover (Keeley *et al.* 2006). Fifth, the ecological importance of biological legacies and of uncommon, structurally complex early-successional stands argues against actions to achieve rapid and complete reforestation. Re-establishing fully stocked stands on sites characterized by low severity fire may actually increase the severity of fire because of fuel loadings outside the historical range of variability. Finally, species dependent on habitat conditions created by high severity fire, with abundant standing dead trees, require substantial areas to be protected from post-fire logging (Hutto 1995).

More ecological science is needed in fire management

Despite the complexity of fire ecology in western forests and uncertainty over the effects of particular management actions, the scientific basis for rational decision-making about fire has improved dramatically in recent years. It is time to systematically incorporate principles of ecological science and existing knowledge of individual forest ecosystems into forest fire and fuel policies.

One barrier to better use of ecological science is that individuals involved in developing fire policies and practices have tended to be specialists in fire and fuel management, not ecologists, conservation biologists, or other broadly trained scientists. It is not surprising, therefore, that current forest law does not adequately incorporate ecological considerations in its implementation and tends to promote a narrow definition of restoration that focuses almost exclusively on fuels (DellaSala *et al.* 2004; Schoennagel *et al.* 2004).

True ecological restoration requires the maintenance of ecological processes, native species composition, and forest structure at both stand and landscape scales. Because forests are highly variable over space and time, few universal principles exist for integrating insights from ecology and conservation biology into fire management policies. Nevertheless, one fundamental principle is that managed forests should not only support the desired fire regime but also viable populations of native species in functional networks of habitat (Hessberg *et al.* 2005). A common-sense conservation goal is to achieve forests that are low maintenance and require minimal repeated treatment. With time, in a landscape of sufficient size, the right end of the restoration continuum (Figure 4) could be reached, where natural fire maintains the system in the desired state. Indeed, wildland fire use is the cheapest and most ecologically appropriate policy for many forests. We envision a future where fire is seen by land managers and the public as the key to healthy forests, but where each forest and each patch of the forest mosaic is recognized for its individuality and managed accordingly. Above all, a guiding principle of forest management should be a precautionary approach that avoids ecological harm.

Acknowledgements

We thank the North American Section of the Society for Conservation Biology for sponsoring this project, with funding from the Wilburforce Foundation and 444 S Foundation.

References

Agee JK. 1993. Fire ecology of Pacific Northwest forests. Washington, DC: Island Press.

Agee JK. 1998. The landscape ecology of western forest fire regimes. *Northwest Sci* **72**: 24–34.

Allen CD, Savage M, Falk D, *et al.* 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol Appl* **12**: 1418–33.

Arno SF. 2000. Fire in western forest ecosystems. In: Brown JK and Smith JK (Eds). Wildland fire in ecosystems. Fort Collins, CO: Rocky Mountain Research Station. USDA Forest Service General Technical Report RMRS-GTR-42 – volume 2.

Belsky A and Blumenthal D. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. *Conserv Biol* **11**: 315–27.

Beyers JL. 2004. Post-fire seeding for erosion control: effectiveness and impacts on native plant communities. *Conserv Biol* **18**: 947–56.

Beschta R, Rhodes J, Kauffman J, *et al.* 2004. Postfire management of forested public lands of the western United States. *Conserv Biol* **18**: 957–67.

Brown PM, Kaufmann MR, and Shepperd WD. 1999. Long-term landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecol* **14**: 513–32.

Brown RT, Agee JK, and Franklin JF. 2004. Forest restoration and fire: principles in the context of place. *Conserv Biol* **18**: 903–12.

Covington WW and Moore MM. 1994. Southwestern ponderosa pine forest structure and resource conditions: changes since Euro-American settlement. *J Forest* **92**: 39–47.

Covington WW, Fule PZ, Moore MM, *et al.* 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. *J Forest* **95**: 23–29.

DellaSala DA, Williams JE, Williams CD, and Franklin JF. 2004. Beyond smoke and mirrors: a synthesis of fire policy and science. *Conserv Biol* **18**: 976–86.

Dombeck MP, Williams JE, and Wood CA. 2004. Wildfire policy and public lands: integrating scientific understanding with social concerns across landscapes. *Conserv Biol* **18**: 883–89.

Donato DC, Fontaine JB, Campbell JL, *et al.* 2006. Post-wildfire logging hinders regeneration and increases fire risk. *Science* **311**: 352.

Ehle DS and Baker WH. 2003. Disturbance and stand dynamics in ponderosa pine forests in Rocky Mountain National Park, USA. *Ecol Monogr* **73**: 543–66.

Gedalof Z, Peterson DL, and Mantua NJ. 2005. Atmospheric, climatic and ecological controls on extreme wildfire years in the northwestern United States. *Ecol Appl* **15**: 154–74.

Habeck JR and Mutch RW. 1973. Fire-dependent forests in the northern Rocky Mountains. *J Quaternary Res* **3**: 408–24.

Hemstrom MA and Franklin JF. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. *J Quaternary Res* **18**: 32–51.

Hessberg PF, Agee JK, and Franklin JF. 2005. Dry forests and wildland fires of the inland northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. *Forest Ecol Manage* **211**: 117–39.

Heyerdahl EK, Brubaker LB, and Agee JK. 2001. Spatial controls of historical fire regimes: a multiscale example from the interior west, USA. *Ecology* **82**: 660–78.

Hutto RL. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (USA)

 © The Ecological Society of America

conifer forests. *Conserv Biol* **9**: 1041–58.
Karr JR, Rhodes JJ, Minshall GW, *et al*. 2004. The effects of postfire salvage logging on aquatic ecosystems in the American west. *BioScience* **54**: 1029–33.
Kaufmann MR, Regan CM, and Brown PM. 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. *Can J Forest Res* **30**: 698–711.
Keeley JE, Allen CD, Betancourt J, *et al*. 2006. A 21st century perspective on postfire seeding. *J Forest* **104**: 103–04.
Kipfmueller KF and Baker WL. 2000. A fire history of a subalpine forest in south-eastern Wyoming, USA. *J Biogeogr* **27**: 71–85.
Lindenmayer DB, Foster DR, Franklin JF, *et al*. 2004. Saving forests or saving fiber? Salvage harvesting policies after natural disturbance impairs ecosystem and species recovery. *Science* **303**: 1303.
Lindenmayer DB and Franklin JF. 2002. Conserving forest biodiversity. Washington, DC: Island Press.
Lindenmayer DB and Noss RF. 2006. Salvage logging, ecosystem processes, and biodiversity conservation *Conserv Biol* **20**: 949–58.
McKenzie D, Gedalof Z, Peterson DL, and Mote P. 2004. Climatic change, wildfire, and conservation. *Conserv Biol* **18**: 890–902.
Millar CI. 1998. Early evolution of pines. In: Richardson DM (Ed). Ecology and biogeography of *Pinus*. Cambridge, UK: Cambridge University Press.
Noss RF (Ed). 2000. The redwood forest. Washington, DC: Island Press.
Noss RF, Beier P, Covington WW, *et al*. 2006b. Integrating restoration ecology and conservation biology: a case study from ponderosa pine forests of the southwestern USA. *Restor Ecol* **14**: 4–10.
Noss RF, Franklin JF, Baker WL, *et al*. 2006a. Ecology and management of fire-prone forests of the western United States. Society for Conservation Biology, North American Section. www.conbio.org/sections/namerica/napolicy.cfm. Viewed 21 Aug 2006.
Odion D, Frost E, Strittholt J, *et al*. 2004. Patterns of fire severity and forest conditions in the western Klamath Mountains, California. *Conserv Biol* **18**: 927–36.
Pierce JL, Meyer GA, and Jull AJT. 2004. Fire-induced erosion and millennial-scale climate change in northern ponderosa pine forests. *Nature* **432**: 87–90.
Romme WH and Despain DG. 1989. Historical perspective on the Yellowstone fires of 1988. *BioScience* **39**: 695–99.
Rummell RS. 1951. Some effects of livestock grazing on ponderosa pine forest and range in central Washington. *Ecology* **32**: 594–607.
Savage M and Swetnam T. 1990. Early nineteenth-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology* **71**: 2374–78.
Schoennagel T, Veblen TT, and Romme WH. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience* **54**: 661–76.
Shinneman DJ and Baker WL. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. *Conserv Biol* **11**: 1276–88.
Skinner C. 1995. Change in spatial characteristics of forest openings in the Klamath Mountains of northwestern California, USA. *Landscape Ecol* **10**: 219–28.
Smucker KM, Hutto RL, and Steele BM. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecol Appl* **15**: 1535–49.
Spies TA, Hemstrom MA, Youngblood A, and Hummel S. 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. *Conserv Biol* **20**: 351–62.
Stephens S and Collins B. 2004. Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. *Northwest Sci* **78**: 12–23.
Taylor AH and Skinner CN. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecol Appl* **13**: 704–19.
Turner MG, Romme WH, and Tinker DB. 2003. Surprises and lessons from the 1988 Yellowstone fires. *Front Ecol Environ* **1**: 351–58.
Veblen TT, Kitzberger T, and Donnegan J. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecol Appl* **10**: 1178–95.
Wallace LL (Ed). 2004. After the fires: the ecology of change in Yellowstone National Park. New Haven, CT: Yale University Press.
Westerling A, Gershunov A, Brown T, *et al*. 2003. Climate and wildfire in the western United States. *B Am Meteorol Soc* **84**: 595–604.

© The Ecological Society of America

esa

ECOSPHERE

Wildland fire deficit and surplus in the western United States, 1984–2012

SEAN A. PARKS,[1,]† CAROL MILLER,[1] MARC-ANDRÉ PARISIEN,[2] LISA M. HOLSINGER,[1] SOLOMON Z. DOBROWSKI,[3] AND JOHN ABATZOGLOU[4]

[1]*Aldo Leopold Wilderness Research Institute, Rocky Mountain Research Station, USDA Forest Service, Missoula, Montana 59801 USA*
[2]*Northern Forestry Centre, Canadian Forest Service, Natural Resources Canada, Edmonton, Alberta T5H 3S5 Canada*
[3]*Department of Forest Management, College of Forestry and Conservation, University of Montana, Missoula, Montana 59812 USA*
[4]*Department of Geography, University of Idaho, Moscow, Idaho 83844 USA*

Citation: Parks, S. A., C. Miller, M.-A. Parisien, L. M. Holsinger, S. Z. Dobrowski, and J. Abatzoglou. 2015. Wildland fire deficit and surplus in the western United States, 1984–2012. Ecosphere 6(12):275. http://dx.doi.org/10.1890/ES15-00294.1

Abstract. Wildland fire is an important disturbance agent in the western US and globally. However, the natural role of fire has been disrupted in many regions due to the influence of human activities, which have the potential to either exclude or promote fire, resulting in a "fire deficit" or "fire surplus", respectively. In this study, we developed a model of expected area burned for the western US as a function of climate from 1984 to 2012. We then quantified departures from expected area burned to identify geographic regions with fire deficit or surplus. We developed our model of area burned as a function of several climatic variables from reference areas with low human influence; the relationship between climate and fire is strong in these areas. We then quantified the degree of fire deficit or surplus for all areas of the western US as the difference between expected (as predicted with the model) and observed area burned from 1984 to 2012. Results indicate that many forested areas in the western US experienced a fire deficit from 1984 to 2012, likely due to fire exclusion by human activities. We also found that large expanses of non-forested regions experienced a fire surplus, presumably due to introduced annual grasses and the prevalence of anthropogenic ignitions. The heterogeneity in patterns of fire deficit and surplus among ecoregions emphasizes fundamentally different ecosystem sensitivities to human influences and suggests that large-scale adaptation and mitigation strategies will be necessary in order to restore and maintain resilient, healthy, and naturally functioning ecosystems.

Key words: climate; fire deficit; fire departure; fire exclusion; fire occurrence; fire suppression; fire surplus; invasive species; protected areas; wilderness; wildland fire.

Received 20 May 2015; revised 29 July 2015; accepted 10 August 2015; **published** 15 December 2015. Corresponding Editor: F. Biondi.

Copyright: © 2015 Parks et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. http://creativecommons.org/licenses/by/3.0/

† **E-mail:** sean_parks@fs.fed.us

INTRODUCTION

The arrival of Euro-American settlers in the late-1800s disrupted the natural ecological role of fire in the western US (Keane et al. 2002), thereby resulting in departures in fire activity compared to earlier periods (Safford and Van de Water 2014). These departures in fire activity have been directly linked to a decoupling of the relationship between climate and fire, which, prior to Euro-American settlement, was fairly strong (Marlon et al. 2012). Consequently, many fire-prone ecosystems in the western US have experienced a reduction in fire activity since Euro-American

settlement compared to earlier periods (e.g., Mallek et al. 2013). Such decreases in fire activity have been attributed to human activities such as fire suppression, livestock grazing, logging, land-type conversion (e.g., to agriculture), and other anthropogenic influences (e.g., roads; Savage and Swetnam 1990, Heyerdahl et al. 2001, Allen et al. 2002, Marlon et al. 2008). Conversely, *increases* in fire activity have also been documented in certain ecosystems or localized areas due to factors such as invasive species that facilitate fire ignition and spread as well as high rates of human-caused ignitions (D'Antonio and Vitousek 1992, Syphard et al. 2007, Balch et al. 2013). Although many of these studies definitively demonstrated that fire activity today is much different in the western US compared to historical conditions (e.g., pre Euro-American settlement), some have questioned the relevance of a past time period in defining reference conditions given that contemporary climate change is altering the biophysical environment (Harris et al. 2006).

At broad spatial scales, climate clearly influences fire activity, although the temporal resolution of analysis can result in different interpretations (Parisien et al. 2014). For example, fire activity has been shown to strongly correlate with climatic normals (e.g., 30 year averages; hereafter "climate;" Krawchuk et al. 2009, Parisien et al. 2011, Moritz et al. 2012). This is likely an indirect influence on fuel conditions via climate's effect on productivity, moisture, and dominant vegetation type (Krawchuk and Moritz 2011, Pausas and Ribeiro 2013, Parks et al. 2014). This climatic effect is in contrast to inter-annual *climatic variability* that also influences fire activity, whereby warm and dry years generally correspond to increased fire activity (Westerling et al. 2006, Heyerdahl et al. 2008, Littell et al. 2009). We suggest that, because climate (i.e., climatic normals) is a strong top-down control on fire activity (although it may be an indirect control), a natural level of fire activity can be defined as that which emerges from the climate. As such, the "expected" amount of fire can be statistically modeled as a function of climate. Indeed, this rationale is often invoked in studies evaluating the effect of climate change on future fire activity (Krawchuk et al. 2009, Moritz et al. 2012, Batllori et al. 2013). This rationale also allows for an evaluation of contemporary departures in fire activity by comparing the expected and observed area burned. Where observed fire activity is less than expected, the result is a "fire deficit" because there is less fire than the climate dictates (Marlon et al. 2012). Where observed fire activity is greater than expected, the result is a "fire surplus."

Because ecosystems with disrupted fire regimes are thought to be less resilient to environmental change (Millar et al. 2007), land managers often cite the need to restore wildland fire as a natural disturbance (NWCG 2001). To accomplish this, land managers need to better understand current departures from natural levels of fire activity, especially considering that restoring wildland fire necessitates that our communities learn to co-exist with fire (Moritz et al. 2014). However, quantifying natural levels of fire activity is challenging for two reasons. First, as climate changes, the natural level of fire activity is a moving target. Second, human activities continue to alter fire regimes (as previously described). Fortunately, protected areas and other lands with little anthropogenic impact can provide a benchmark for quantifying natural levels of fire activity as a function of climate. For example, Parks et al. (2014) found that the relationship between climate and fire activity was reasonably strong in the western US when models were built using samples primarily comprised of protected areas; the relationship was weak when models were built using samples irrespective of the protected area composition (Appendix A). Archibald et al. (2010) had a similar finding in their study of fire and climate variability in southern Africa. A comparison of expected (according to the natural benchmark) to observed fire activity then allows for a formal evaluation of fire deficit and surplus for lands of all management designations.

We sought to quantify departures from contemporary natural levels of expected fire activity and identify areas of fire deficit and surplus in the western US for the 1984–2012 time period. This was achieved by developing a boosted regression tree (BRT) model to predict area burned as a function of several climatic variables for 500 km^2 hexagonal polygons (hereafter "hexels"). The model was built using fire and climate data from a subset of hexels in the western US having substantial area in a protected

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

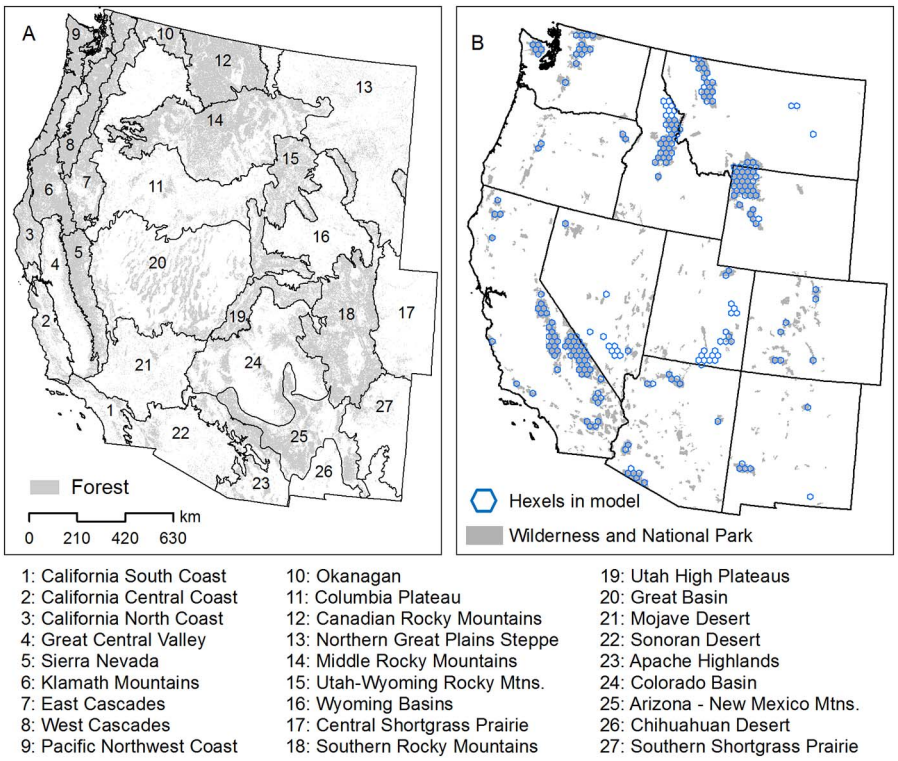


Fig. 1. Study area of the western US for which we quantify departures in expected area burned. Map showing forested areas and ecoregion boundaries (A) and showing designated wilderness areas and national parks as well as the hexels we used to build the model of area burned (B).

status (e.g., wilderness and parks) or otherwise having a low anthropogenic influence. These hexels serve as a natural benchmark (e.g., Appendix A) and are representative of a broad gradient in climate (Appendix B) and include ecosystems such as desert, dry conifer forest, and cold conifer forest. We then quantified the degree of fire deficit or surplus as the difference between expected (as predicted with the BRT model) and observed area burned from 1984 to 2012 for all hexels in the western US and provided ecoregional summaries. Our study is relevant to the contemporary time period (i.e., 1984–2012) and does not reflect prior time periods in which the climate was different or indigenous burning was common.

Methods

We quantified departures in expected area burned from 1984 to 2012 for each 500 km^2 hexagonal polygon (i.e., "hexels") in the western US (Fig. 1). We chose this hexel size based on previous work (Parks et al. 2014), although we acknowledge that the resolution of analysis may influence the relationship between fire and its environment (Parisien et al. 2011, Parks et al. 2011). We built a model of area burned as a function of climate and then used model results to quantify fire departures.

We selected a subset of hexels with low human influence to build the model because the relationship between climate and fire is reasonably strong in areas of low human impact but weakens as anthropogenic influences increase (Archibald et al. 2009, Parks et al. 2014; Appendix A). Consequently, areas of low human impact act as "controls" and therefore characterize the expected relationship between fire and climate were human activities not an overarching influence. We selected hexels comprised of at least 75% designated wilderness and national park or had an average "human footprint" (HFP; Leu et al. 2008) $\leq$1.5 (on a scale of 1–10). We also

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 1. Climatic variables evaluated as independent variables in the statistical model describing area burned. Only those that had a correlation coefficient <0.9 (bold) to each other were included in the final model ($n = 5$). The coefficient of variation (among years) of the five selected variables were also included in the statistical model for a total of 10 variables. These variables represent climatic conditions from 1984 to 2012.

Variable abbreviation	Description	Units
AET	Actual evapotranspiration (annual average)	mm/year
DMC†	Duff moisture code (annual average)	dimensionless
ERC‡	Energy release component (annual average)	dimensionless
PRECIP	Precipitation (annual average)	mm/year
SWE	Snow water equivalent (monthly average)	mm/month
SMO	Soil moisture (monthly average)	mm/month
TEMP	Temperature (annual average)	°C
VPD	Vapor pressure deficit (monthly average)	kPa
WD	Water deficit (annual average)	mm/year

† ERC is a fire danger index in the National Fire Danger Rating System (NFDRS; Cohen and Deeming 1985).
‡ DMC is a fire danger index in the Canadian Forest Fire Danger Rating System (CFFDRS; van Wagner 1987).

excluded hexels with more than 50% nonfuel (e.g., open water and barren). These selection criteria resulted in 235 hexels for which we built the model of area burned (Fig. 1). Despite representing only a small proportion of the western US (~4%), the hexels span broad climatic gradients ranging from warm deserts to cold forests (Appendix B). Although human-ignited fires may blur the relationship between climate and fire, only about 8% of the area burned from this subset of hexels was due to such fires (for the years 1992–2012; Short 2014).

Area burned (ha) was calculated within each hexel using a fire atlas covering all fires ≥400 ha from 1984 to 2012 (Eidenshink et al. 2007). Area burned was adjusted to account for unburnable areas (e.g., open water) within each hexel by dividing area burned by the proportion of the hexel that was composed of burnable fuel types (Rollins 2009). Several climatic variables known to influence fire activity were evaluated for inclusion into the model as independent variables (e.g., Littell and Gwozdz 2011, Abatzoglou and Kolden 2013, Parks et al. 2014; Table 1). Gridded monthly temperature and precipitation data were obtained from the parameter-elevation regression on independent slopes model (PRISM; Daly et al. 2002) that uses station data and physiographic factors to map climate at a spatial resolution of ~800 m. Abatzoglou (2013) combined monthly data from PRISM and hourly estimates from coarser scale analyses from the North American Land Data Assimilation System Phase 2 (NLDAS-2; Mitchell et al. 2004) to produce daily and sub-daily surface meteorological variables at a ~4-km resolution that captures temperature, humidity, winds, solar radiation, and precipitation, which were subsequently used to estimate the energy release component (ERC; Cohen and Deeming 1985), duff moisture code (DMC; van Wagner 1987), and reference evapotranspiration. These data were collectively used to run the climatic water balance model following Dobrowski et al. (2013) to estimate monthly actual evapotranspiration (AET), snow water equivalent (SWE), soil moisture (SMO), and water deficit (WD). This model operates on a monthly time-step and accounts for atmospheric demand (via the Penman-Monteith equation), soil water storage, and includes the effect of temperature and radiation on snow hydrology via a snow melt model. All variables were characterized by averaging or summing monthly values over each year, then averaging the values over 1984–2012, and finally, averaging within each hexel. Those variables with a correlation coefficient of ≥0.9 (for the 235 hexels used to build the model) were excluded from the model (Table 1). For the five variables that met this correlation criterion, we also included in the model variables representing inter-annual variability (coefficient of variation).

We built our model of area burned as a function of climate using boosted regression trees (BRT) within the R statistical program (R Development Core Team 2007; "gbm" package). BRT is a machine-learning approach that does not require a priori model specification (De'ath 2007). We square-root-transformed area burned to homogenize variance in model residuals and

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

used a Poisson distribution. We followed the recommendations of Elith et al. (2008) for selecting BRT options; we set the bagging fraction to 0.5, learning rate to 0.0025, and tree complexity to 5. We used a custom script from Elith et al. (2008) to determine the necessary number of trees, thereby reducing the potential for overfitting the model. We evaluated model fit using 10-fold cross-validated correlation between predicted and observed values of area burned.

We quantified departures in expected area burned for each hexel in the western US by subtracting predicted from observed area burned for the 1984–2012 time period; negative values indicate less area burned than expected (i.e., a fire deficit), and positive values indicate more area burned (i.e., a fire surplus). We "clamped" predicted area burned to the maximum value in the training hexels to avoid predicting outside of the observed range of area burned. We summarized deficits and surpluses, as well as the expected and observed fire rotation, for each ecoregion (Olsen and Dinerstein 2002; Fig. 1); results for ecoregions with minimal overlap with the study area are not shown (e.g., Black Hills). Hexels on the edge of study area boundary are omitted from the ecoregional summaries if $>50\%$ of its area overlaps with the ocean, Mexico, Canada, or areas east of the study area. Hexels are defined as unburnable if $\geq 50\%$ is characterized as irrigated agriculture, barren, urban, or water (Rollins 2009) and are excluded from the ecoregional summaries.

Results

The BRT performed well; the cross-validated correlation between predicted and observed area burned was 0.80 (see Appendix C for variable importance and response curves for selected variables). Departures from expected area burned from 1984 to 2012 were spatially heterogeneous across the western US (Fig. 2). Some ecoregions exhibited large fire deficits (e.g., California North Coast and Apache Highlands), others a fire surplus (e.g., California South Coast and Columbia Plateau), and others no substantial departure (e.g., West Cascades and Sonoran Desert; Fig. 2, Table 2). Most forested ecoregions experienced a fire deficit, with the notable exception of mesic forested ecoregions in the Pacific Northwest, which showed no substantial departure from expected area burned. Large geographic expanses of fire surplus were apparent in some non-forested regions (e.g., the southern Columbia Plateau and northern Great Basin), although a fire deficit was observed in two non-forested ecoregions (i.e., Central Shortgrass Prairie and Southern Shortgrass Prairie; Fig. 2, Table 2).

Discussion

Our results reveal a striking pattern of departures from expected area burned across the western US from 1984 to 2012. We found that fire deficits were more prevalent in forested ecoregions compared to non-forested ecoregions. In several non-forested ecoregions, large expanses of fire surplus were evident. The contrasting patterns of fire deficit and surplus between forested and non-forested ecoregions emphasize fundamentally different ecosystem sensitivities to human influences. However, there were also large expanses that experienced no substantial departure from expected area burned. Such areas generally corresponded to two types of ecosystems that typically experience little fire: very dry ecosystems that are biomass limited (i.e., warm and cold deserts that have not been invaded by annual grasses) and wet ecosystems (temperate rainforest) that are rarely conducive to burning (Krawchuk and Moritz 2011, Parks et al. 2014).

Most forested areas in the western US experienced a fire deficit from 1984 to 2012. These deficits strongly support the widespread notion that fire activity is reduced by human activities that exclude fire. Although our findings are only relevant to climate and fire over the 1984–2012 time period, they corroborate the findings of Marlon et al. (2012) and multiple fire history studies that indicated a sharp reduction in fire activity since the arrival of Euro-Americans, e.g., in the Sierra Nevada (Taylor 2000, Beaty and Taylor 2008), Klamath Mountains (Taylor and Skinner 2003), California North Coast (Stuart and Salazar 2000), East Cascades (Wright and Agee 2004), Southern Rocky Mountains (Grissino-Mayer et al. 2004), Middle Rocky Mountains (Heyerdahl et al. 2001), Canadian Rocky Mountains (Power et al. 2006), Utah High Plateaus (Stein 1988, Brown et al. 2008), Apache High-

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

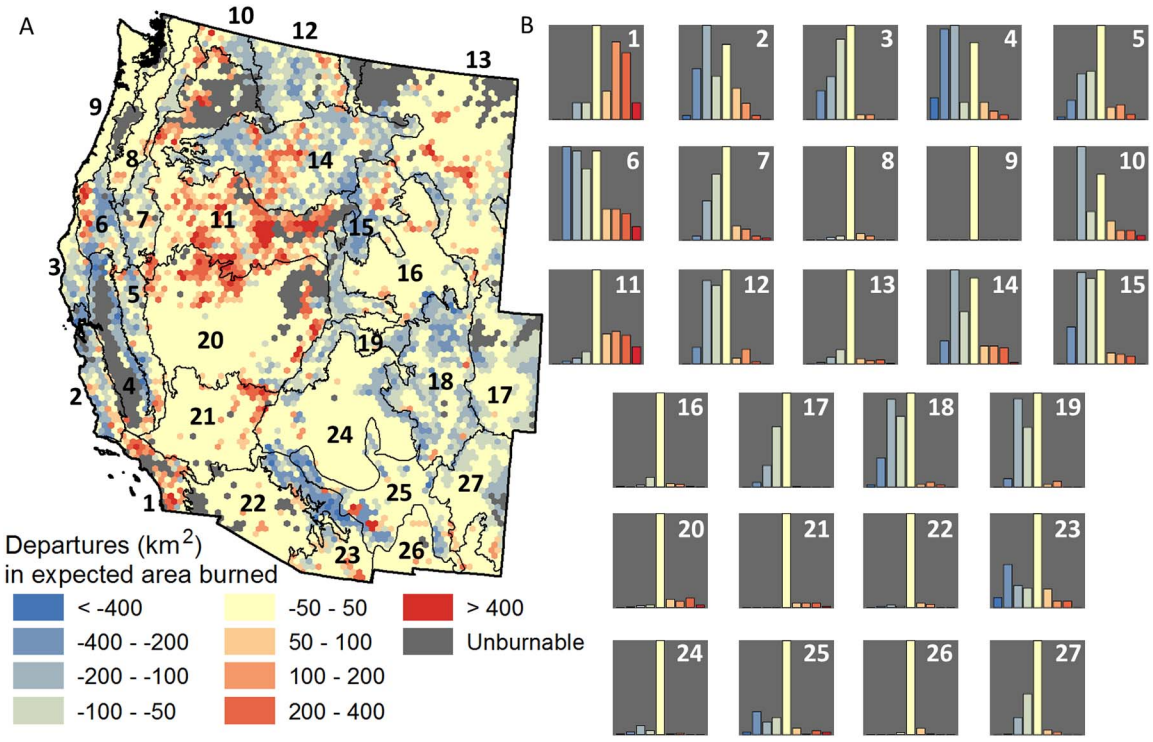


Fig. 2. Map depicting departures in expected area burned from 1984 to 2012 (A). Blue hexels represent less fire than expected (i.e., a fire deficit); red hexels represent more than expected (i.e., a fire surplus); yellow hexels indicate no substantial departure; dark gray hexels are unburnable. Histograms of each ecoregion (B) correspond to fire departure categories shown in the map legend (A).

lands (Baisan and Swetnam 1990), and Arizona-New Mexico Mountains (Swetnam and Dieterich 1985). Decreased fire activity has resulted in substantial changes to some forested ecosystems. For example, reduced rates of burning have resulted in altered species composition (i.e., increases in shade-tolerant species), increased tree density, and increased landscape homogeneity (Taylor 2000, Naficy et al. 2010, Fry et al. 2014, Stephens et al. 2015). A major concern of these site- and landscape-level ecosystem changes is the increased likelihood of uncharacteristically large and severe wildland fire in future years (Hessburg et al. 2005, Stephens 2005, Calkin et al. 2015). Although such fires may contribute to a reduction in the fire deficit, the uncharacteristic manner in which they burn can exceed ecological thresholds and result in conversion to non-forest types (Savage and Mast 2005). A few forested areas did not experience a fire deficit (i.e., Pacific Northwest Coast and West Cascades ecoregions), which is coherent with our knowledge of the fire regime characteristics of these regions where fires are infrequent (fire return intervals of 200–1000 years; Agee 1993).

The pattern of fire surpluses and deficits in non-forested ecoregions is consistent with our knowledge of the impact of human activities on area burned. For example, in the Columbia Plateau and Great Basin ecoregions, the large expanse of fire surplus is likely the result of cheatgrass invasion (*Bromus tectorum*; Fig. 3; Knapp 1996, Bradley and Mustard 2008), a non-native annual grass that was introduced to North America during the 1800s that is known to increase fire activity (Knick and Rotenberry 1997, Balch et al. 2013). Similarly, the fire surplus in the Mojave Desert ecoregion is likely due to invasion by the annual grass red brome (*Bromus rubens*; Hunter 1991, Salo et al. 2005, Brooks and Matchett 2006), another grass introduced from Europe. In many of these affected areas, there is generally a positive feedback where fire facilitates invasive grass establishment, which in turn

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 2. Ecoregional summary of fire departures in the western US†; values were summed across hexels within each ecoregion.

ID	Ecoregion name	Area (km^2)	Observed area burned (km^2)	Expected area burned (km^2)	Total fire departure (km^2)‡	Expected fire rotation§ (years)	Observed fire rotation§ (years)
1	California South Coast	28376	13256	6268	6987	131	62
2	California Central Coast	39505	7330	14269	−6939	80	156
3	California North Coast	27828	2798	7714	−4916	105	288
4	Great Central Valley	38340	4499	15905	−11406	70	247
5	Sierra Nevada	50000	7121	11793	−4672	123	204
6	Klamath Mountains	50144	10323	15541	−5218	94	141
7	East Cascades	65500	6095	10076	−3981	189	312
8	West Cascades	43000	1774	1992	−217	626	703
9	Pacific Northwest Coast	40177	137	1179	−1042	988	8505
10	Okanagan	24549	3308	5459	−2151	130	215
11	Columbia Plateau	234000	64668	15973	48695	425	105
12	Canadian Rocky Mountains	81230	5957	16871	−10914	140	395
13	Northern Great Plains Steppe	236458	14347	17922	−3575	383	478
14	Middle Rockies	210000	38255	59794	−21539	102	159
15	Utah-Wyoming Rocky Mountains	108500	12393	29836	−17444	105	254
16	Wyoming Basins	132000	3247	5856	−2609	654	1179
17	Central Shortgrass Prairie	108156	650	15094	−14445	208	4825
18	Southern Rocky Mountains	160000	5489	34228	−28739	136	845
19	Utah High Plateaus	45500	2685	9457	−6772	140	491
20	Great Basin	269000	31827	10853	20974	719	245
21	Mojave Desert	128500	8506	475	8031	7845	438
22	Sonoran Desert	101830	3023	2732	291	1081	977
23	Apache Highlands	83987	12359	26610	−14251	92	197
24	Colorado Plateau	197000	3505	12142	−8637	471	1630
25	Arizona-New Mexico Mountains	114572	13491	25820	−12329	129	246
26	Chihuahuan Desert	58407	1347	1221	127	1387	1257
27	Southern Shortgrass Prairie	94031	2761	11402	−8641	239	988

† Hexels are considered unburnable if ≥50% is characterized as irrigated agriculture, barren, urban, or water and are excluded from all calculations.

‡ Negative values indicate a fire deficit and positive values a fire surplus.

§ Fire rotation is defined as the number of years necessary to burn an area the size of the ecoregion and for the 29 year record (1984–2012) is calculated as follows: 29/(expected [or observed] area burned/area of the ecoregion).

increases fire frequency because the invading grass produces a continuous bed of flammable fine fuels (Brooks et al. 2004). Although the Sonoran Desert and Chihuahuan Desert ecoregions exhibited no substantial fire departure from 1984–2012, natural and climate-induced range expansions of invasive annual grasses could put them at risk in the future (Salo 2004, Abatzoglou and Kolden 2011). In addition to the effects from invasive and exotic plant species, the prevalence of human-caused ignitions are implicated in increased fire activity and the associated fire surplus found in the California South Coast ecoregion (Syphard et al. 2007, Keeley et al. 2011, Keeley and Brennan 2012). The fire deficits we found for the Central Shortgrass Prairie and Southern Shortgrass Prairie ecoregions are areas that naturally would support periodic fire, but fire suppression and grazing by domestic cattle has reduced fire activity in these areas (Axelrod 1985, Brockway et al. 2002).

Other studies that also evaluated potential departures in fire activity include Mallek et al. (2013), who used the results of numerous published dendrochronology studies to infer historical annual area burned for several forest types in the Sierra Nevada and made comparisons to contemporary rates of burning. Also, Ager et al. (2014) compared burn probability maps (generated with simulation models) to those of the Landfire "mean fire return interval" product (Rollins 2009) for National Forests in the western US to identify which pixels had higher or lower burn probabilities compared to presumed historical conditions. Similar to our findings, these studies found that contemporary fire activity in forested regions, for the most part, was less than that of the pre-European reference period. However, formal comparisons between our study and these previous studies are not appropriate due to differences in the reference period, spatial resolution, and spatial extent of

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

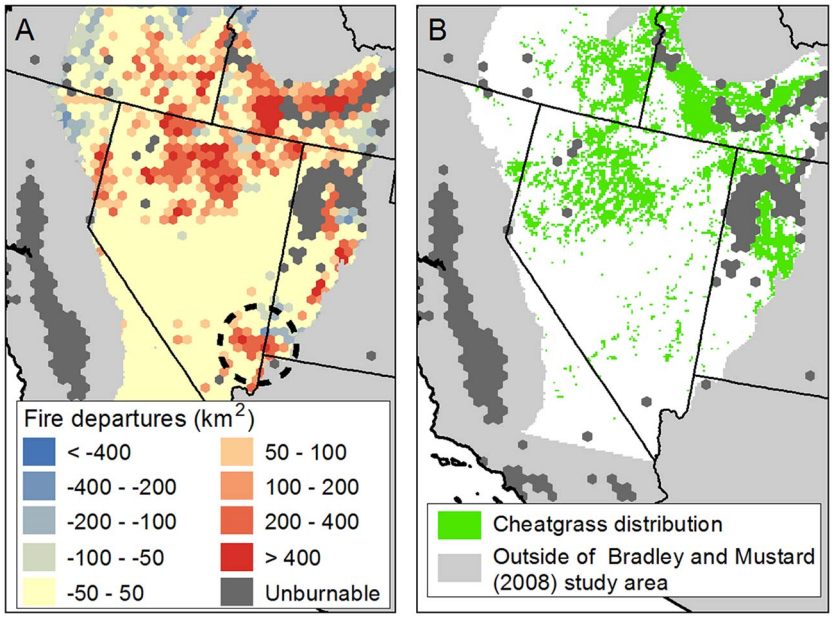


Fig. 3. Departures in expected area burned (km^2) within the Bradley and Mustard (2008) study area (A) and cheatgrass (*Bromus tectorum*) distribution according to Bradley and Mustard (2008) (B). Note the high spatial correspondence between fire surplus and cheatgrass distribution. The large expanse of fire surplus in southeastern Nevada (shown by the dashed circle) is likely due to a different invasive annual grass, red brome (*Bromus rubens*; Salo 2005).

analyses.

Multiple lines of evidence have attributed departures in fire activity between contemporary and historical (i.e., pre-Euro settlement) eras to human activities. Studies using both dendrochronology (i.e., cross-dated fire scar records; e.g., Heyerdahl et al. 2001, Mallek et al. 2013) and charcoal records (e.g., Colombaroli and Gavin 2010) have inferred that humans are at least partly responsible for reductions in rates of burning after about 1900. Our findings suggest that humans continue to influence fire activity today and show how this influence varies among ecosystems. As such, our approach to quantifying departures in fire activity complements earlier research and offers certain advantages. For example, because our model of expected area burned was built from a broad spatial extent, it incorporates all major ecosystems in the western US (e.g., shrub, forest, desert). Specifically, our method is not limited to tree-dominated ecosystems (cf. dendrochronology) or those that have permanent or ephemeral water bodies (cf. charcoal records). Furthermore, because we used contemporary fire and climate data in our study, we defined a contemporary, climatically driven baseline for expected fire activity. As such, in quantifying departures in fire activity, we avoid the use of a past reference period in which climate and indigenous burning practices were quite different (Sheppard et al. 2002, Stephens et al. 2007).

Several factors should be considered when interpreting our results. We assume a space-for-time substitution in calibrating our model; the large sample domain ensures adequate sampling of fires and allows us to infer relationships between fire and climate. Nevertheless, the temporal window of our analysis (1984–2012) is relatively short for many ecosystems (Agee 1993). Consequently, we may not have adequately characterized departures from expected area burned in certain regions, especially in cool/wet forested areas that show an apparent fire surplus only because of large, infrequent fires (sensu Meyn et al. 2007) that have occurred during our study period (e.g., Yellowstone National Park in 1988). For this reason, it is inappropriate to focus

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

on any single hexel or small group of hexels to infer departures in expected fire activity. Instead, it is most appropriate to evaluate fire surplus and deficit over large geographical regions, which explains our rational for providing ecoregional summaries (Fig. 2, Table 2). The temporal window we analyzed (i.e., 1984–2012) also coincides with increased fire activity compared to earlier decades (e.g., 1940–1970; Littell et al. 2009). Consequently, had we analyzed fire and climate data from a different time period, our results would certainly be different. Periodic updates to our model and map are clearly warranted to provide a longer-term perspective on departures in expected fire activity, especially given the heterogeneous nature of fire and that negative feedbacks associated with recurring fires will likely limit future burning in some areas (Héon et al. 2014, Parks et al. 2015). Lastly, our study relies heavily on data from protected areas, which, despite representing the majority of climates in the western US, admittedly do not represent the complete range of climatic conditions (Batllori et al. 2014). Nevertheless, the climatic variability encompassed in the data we used to build the model (Appendix B) translates into a broad range of ecosystem and vegetation types, for example, warm desert (Death Valley National Park [NP]), dry conifer forest (Gila Wilderness), and cold forest (Yellowstone NP). As such, we suggest that poorly represented climates have only a marginal effect on our results.

Conclusions

Previous studies conducted at a variety of temporal and spatial scales identified a sharp drop in fire activity with the arrival of Euro-American settlers in forest-dominated landscapes of the western US (e.g., Marlon et al. 2012, Mallek et al. 2013). Our study makes no comparisons to time periods and climates prior to 1984 but demonstrates that most forested regions continue to experience less fire than expected, or a fire deficit. Our study also demonstrates that some non-forested regions experienced more fire than expected, or a fire surplus, over the 1984–2012 time period. The findings of our study, as well as other efforts such as the Landfire "Vegetation departure" (Rollins 2009) product, suggest that multiple large-scale adaptation and mitigation strategies will be necessary in order to restore and maintain resilient, healthy, and naturally functioning ecosystems (cf. Hessburg et al. 2015). For example, forested areas experiencing a fire deficit may be candidates for restoration treatments (e.g., mechanical fuel treatments, prescribed fire, wildland fire use) intended to promote resilience to future disturbances (Stephens and Ruth 2005, Millar et al. 2007). Conversely, areas experiencing a fire surplus may be indicative of highly altered and degraded ecosystems (Bradley and Mustard 2008, Brooks 2012) that are in need of restoration and ignition management (e.g., fire suppression and prevention). Protected areas and other areas with low anthropogenic influence served as a natural benchmark in which fire activity and climate are relatively tightly linked, and as such, are an invaluable data source for assessing perturbations to fire regimes across multiple ecosystem types.

Acknowledgments

We thank two anonymous reviewers for thoughtful comments that significantly improved this manuscript. We acknowledge National Fire Plan funding from the Rocky Mountain Research Station.

Literature Cited

Abatzoglou, J. T. 2013. Development of gridded surface meteorological data for ecological applications and modelling. International Journal of Climatology 33:121–131.

Abatzoglou, J. T., and C. A. Kolden. 2011. Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. Rangeland Ecology and Management 64:471–478.

Abatzoglou, J. T., and C. A. Kolden. 2013. Relationships between climate and macroscale area burned in the western United States. International Journal of Wildland Fire 22:1003–1020.

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Ager, A. A., M. A. Day, C. W. McHugh, K. Short, J. Gilbertson-Day, M. A. Finney, and D. E. Calkin. 2014. Wildfire exposure and fuel management on western US national forests. Journal of Environmental Management 145:54–70.

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

restoration of Southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications 12:1418–1433.

Archibald, S., A. Nickless, N. Govender, R. J. Scholes, and V. Lehsten. 2010. Climate and the inter-annual variability of fire in southern Africa: a meta-analysis using long-term field data and satellite-derived burnt area data. Global Ecology and Biogeography 19:794–809.

Archibald, S., D. P. Roy, B. W. van Wilgen, and R. J. Scholes. 2009. What limits fire? An examination of drivers of burnt area in Southern Africa. Global Change Biology 15:613–630.

Axelrod, D. I. 1985. Rise of the grassland biome, central North America. Botanical Review 51:163–201.

Baisan, C. H., and T. W. Swetnam. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. Canadian Journal of Forest Research 20:1559–1569.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gomez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). Global Change Biology 19:173–183.

Batllori, E., C. Miller, M.-A. Parisien, S. A. Parks, and M. A. Moritz. 2014. Is U.S. climatic diversity well represented within the existing federal protection network? Ecological Applications 24:1898–1907.

Batllori, E., M. A. Parisien, M. A. Krawchuk, and M. A. Moritz. 2013. Climate change-induced shifts in fire for Mediterranean ecosystems. Global Ecology and Biogeography 22:1118–1129.

Beaty, R. M., and A. H. Taylor. 2008. Fire history and the structure and dynamics of a mixed conifer forest landscape in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. Forest Ecology and Management 255:707–719.

Bradley, B. A., and J. F. Mustard. 2008. Comparison of phenology trends by land cover class: a case study in the Great Basin, USA. Global Change Biology 14:334–346.

Brockway, D. G., R. G. Gatewood, and R. B. Paris. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. Journal of Environmental Management 65:135–152.

Brooks, M. L. 2012. Effects of high fire frequency in creosote bush scrub vegetation of the Mojave Desert. International Journal of Wildland Fire 21:61–68.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. BioScience 54:677–688.

Brooks, M. L., and J. R. Matchett. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980-2004. Journal of Arid Environments 67:148–164.

Brown, P. M., E. K. Heyerdahl, S. G. Kitchen, and M. H. Weber. 2008. Climate effects on historical fires (1630-1900) in Utah. International Journal of Wildland Fire 17:28–39.

Calkin, D. E., M. P. Thompson, and M. A. Finney. 2015. Negative consequences of positive feedbacks in US wildfire management. Forest Ecosystems 2:1–10.

Cohen, J. D., and J. E. Deeming. 1985. The national fire danger rating system: basic equations. GTR-PSW-82. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.

Colombaroli, D., and D. G. Gavin. 2010. Highly episodic fire and erosion regime over the past 2,000 y in the Siskiyou Mountains, Oregon. Proceedings of the National Academy of Sciences USA 107:18909–18914.

Daly, C., W. P. Gibson, G. H. Taylor, G. L. Johnson, and P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research 22:99–113.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

De'ath, G. 2007. Boosted trees for ecological modeling and prediction. Ecology 88:243–251.

Dobrowski, S. Z., J. Abatzoglou, A. K. Swanson, J. A. Greenberg, A. R. Mynsberge, Z. A. Holden, and M. K. Schwartz. 2013. The climate velocity of the contiguous United States during the 20th century. Global Change Biology 19:241–251.

Eidenshink, J., B. Schwind, K. Brewer, Z. L. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology 3:3–21.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77:802–813.

Fry, D. L., S. L. Stephens, B. M. Collins, M. P. North, E. Franco-Vizcaino, and S. J. Gill. 2014. Contrasting spatial patterns in active-fire and fire-suppressed Mediterranean climate old-growth mixed conifer forests. PLoS ONE 9(2):e88985.

Grissino-Mayer, H. D., W. H. Romme, M. L. Floyd, and D. D. Hanna. 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. Ecology 85:1708–1724.

Harris, J. A., R. J. Hobbs, E. Higgs, and J. Aronson. 2006. Ecological restoration and global climate change. Restoration Ecology 14:170–176.

Héon, J., D. Arseneault, and M.-A. Parisien. 2014. Resistance of the boreal forest to high burn rates. Proceedings of the National Academy of Sciences

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

USA 111:13888–13893.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211:117–139.

Hessburg, P. F., et al. 2015. Restoring fire-prone Inland Pacific landscapes: seven core principles. Landscape Ecology 30: 1805–1835.

Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial controls of historical fire regimes: a multi-scale example from the interior west, USA. Ecology 82:660–678.

Heyerdahl, E. K., P. Morgan, and J. P. Riser. 2008. Multi-season climate synchronized historical fires in dry forests (1650-1900), northern Rockies, USA. Ecology 89:705–716.

Hunter, R. 1991. *Bromus* invasions on the Nevada Test Site: present status of *B. rubens* and *B. tectorum* with notes on their relationship to disturbance and altitude. Great Basin Naturalist 51:176–182.

Keane, R. E., K. C. Ryan, T. T. Veblen, C. D. Allen, J. A. Logan, and B. Hawkes. 2002. The cascading effects of fire exclusion in Rocky Mountain ecosystems. Pages 133–521 *in* J. S. Baron, editor. Rocky Mountain futures: an ecological perspective. Island Press, Washington, D.C., USA.

Keeley, J. E., and T. J. Brennan. 2012. Fire-driven alien invasion in a fire-adapted ecosystem. Oecologia 169:1043–1052.

Keeley, J. E., J. Franklin, and C. D'Antonio. 2011. Fire and invasive plants in California Landscapes. Pages 193–222 *in* D. McKenzie, C. Miller, and D. A. Falk, editors. The landscape ecology of fire. Springer, Amsterdam, The Netherlands.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert: history, persistence, and influences to human activities. Global Environmental Change, Human and Policy Dimensions 6:37–52.

Knick, S. T., and J. T. Rotenberry. 1997. Landscape characteristics of disturbed shrubsteppe habitats in southwestern Idaho (USA). Landscape Ecology 12:287–297.

Krawchuk, M. A., and M. A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. Ecology 92:121–132.

Krawchuk, M. A., M. A. Moritz, M.-A. Parisien, J. Van Dorn, and K. Hayhoe. 2009. Global pyrogeography: the current and future distribution of wildfire. PloS ONE 4:e5102.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Littell, J. S., and R. B. Gwozdz. 2011. Climatic water balance in regional fire years in the Pacific Northwest, USA: linking regional climate and fire and at landscape scales. Pages 177–139 *in* D. McKenzie, C. Miller, and D. A. Falk, editors. The landscape ecology of fire. Springer, Amsterdam, The Netherlands.

Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916-2003. Ecological Applications 19:1003–1021.

Mallek, C., H. Safford, J. Viers, and J. Miller. 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. Ecosphere 4:art153.

Marlon, J. R., P. J. Bartlein, C. Carcaillet, D. G. Gavin, S. P. Harrison, P. E. Higuera, F. Joos, M. J. Power, and I. C. Prentice. 2008. Climate and human influences on global biomass burning over the past two millennia. Nature Geoscience 1:697–702.

Marlon, J. R., et al. 2012. Long-term perspective on wildfires in the western USA. Proceedings of the National Academy of Science USA 109:E535–E543.

Meyn, A., P. S. White, C. Buhk, and A. Jentsch. 2007. Environmental drivers of large, infrequent wildfires: the emerging conceptual model. Progress in Physical Geography 31:287–312.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17:2145–2151.

Mitchell, K. E., et al. 2004. The multi-institution North American Land Data Assimilation System (NLDAS): utilizing multiple GCIP products and partners in a continental distributed hydrological modeling system. Journal of Geophysical Research, Atmospheres 109:D07S90.

Moritz, M. A., et al. 2014. Learning to coexist with wildfire. Nature 515:58–66.

Moritz, M. A., M.-A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. Ecosphere 3:art49.

Naficy, C., A. Sala, E. G. Keeling, J. Graham, and T. H. DeLuca. 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. Ecological Applications 20:1851–1864.

NWCG [National Wildfire Coordinating Group]. 2001. Review and update of the 1995 federal wildland fire management policy. National Wildfire Coordinating Group, Interagency Fire Center, Boise, Idaho, USA.

Olsen, D. M., and E. Dinerstein. 2002. The global 200: priority ecoregions for global conservation. Annals of the Missouri Botanical Garden 89(2):199–224.

Parisien, M.-A., S. A. Parks, M. A. Krawchuk, M. D.

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Flannigan, L. M. Bowman, and M. A. Moritz. 2011. Scale-dependent controls on the area burned in the boreal forest of Canada, 1980-2005. Ecological Applications 21:789–805.

Parisien, M.-A., S. A. Parks, M. A. Krawchuk, J. M. Little, M. D. Flannigan, L. M. Gowman, and M. A. Moritz. 2014. An analysis of controls on fire activity in boreal Canada: comparing models built with different temporal resolutions. Ecological Applications 24:1341–1356.

Parks, S. A., L. M. Holsinger, C. Miller, and C. R. Nelson. 2015. Wildland fire as a self-regulating mechanism: the role of previous burns and weather in limiting fire progression. Ecological Applications 25:1478–1492.

Parks, S. A., M.-A. Parisien, and C. Miller. 2011. Multi-scale evaluation of the environmental controls on burn probability in a southern Sierra Nevada landscape. International Journal of Wildland Fire 20:815–828.

Parks, S. A., M.-A. Parisien, C. Miller, and S. Z. Dobrowski. 2014. Fire activity and severity in the western US vary along proxy gradients representing fuel amount and fuel moisture. PLoS ONE 9:e99699.

Pausas, J. G., and E. Ribeiro. 2013. The global fire productivity relationship. Global Ecology and Biogeography 22:728–736.

Power, M. J., C. Whitlock, P. Bartlein, and L. R. Stevens. 2006. Fire and vegetation history during the last 3800 years in northwestern Montana. Geomorphology 75:420–436.

R Development Core Team. 2007. R: a language and environment for statistical computing. R Foundation for Computing, Vienna, Austria.

Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. International Journal of Wildland Fire 18:235–249.

Safford, H. D., and K. P. Van de Water. 2014. Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on National Forest lands in California. Research Paper PSW-RP-266. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Salo, L. F. 2004. Population dynamics of red brome (*Bromus madritensis* subsp. *rubens*): times for concern, opportunities for management. Journal of Arid Environments 57:291–296.

Salo, L. F. 2005. Red brome (*Bromus rubens* subsp. *madritensis*) in North America: possible modes for early introductions, subsequent spread. Biological Invasions 7:165–180.

Salo, L. F., G. R. McPherson, and D. G. Williams. 2005. Sonoran desert winter annuals affected by density of red brome and soil nitrogen. American Midland Naturalist 153:95–109.

Savage, M., and J. N. Mast. 2005. How resilient are southwestern ponderosa pine forests after crown fires? Canadian Journal of Forest Research 35:967–977.

Savage, M., and T. W. Swetnam. 1990. Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. Ecology 71:2374–2378.

Sheppard, P. R., A. C. Comrie, G. D. Packin, K. Angersbach, and M. K. Hughes. 2002. The climate of the US Southwest. Climate Research 21:219–238.

Short, K. C. 2014. A spatial database of wildfires in the United States, 1992-2011. Earth System Science Data 6:1–27.

Stein, S. J. 1988. Fire history of the Paunsaugunt plateau in southern Utah. Great Basin Naturalist 48:58–63.

Stephens, S. L. 2005. Forest fire causes and extent on United States Forest Service lands. International Journal of Wildland Fire 14:213–222.

Stephens, S. L., J. M. Lydersen, B. M. Collins, D. L. Fry, and M. D. Meyer. 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. Ecosphere 6:79.

Stephens, S. L., R. E. Martin, and N. E. Clinton. 2007. Prehistoric fire area and emissions from California's forests, woodlands, shrublands, and grasslands. Forest Ecology and Management 251:205–216.

Stephens, S. L., and L. W. Ruth. 2005. Federal forest-fire policy in the United States. Ecological Applications 15:532–542.

Stuart, J. D., and L. A. Salazar. 2000. Fire history of white fir forests in the coastal mountains of northwestern California. Northwest Science 74:280–285.

Swetnam, T. W., and J. H. Dieterich. 1985. Fire history of ponderosa pine forests in the Gila Wilderness, New Mexico. Pages 390–397 *in* J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch, editors. Proceedings of the Symposium and Workshop on Wilderness Fire. USDA Forest Service, Ogden, Utah, USA.

Syphard, A. D., V. C. Radeloff, J. E. Keeley, T. J. Hawbaker, M. K. Clayton, S. I. Stewart, and R. B. Hammer. 2007. Human influence on Califoirnia fire regimes. Ecological Applications 17:1388–1402.

Taylor, A. H. 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, USA. Journal of Biogeography 27:87–104.

Taylor, A. H. and C. N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications 13:704–719.

van Wagner, C. E. 1987. Development and structure of

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

the Canadian forest fire weather index system. Forest Technical Report 35:37.CanadianForest Service, Ontario, Canada.
Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313:940–943.
Wright, C. S., and J. K. Agee. 2004. Fire and vegetation history in the eastern Cascade Mountains, Washington. Ecological Applications 14:443–459.

Supplemental Material

Ecological Archives

Appendices A–C are available online: http://dx.doi.org/10.1890/ES15-00294.1.sm

21508925, 2015, 12, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/ES15-00294.1, Wiley Online Library on [01/02/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/262808761

Does Riparian Forest Restoration Thinning Enhance Biodiversity? The Ecological Importance of Large Wood

Article *in* JAWRA Journal of the American Water Resources Association · June 2014

DOI: 10.1111/jawr.12206

CITATIONS
44

READS
772

2 authors:



Michael M. Pollock
National Oceanic and Atmospheric Administration
65 PUBLICATIONS **6,555** CITATIONS

SEE PROFILE



Timothy Beechie
National Oceanic and Atmospheric Administration
141 PUBLICATIONS **9,630** CITATIONS

SEE PROFILE

All content following this page was uploaded by Michael M. Pollock on 15 February 2019.

The user has requested enhancement of the downloaded file.

JOURNAL OF THE AMERICAN WATER RESOURCES ASSOCIATION
Vol. 50, No. 3 AMERICAN WATER RESOURCES ASSOCIATION June 2014

DOES RIPARIAN FOREST RESTORATION THINNING ENHANCE BIODIVERSITY? THE ECOLOGICAL IMPORTANCE OF LARGE WOOD[1]

Michael M. Pollock and Timothy J. Beechie[2]

ABSTRACT: Intact riparian ecosystems are rich in biological diversity, but throughout the world, many have been degraded. Biodiversity declines, particularly of vertebrates, have led to experimental efforts to restore riparian forests by thinning young stands to accelerate creation of large diameter live trees. However, many vertebrates depend on large diameter deadwood that is standing as snags or fallen to the forest floor or fallen into streams. Therefore, we reviewed the sizes of deadwood and live trees used by different vertebrate species to understand which species are likely to benefit from different thinning treatments. We then examined how riparian thinning affects the long-term development of both large diameter live trees and deadwood. To this end, we used a forest growth model to examine how different forest thinning intensities might affect the long-term production and abundance of live trees and deadwood. Our results suggest that there are long-term habitat tradeoffs associated with different thinning intensities. Species that utilize large diameter live trees will benefit most from heavy thinning, whereas species that utilize large diameter deadwood will benefit most from light or no thinning. Because far more vertebrate species utilize large deadwood rather than large live trees, allowing riparian forests to naturally develop may result in the most rapid and sustained development of structural features important to most terrestrial and aquatic vertebrates.

(KEY TERMS: riparian ecology; rivers/streams; restoration; forests; fish; fluvial processes; forest management; forest structure; large wood.)

Pollock, Michael M. and Timothy J. Beechie, 2014. Does Riparian Forest Restoration Thinning Enhance Biodiversity? The Ecological Importance of Large Wood. *Journal of the American Water Resources Association* (JAWRA) 50(3): 543-559. DOI: 10.1111/jawr.12206

INTRODUCTION

Throughout much of the world, old, complex, and biologically diverse forested riparian ecosystems have been cleared and replaced by young, structurally simple forests (Naiman *et al.*, 1993; Sala, 2000; Stromberg *et al.*, 2004). In the Pacific coastal states of North America, extensive degradation of riparian forests has led to the decline of numerous aquatic and terrestrial species that depend upon them, a number of which are now listed under the United States (U.S.) Endangered Species Act (ESA) (Nehlsen *et al.*, 1991; USDA and USDI, 1994). In such forests, much of the decline in biodiversity is due to the loss of four major structural features; large live trees, large snags, large down wood on the forest floor, and large down wood in streams (Bauhus *et al.*, 2010; Bunnell and Houde, 2010; Marcot *et al.*, 2010). Notable among the ESA-listed species that utilize riparian ecosys-

[1]Paper No. JAWRA-13-0084-P of the *Journal of the American Water Resources Association* (JAWRA). Received April 3, 2013; accepted March 14, 2014. © 2014 American Water Resources Association. This article is a U.S. Government work and is in the public domain in the USA. **Discussions are open until six months from print publication.**

[2]Research Scientists, Northwest Fisheries Science Center-Watershed Program, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd. E, Seattle, Washington 98112 (E-Mail/Pollock: michael.pollock@noaa.gov).

tems are several salmonids of the genera *Oncorhynchus* and *Salvelinus*, which rely on habitat created by large wood falling into streams; northern spotted owls *Strix occidentalis*, which depend on large live and deadwood for nest sites and habitat for their prey; and marbled murrelets *Brachyramphus marmoratus*, which require large live trees for nesting (USDA and USDI, 1994).

Large living trees and deadwood provide important habitat for a range of other species. Diverse epiphytic communities are found in the crowns of large live trees (Muir *et al.*, 2006), while large snags and down wood provide nesting, roosting, denning, and foraging habitat for numerous birds and mammals (Bunnell *et al.*, 1999; Bunnell and Houde, 2010; Marcot *et al.*, 2010). For numerous aquatic organisms, large wood that falls into streams is essential for the maintenance of habitat because it forms pools, traps, and sorts gravels, increases hyporheic exchange, modulates stream temperature, and provides cover and increased habitat complexity (Beechie and Sibley, 1997; Moore *et al.*, 2005). Large wood that falls to the forest floor provides thermal and moisture refugia for amphibians, habitat for small mammals, and establishment sites for numerous plant species (Harmon and Franklin, 1989; Carey *et al.*, 1999; Kluber *et al.*, 2009). Standing and down wood in various stages of decay creates habitat heterogeneity that supports a complex and diverse fungal community (Norden *et al.*, 2004; Berglund *et al.*, 2005). Large wood ultimately decomposes and helps to provide a humic-rich forest floor with high moisture holding capacity and a biologically complex and diverse soil taxa (Harmon *et al.*, 1986; Coleman and Whitman, 2005). Much of the riparian forest structure needed to maintain biologically diverse aquatic and terrestrial communities is provided by large standing and fallen deadwood.

Rapid biodiversity declines in forested ecosystems have led to experimental efforts to accelerate the development of complex forest ecosystem structure, and in particular to more rapidly create large live and deadwood from young forests (Davis *et al.*, 2006; Puettmann *et al.*, 2009; Bauhus *et al.*, 2010). In the U.S. Pacific Northwest and elsewhere, riparian forest reserves have been established for the primary purpose of recovering species with declining populations (USDA and USDI, 1994). However, many riparian forest reserves are degraded from past land use activities and are now dominated by young, simplified forests. There is an emerging debate as to what types of active and passive management are the best approaches for restoring the structural complexity needed to maintain both terrestrial and aquatic biodiversity as these young forests mature (Beechie *et al.*, 2000; Puettmann *et al.*, 2009; Bauhus *et al.*, 2010; Marcot *et al.*, 2010).

To help resolve this debate, in this article we review and summarize available quantitative data describing the different sizes of large live trees and deadwood that are used by vertebrate species, to better understand which species are likely to benefit from restoration thinning. We then use a forest growth model, Forest Vegetation Simulator (FVS), to simulate how four common restoration thinning intensities (high, medium, low, and no thin) are likely to affect the long-term production of large live trees and large deadwood. We focus our analysis on the sizes of wood important to aquatic and terrestrial vertebrate species found in the Pacific Northwest that are known to use riparian forests, with an emphasis on the structural attributes required by species in population decline.

THE STRUCTURAL HABITAT REQUIREMENTS OF SPECIES THAT UTILIZE RIPARIAN FORESTS

From the perspective of enhancing and maintaining biological diversity in riparian forests, it is helpful to understand the specific structural attributes a given species needs. There has been some effort to understand the specific habitat needs of vertebrate species, while the needs of specific plants, fungi, and invertebrate fauna are not as well known, although data are accumulating (Bunnell *et al.*, 2008; Bunnell and Houde, 2010). However, to date, there has been no synthesis that summarizes how different species utilize specific sizes and types of large wood in riparian forests. To this end, we provide a review of the specific structural components of forests that have been directly linked to usage by vertebrate species. Initially, we used Web of Knowledge, Google, and Google Scholar to search for studies published in peer-review journals examining quantifiable forest structural attributes that are correlated with usage by Pacific Northwest forest vertebrate species. In reviewing the literature, we found that researchers consistently identified one or more of four measurable forest structural attributes that could be related to the habitat requirements of specific species: (1) large down wood in streams, (2) large down wood on the forest floor, (3) large standing snags, and (4) large living trees, often with large limbs and structural irregularities such as cavities and irregular, broken branches, and broken tops. A fifth structural attribute often identified as important for certain species was canopy gaps (e.g., Spies, 1989). However, this attribute was frequently discussed conceptually, and limited quantitative information was available as to the specific size, frequency, and general nature of

canopy gaps that were needed by specific species. Therefore, we limited our review of this attribute to a generalized qualitative discussion, and focused our review effort on identifying studies examining relationships between specific species and the four quantifiable structural attributes of riparian forests previously identified. Many of the studies we examined established relationships between specific forest structural elements and vertebrate species abundance that were not limited to riparian forests, particularly for terrestrial vertebrates, but all of the species we discuss in this review utilize riparian forests.

Table 1 summarizes specific sizes of instream wood, forest floor wood, snags, and live trees associated with certain vertebrate species that we were able to identify in the scientific literature. Each of these attributes and the species associated with them are discussed below.

Trees That Fall into Streams

Salmonids and other aquatic species benefit from the presence of large diameter riparian trees that have fallen into streams. The loss wood inputs from riparian forests is thought to be a major factor in the degradation of freshwater habitat (Gregory *et al.*, 2003; Cluer and Thorne, 2014). Large wood ranging from 15 to 200 cm in diameter and over 2 m in length has been found to structure stream habitat in ways that are beneficial, primarily by forming wood jams, reducing sediment transport, and creating pools (Table 1; Bilby, 1981; Montgomery *et al.*, 1996; Beechie and Sibley, 1997; Fox and Bolton, 2007).

Complex wood jams, that is, the accumulations of many pieces of large wood in streams and rivers, are particularly important because they fundamentally alter transport rates of both sediment and water and in doing so, create complex instream and floodplain habitat (see overview in Cluer and Thorne, 2014). By slowing the flow of water and sediment, complex wood jams help to push water onto floodplains, increasing the dynamic nature of riparian ecosystems and in doing so creating multithreaded channels, mid-channel islands, off-channel habitat, and wetlands which fundamentally enhance riparian species richness by creating a diversity of habitats (Naiman *et al.*, 1993; Walter and Merritts, 2008; Cluer and Thorne, 2014). Thus, arguably, the most important role of riparian forests in terms of enhancing biological diversity is to produce wood of a size distribution and abundance sufficient for large, complex wood jams to form.

Complex wood jams are composed of wood across a wide range of sizes (length and diameter) that is generally commensurate with the size of riparian trees available to fall into streams. Wood jams are composed of a framework of large structural pieces that then serve to trap smaller pieces, which fill in the interstices such that sediment accumulates behind jams and flow is routed around them. However, all wood jams initially require at least one piece which is large enough to be stable during high flows and which forms the initial frame against which other pieces can accumulate (Bilby and Ward, 1989; Fox and Bolton, 2007). The size of such a "key" piece varies with stream characteristics. The size (volume) of the key piece of large wood needed to form stable jams is proportional to the bankfull width for low gradient streams, and wood volume ranges from 1 to 11 m^3 for streams up to 100-m wide or measured by diameter or length ranges from 40 to 70 cm or 8 to 24 m, respectively, for streams up to 20-m wide (WFPB, 1995; Fox and Bolton, 2007) but in high gradient headwater streams, at least one piece of large diameter wood (60-200 cm) is needed to form stable wood jams even if the streams are small (Montgomery *et al.*, 1996). Thus, restoration of riparian forests for the purposes of providing wood to streams such that complex jams can form requires consideration of both the size and abundance of large trees.

Individual riparian trees that fall into streams can also provide important habitat for aquatic organisms, primarily by creating cover and helping to form pools. Similar to key pieces, the minimum size of large wood needed to independently form pools can be predicted from the width of the stream, and ranges from 15 to 75 cm diameter for streams ranging in width from 4 to 23 m (Table 1; Beechie and Sibley, 1997).

Standing Snags and Trees That Fall to the Forest Floor

Numerous terrestrial vertebrates that utilize riparian forests are associated with large trees that have fallen completely or partially to the forest floor (a portion of the tree may have also fallen into a stream or remain standing as a snag). The size of tree utilized by such species ranges from 13 cm to >200 cm diameter, with the average diameter of deadwood used ranging from 53 to 123 cm, depending on the species (Table 1). A number of forest vertebrates are also positively associated with the percent cover of all deadwood on the forest floor, often defined as logs >10 cm or >30 cm diameter (Marcot *et al.*, 2010). Large diameter snags or down wood are used in a number of ways that vary by species (Table 1). Such uses include nesting, denning, resting, foraging, and roosting. For example, the widely distributed wood duck *Aix sponsa* requires large riparian snags with cavities for nesting and the loss of such structures is thought to have resulted in population declines (Soulliere, 1988). Several small

TABLE 1. Examples of Species of Pacific Coastal Forests Use of Large Diameter Deadwood and Live Trees in Aquatic and Terrestrial Habitats, with an Emphasis on ESA-Listed Species (salmonids, the northern spotted owl [and its prey base], and the marbled murrelet). Size range numbers refer to bole diameter breast height (dbh), unless otherwise noted (cf. Bunnell *et al.*, 1999; Bunnell and Houde, 2010).

Species	Wood Type	Function	Size Range	Average Diameter (cm)	Average Length or Height (m)	References
Oncorhynchus, *Salmo,* and *Salvelinus* (salmonids) and other aquatic species	Instream down wood	Forms pools independently, in the absence of other wood or obstructions	0.15-0.75 m diameter for streams with bankfull widths between 4 and 23 m according to the equation: Diameter = 0.028*BFW + 0.0057	—	—	Beechie and Sibley (1997)
Salmonids and other aquatic species	Instream down wood	Independently stable during large floods. "Key" piece forms jams	Varies with stream size: wood piece volumes from 1.0 to 10.8 m^3 for streams 1-100 m wide.	—	—	Fox and Bolton (2007)
Salmonids and other aquatic species	Instream down wood	Independently stable during large floods. "Key" piece forms jams	Varies with stream size: wood diameters from 40 to 70 cm and lengths from 8 to 24 m for streams 1-20 m wide.	—	—	WFPB (Washington Forest Practices) (1995)
Salmonids and other aquatic species	Instream down wood	Stabilize valley spanning jams in high gradient channels	60-200 cm diameter	—	—	Montgomery *et al.* (1996)
Salmonids and other aquatic species	Instream down wood	Accumulates on larger "key" pieces to form debris jams	>10 cm dbh, 2 m length	—	—	Bilby (1981), Bilby and Likens (1980), Bilby and Ward (1989)
Strix occidentalis (northern spotted owl)	Riparian down wood	Preferred foraging areas	Foraging positively related to all CWD volumes, and big log (dbh > 50 cm and L > 8 m) volumes and densities	—	—	North *et al.* (1999)
G. sabrinus (northern flying squirrel), *Neotamias townsendii* (Townsend's chipmunk)	Riparian down wood	Preferred habitat for spotted owl prey species	12% cover of large wood	—	—	Carey (1995)
Myotis lucifugus (little brown myotis)	Riparian down wood	Roosting	—	55	8	Bunnell and Houde (2010)
Martes pennanti (fisher)	Riparian down wood	Resting	50-200	95		Zielinski *et al.* (2004)
Martes americana (marten)	Riparian down wood	Denning	—	53	—	Ruggiero *et al.* (1998)
M. americana	Riparian down wood	Resting	—	66	17	Bull and Heater (2000)
Ursus americanus (black bear)	Riparian down wood	Denning	—	108	17	Bull *et al.* (2000)
U. americanus	Riparian down wood	Denning	—	123		Davis (1992)
Ensatina eschscholtzii	Riparian down wood	General habitat	0-800 m^3/ha, density = 0.11* (CWD Volume)^0.66	—	—	Butts and McComb (2000)

(continued)

TABLE 1. Continued.

Species	Wood Type	Function	Size Range	Average Diameter (cm)	Average Length or Height (m)	References
Ensatina eschscholtzii	Riparian down wood	General habitat	91% of observations related to CWD	—	—	Bury and Corn (1988)
Aneides ferreus (clouded salamander)	Riparian down wood	General habitat	84% of observations related to CWD	—	—	Bury and Corn (1988)
Batrachoseps wrightorum (slender salamander)	Riparian down wood	General habitat	64% of observations related to CWD	—	—	Bury and Corn (1988)
S. occidentalis	Snags	Preferred foraging areas	Vol > 142 m^3/ha, 70% of snag volume was from snags >50 cm dbh. 15 large snags >50 cm/ha in medium and high use areas	86	—	North *et al.* (1999)
G. sabrinus (northern flying squirrel), *Neotamias townsendii* (Townsend's chipmunk)	Snags	Preferred habitat for spotted owl prey species	23 large (>50 cm) snag/ha	—	—	Carey (1995)
Myotis californicus (California myotis)	Snags	Roosting	—	56	27	Brigham *et al.* (1997)
Myotis volans (long-legged myotis)	Snags	Roosting	95% CI = 83-110	97	38	Ormsbee and McComb (1998)
Myotis thysanodes (fringed myotis)	Snags	Roosting	58.5-167	121	41	Weller and Zabel (2001)
M. americana	Snags	Denning	—	55	—	Ruggerio *et al.* (1998)
M. pennanti	Snags	Resting	66-200	119		Zielinski *et al.* (2004)
Aix sponsa (wood duck)	Snags	Cavity nesting	>31 cm	—	—	Soulliere (1988)
Colaptes auratus (common flicker)	Snags	Cavity nesting	36-112 cm	61	11	Mannan *et al.* (1980)
Dryocopus pileatus (pileated woodpecker)	Snags	Cavity nesting	46-172 cm	78	15	Mannan *et al.* (1980)
Picoides villosus (hairy woodpecker)	Snags	Cavity nesting	48-172 cm	92	18	Mannan *et al.* (1980)
Sphyrapicus varius (sapsucker)	Snags	Cavity nesting	56-216 cm	101	17	Mannan *et al.* (1980)
Sitta canadensis (nuthatch)	Snags	Cavity nesting	74-185 cm	118	28	Mannan *et al.* (1980)
Oecile rufescens (chickadee)	Snags	Cavity nesting	53-160 cm	103	18	Mannan *et al.* (1980)
C. auratus	Snags	Foraging	19-167 cm	95	23	Mannan *et al.* (1980)
D. pileatus	Snags	Foraging	20-185 cm	103	30	Mannan *et al.* (1980)
P. villosus	Snags	Foraging	13-173 cm	62	20	Mannan *et al.* (1980)

(continued)

TABLE 1. Continued.

Species	Wood Type	Function	Size Range	Average Diameter (cm)	Average Length or Height (m)	References
Haliaeetus leucocephalus (bald eagle)	Live trees	Nesting	53-277 cm dbh, 21-87 m, for a range of forest types	137	43	Anthony *et al.* (1982)
H. leucocephalus (bald eagle)	Live trees	Nesting	53-277 cm dbh, 21-87 m, for a range of forest types	137	43	Anthony *et al.* (1982)
Pandion haliaetus (osprey)	Live trees	Nesting	28-136 cm dbh, 6-33 m	59	23	Swenson (1981)
S. occidentalis	Live trees	Platform nesting	36-179 cm dbh	106	42	Forsman *et al.* (1984)
S. occidentalis	Live trees	Cavity nesting	74-205 cm dbh	135	38	Forsman *et al.* (1984)
S. occidentalis	Live trees	Roosting	Range of means: 15-115 cm, varies with location and weather	83	—	Forsman *et al.* (1984)
S. occidentalis	Live trees	Dispersal habitat	>40% canopy cover of trees >28 cm dbh	—	—	USFWS (2004, 2010)
Brachyramphus marmoratus (marbled murrelet)	Live trees	Platform nesting	Large trees >82 cm dbh comprising >10% of the canopy cover	—	—	Meyer and Miller (2002)
B. marmoratus	Live trees	Platform nesting	Dominated by conifers >50 cm dbh	—	—	Ripple *et al.* (2003)
B. marmoratus	Live trees	Platform nesting	Mean dbh of trees >77 cm (OR) or >91 cm (CA)	—	—	Meyer *et al.* (2002)
B. marmoratus	Live trees	Platform nesting	>70% crown closure from trees >53 cm dbh (WA)	—	—	Raphael *et al.* (2002)
B. marmoratus	Live trees	Platform nesting	High density of trees >80 cm within 50 m of nest	—	—	Rodway and Regehr (2000)
B. marmoratus	Live trees	Platform nesting	49-533 cm dbh, range of means, varies with location	116-278	51-73	Hamer and Nelson (1995)
M. americana	Live trees	Resting	—	61	25	Bull and Heater (2000)
M. pennanti	Live trees	Resting	35-205	125		Zielinski *et al.* (2004)
U. americanus	Live trees	Denning	—	112	24	Bull *et al.* (2000)
U. americanus	Live trees	Denning	—	159		Davis (1996)

mammals, such as the northern flying squirrel *Glaucomys sabrinus* form the prey base for avian predators with declining populations such as the spotted owl and are among the species utilizing riparian forests that are associated with abundant large dead standing and down wood. This presumably is why such avian predators prefer to forage in stands with abundant standing and fallen deadwood (Table 1; North *et al.*, 1999). The fruiting bodies of hypogeous fungi are a food source of northern flying squirrels and are also associated with down logs, suggesting that there are complex, indirect paths through which trees that fall to the forest floor support biologically diverse ecosystems (Amaranthus *et al.*, 1994; Carey, 2000).

Although species associations with specific sizes of large deadwood are known (Table 1), mechanistically speaking, the reasons why a particular species is associated with a particular size class of deadwood are not always well understood (cf. Bunnell *et al.*, 1999). Potential functions provided by large dead terrestrial wood that would not occur in smaller deadwood includes temperature (hot and cold) and humidity refugia which are particularly important to riparian-dependent taxa such as amphibians (Ruggiero *et al.*, 1998; Kluber *et al.*, 2009), large internal cavity volumes for nests and dens (Bull *et al.*, 2000; Zielinski *et al.*, 2004), cavities between the bark and bole (Bunnell *et al.*, 2002), and sustained structural integrity, particularly during advanced stages of decay (Mannan *et al.*, 1980). For some species, the size of the deadwood may not matter so much as the mechanism by which the tree died and what happened to the tree while it was alive. As an example, the slow death of a tree by heart rot creates a large cavity that is useful as a denning site for several species (e.g., black bear *Ursus americanus*, fisher *Martes pennanti*, and marten *M. americana*), suggesting that variation in the mechanisms of tree death is another consideration for the maintenance of biodiversity (Bunnell and Houde, 2010).

A number of vertebrates utilize snags and down wood >100 cm diameter, suggesting that similar to species found in aquatic environments, terrestrial species will also benefit from wood of this very large size (Table 1). However, many of these species will also utilize deadwood 50-100 cm diameter and some will utilize deadwood as small as 10 cm diameter (Marcot *et al.*, 2010).

Large Live Trees

Large live riparian trees are utilized by numerous raptors, including the bald eagle *Haliaeetus leucocephalus*, osprey *Pandion haliaetus*, and the northern spotted owl for nesting and roosting, by pileated woodpeckers *Dryocopus pileatus* for foraging and nesting, and by marbled murrelets for nesting (Table 1). The marbled murrelet and spotted owl are both ESA listed. These two species prefer to build nests on the limbs or the broken tops of very large diameter live trees (Forsman *et al.*, 1984; Huff *et al.*, 2006). Marble murrelets nest in forests that are dominated by large diameter (>50 cm) live trees, and the diameter of individual trees used as nesting sites averages from 49 cm to >500 cm along the west coast from northern California to Alaska, generally decreasing in size with increasing latitude (Table 1).

Spotted owls also build nests in large diameter live trees, either on the platforms of irregular branches such as those misshapen by mistletoe infections, or in cavities atop the boles of trees with broken tops. Platform nests are found in live trees averaging 106 cm diameter and ranging from 36 to 179 cm diameter, while cavity nests are found in live trees averaging 135 cm diameter and ranging from 74 to 205 cm diameter (Table 1; Forsman *et al.*, 1984). Spotted owls also roost in live trees ranging from 15 to 115 cm diameter, depending on location (Forsman *et al.*, 1984).

Canopy Gaps

Canopy gaps have been identified as a structural attribute important to the maintenance of biodiversity primarily because gaps allow more light to reach the forest floor and this can improve the growth of understory vegetation and increase floristic diversity (Halpern and Spies, 1995; Van Pelt and Franklin, 1999). Trees adjacent to canopy gaps also extend their branches into gaps, resulting in larger diameter branches which should create more sites for the establishment of epiphytes and may benefit species such as the marbled murrelet, which nest on "platforms" created by epiphytes growing on large diameter or irregular branches (Hamer and Nelson, 1995; Naslund *et al.*, 1995). Gap creation in Douglas-fir forests also results in short-term increases in the abundance of some songbirds, but causes declines in others (Hagar, 2009).

The character of canopy gaps is complex and metrics for quantifying the value of different types or sizes of gaps have not been well developed. Although active management may create canopy gaps, it is also noteworthy that canopy gaps naturally develop as trees die and fall and knock down neighboring trees, and that the character of natural gaps may differ from artificial gaps, depending in part on whether tree boles are removed during active management (Van Pelt and Franklin, 1999). If a tree dies naturally and falls over to create a gap, it also creates topographical and substrate heterogeneity (e.g., pit and mound topography) that can help increase floristic diversity (Beatty, 1984; Pollock *et al.*, 1998). When trees die and fall, they also may break tops and branches and scrape the boles of

adjacent trees. This can create irregularly shaped branches and apical and lateral cavities, all of which are habitat features used by a variety of species and are a useful index of biodiversity (Michel and Winter, 2009). Additional research is needed to assess the role of variation in the cause of tree death and tree fall in the creation of canopy gaps essential to the maintenance of biodiversity.

EVALUATION OF FOREST THINNING AS A RESTORATION PRACTICE

In the Pacific Northwest, a commonly applied riparian restoration technique is to thin young forests to help promote the development of complex forest structure. The rationale for such thinning is that it should increase the growth rates of the remaining trees and thus more rapidly develop a forest of large diameter trees (Davis *et al.*, 2006). Thinning young forests may also help to create canopy gaps, another structural attribute of older forests that is often missing in dense young stands (Spies, 1989). If such restoration approaches can accelerate the development of complex riparian forest structure, then the restoration of biologically diverse aquatic and terrestrial communities could also be accelerated (Puettmann *et al.*, 2009; Bauhus *et al.*, 2010).

To demonstrate how the potential effects of such restorative treatments on forest structure could be assessed, we used a forest growth model FVS to examine how the size and abundance of large live and dead trees might be affected over the long term in response to various restoration treatments intended to improve the condition of young, degraded conifer stands typical of Pacific Northwest riparian forests. We projected how these stands would respond to three different levels of active restorative thinning treatments and compared them to a passive, no thin treatment. Details of the forest growth model calibration and parameterization, and initial stand conditions have been previously described by Pollock *et al.* (2012) and are detailed below.

PARAMETERIZATION AND CALIBRATION OF THE FOREST GROWTH MODEL, FOREST VEGETATION SIMULATOR

Site Description of Stands Used in the Simulation

For our analysis, we simulated the growth of planted stands of 30- to 40-year-old Douglas-fir forests in the Coast Range of western Oregon. The geology of the Coast Range consists primarily of marine sandstone and shale, with localized basalt intrusions. The terrain is mountainous and highly dissected. Elevations range from sea level to 1,250 m. The climate is temperate maritime with warm dry summers, and mild wet winters. Most of the peak flows occur in late fall or winter and low flows occur in late summer. The watershed is heavily forested in conifers, with Douglas-fir *Pseudotsuga menziesii* the most abundant species. In these forests, the main successional pathway is characterized by Douglas-fir colonization after fire, Douglas-fir dominance during the first 200-300 years, and then slow succession to a "climax" forest dominated by the shade-tolerant (but fire intolerant) western red cedar *Thuja plicata*, western hemlock *Tsuga heterophylla*, and Sitka spruce *Picea sitchensis* (Munger, 1940). However, because the historic fire return interval in these forests averaged between 180 and 230 years (Long and Whitlock, 2002), many of these stands were continually dominated by Douglas-fir, since stands were often reset by fire prior to succeeding to western hemlock and western red cedar dominance.

Model Parameterization and Calibration

To project long-term changes in stand structure, we used the model FVS and the post-processor Fires and Fuel Extension (FFE) (USFS, 2010c). FVS is a distance-independent, individual tree forest growth model developed by the U.S. Forest Service that has been used to project forest stand development in the Pacific Northwest and most other forested regions of the U.S. (Bragg, 2000; Wilhere, 2001; Crookston and Dixon, 2005). Extensive information concerning FVS, including its development, its use, software downloads, reference documents, and related publications can be found at www.fs.fed.us/fmsc/fvs/. Other forest growth models have been developed to simulate the development of Pacific Northwest forests (e.g., Zelig and Organon), but these have significant shortcomings (Pabst *et al.*, 2008; Hann *et al.*, 2009). Zelig is not publically available, lacks institutional support, and has a complex user interface such that a very small number of scientists understand how to use it. Relative to Zelig, Organon is more widely used, but its growth and mortality parameters are not easily adjusted to calibrate the model to real stand data. On the other hand, most of the growth and mortality parameters in FVS can be adjusted, and this enabled us to calibrate the model against real stand data, as we describe below.

The key parameters affecting the FVS model behavior are tree growth rates and mortality rates.

TABLE 2. Long-Term Annual Mortality Rates for *Pseudotsuga menziesii* in Young, Mature, and Old *P. menziesii*-Dominated Stands in the Pacific Northwest.

Site	Age Start (year)	Age End (year)	Interval (year)	TPH Start	TPH End	Mortality Rate (%)	Source
Mt Hood, nw Oregon	45	109	64	847	306	1.6	Bible (2001)
Gifford Pinchot, sw Washington	50	117	67	557	181	1.7	Bible (2001)
WNF, nw Oregon	54	90	36	464	277	1.4	Munger (1946)
WNF, nw Oregon	54	90	36	529	289	1.7	Munger (1946)
WNF, nw Oregon	54	90	36	469	287	1.4	Munger (1946)
Willamette, nw Oregon	55	137	82	489	208	1.0	Bible (2001)
Hagen RNA, nw Oregon	90	102	12	284	246	1.2	Bible (2001)
RS26, nw Oregon	130	148	18	385	335	0.8	Bible (2001)
Bagby, nw Oregon	270	288	18	127	104	1.1	Bible (2001)
Ohanepecosh, sw Washington	277	288	11	138	126	0.8	Bible (2001)
Munger, sw Washington	400	450	50	53	38	0.7	Bible (2001)
WS202, nw Oregon	460	472	12	89	82	0.7	Bible (2001)

Note: TPH, trees per hectare; WNF, Willamette National Forest; RNA, Research Natural Area; nw, northwest; sw, southwest.

We used a maximum stand density index of 1,250, which is typical for the area, to project competition mortality rates in young stands. We set a minimum background mortality rate of 0.7% for all stands, a somewhat conservative estimate relative to Douglas-fir mortality rates in older stands or thinned stands (Table 2, Munger, 1946; Bible, 2001). Maximum tree height was set at 76 m because that is the typical site potential tree height in the study area.

To ensure that simulated changes in diameter, stand density, and height were consistent with local conditions, the model was calibrated against 66 Douglas-fir dominated reference stands from the area ranging from 23 to 139 years in age.

We also wanted to assess the effects of the different treatments on potential understory tree growth, since understory growth over the course of 200 years may produce some large diameter live and dead trees. To ensure opportunities for understory tree growth, we simulated the planting of seedlings of the shade-tolerant species, western red cedar, western hemlock, and Sitka spruce, at densities of 60 trees/ha every 10 years. We anticipated that most of these would not survive, particularly in the young stands, because of a dense overstory canopy, but that some would begin to survive as the overstory trees began to die and the canopy opened up, consistent with typical successional processes. However, we also expected that the heavier thinning treatments would reduce the overstory canopy sufficient to allow growth of the shade-tolerant species in the understory at a relatively young age, consistent with empirical studies (Comfort *et al.*, 2010).

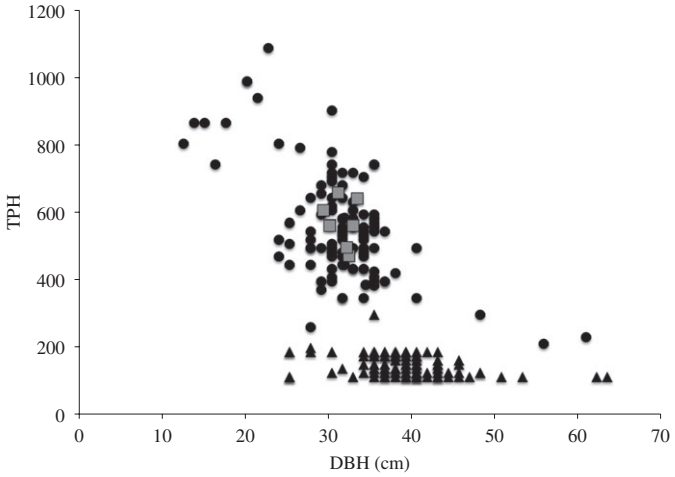


FIGURE 1. Graph Showing Empirical Pre-Treatment Data (black circles) and Proposed (by the USFS, 2010b) Post-Treatment (black triangles) Stand Densities and Average Tree Diameter for the 130 Stands from Which We Modeled Seven for the Purposes of Estimating Long-Term Changes in Large Live Tree and Large Deadwood Production. Gray squares represent the seven stands modeled, and are generally representative of average condition of the larger group of stands, but do not encompass the full range of stand densities.

Initial Stand Conditions

The United States Forest Service (USFS) provided detailed data on seven 30- to 40-year-old Douglas-fir dominated stands in the Siuslaw River basin from a group of 130 stands that will be thinned for the purposes of restoring forest functions (Figure 1). Most of the stands to be thinned originated 30-50 years ago, when Douglas-fir was planted following clear-cut harvest of the original forest. The average stand age proposed for restorative thinning (n = 130) is 35 years (SD = 9.0) and ranges from 14 to 64 years. Stand densities currently average 558 trees/ha (range = 210-1087 trees/ha) and post-treatment will average 147 trees/ha (range = 111-296 trees/ha). The proposed treatment is typical of USFS and Bureau of

Land Management plans to restore biologically diverse forests on riparian reserve lands (e.g., USFS, 2010a; BLM, 2011).

Comparison of our calibrated model outputs with the reference stands showed that our projected changes in diameter, height, and stand density all followed patterns generally consistent with the reference stands, suggesting that the model was appropriately calibrated (Figure 2). The projected changes in average tree height trended toward the higher end of what was observed in the reference stands (Figure 2c) which we attribute to the fact that tree tops in the natural world are often damaged from wind, disease or insects, something that the FVS model does not take into account.

We also compared the thinning treatments with the individual trees in the reference stands used to calibrate the model to verify that all of the treatments produced age-diameter and age-height relationships within the range of natural variation (Figure 3). We found that many trees in the natural environment were growing more rapidly than the trees even in our heaviest thin (Figure 3). This was surprising because the heaviest thin was intended to maximize live tree growth by eliminating any potential for competition.

Caveats

We simulated the growth of stands in the absence of major disturbances. In reality, many stands experience pulses of mortality caused by disturbances such as wind, insect outbreaks, pathogens, and fire. Thus, our mortality estimates are likely lower than what many stands will actually experience. This suggests that recognition of the potential for natural disturbance is important when considering application of restorative treatments. Heavy thins in particular, followed by a disturbance could result in a loss of most of the overstory and delay the creation of a forest with desirable structural attributes (e.g., see Mitchell and Rodney, 2001; Ruel *et al.*, 2001).

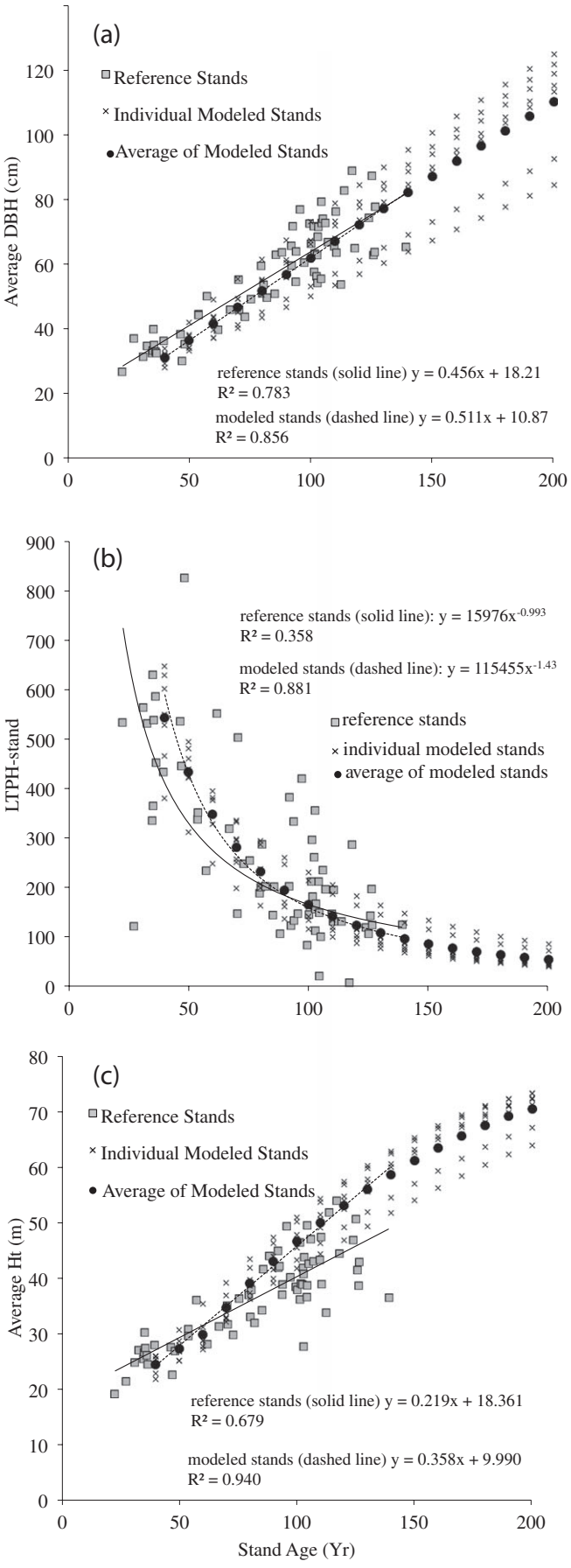


FIGURE 2. Graph Showing Comparison of Forest Vegetation Simulator Model Growth Projection of the Seven Modeled Stands (a) Diameter, (b) Stand Density, and (c) Height, Relative to the Static State of 66 Reference Stands 23-139 Years of Age (see Pollock *et al.*, 2012). The static reference stands are represented by gray diamonds, the crosses represent the modeled trajectory of the seven individual stands described in Figure 1, and the black circles represent the median trajectory of the seven modeled stands. Regression lines help to assess the extent to which the range of modeled stands is representative of the empirically observed range of natural conditions.

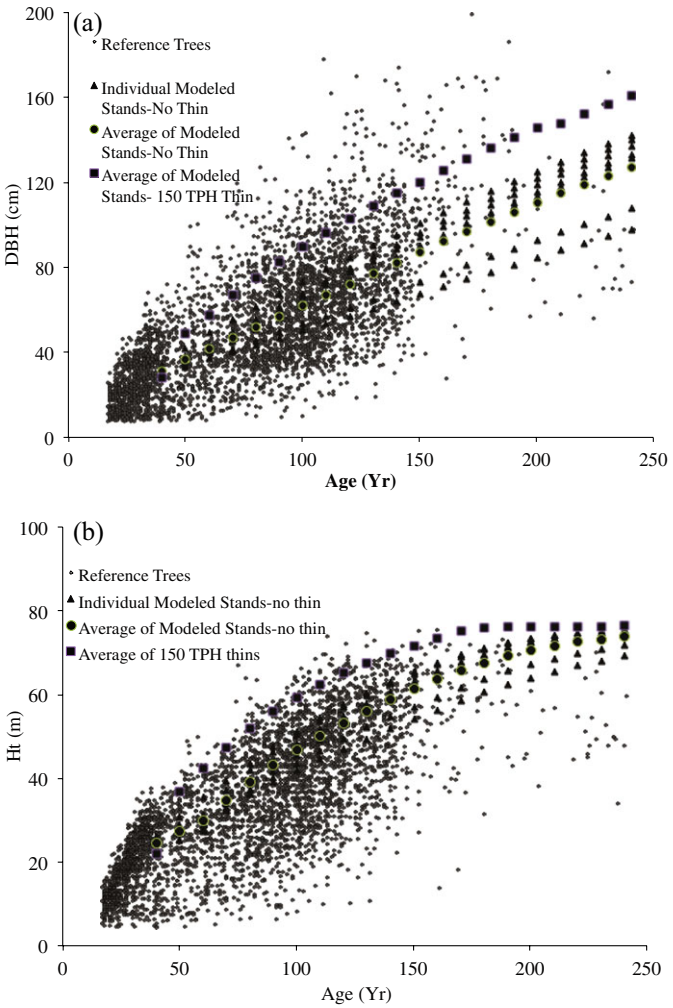


FIGURE 3. Graph Showing the Comparison of the Projected Average Diameter (a) and Height (b) Changes over Time of the Four Simulated Treatments with the Height and Diameter of 3,946 Live Trees in the Area, Ranging in Age from 17 to 250 Years. Tree data were obtained from the USFS Forest Inventory and Analysis database and were limited to productive (site index >120) Douglas-fir-dominated stands that were growing within the coastal region of northwest Oregon. These data help to verify that simulated tree growth in the model was parameterized consistent with growth rates for real live trees.

We found that model projections from the thinning treatments created tree sizes and densities within the natural range of variation. For individual trees, we found that growth rates in the heavy thinning treatment trended toward the upper end of growth rates observed in real stands. This is expected, since the heavy thinning treatments were intended to maximize growth rates of the remaining trees. While such data are reassuring that the model is making reasonable predictions, we note that natural analogues for a stand that has 75% of its overstory removed around age 40 (as was the case for our heaviest thinning treatment) are rare, and forest growth models are not necessarily calibrated for stands that have developed along such a trajectory.

In addition, stochastic events can change stand developmental trajectories and the input data used to parameterize the initial stand conditions do not contain the variation in tree density inherent in any natural stand. As such, using forest growth models (or any models for that matter) in a relative (rather than absolute) context is useful to compare the results of different treatments under controlled conditions where the effects of changing a limited number of variables can be assessed. While forest growth models are no substitute for empirical data, they are currently still the only tool available for predicting the long-term effects of thinning and as such represent our collective best estimate as to how stands will respond to different management scenarios.

Simulated Restoration Treatments

We projected changes in the average mortality, size, and abundance of large diameter live trees, snags, and down wood of seven 30- to 40-year-old stands that averaged about 600 trees/ha, under three restorative treatments; thinning to 400, 250, and 150 trees/ha (light, moderate, and heavy thins). We then compared these to a projection of the stands if left untreated (no thin). Because the restoration thinning is intended to accelerate the development of large diameter trees, all the thinning scenarios removed the smaller diameter trees until the target density was reached, such that the largest trees remained. We assumed that all thinned trees were removed from the site and did not include them in mortality counts. Every 10 years in the simulation, we categorized the live and dead trees by diameter classes; 30-50 cm, 50-100 cm, and >100-cm-diameter breast height. We used these categories because they were representative of size class categorization used to assess live and dead tree habitat value for a variety of taxa (see Table 1).

RESULTS

Deadwood Production

Tree mortality is the number of trees dying in any given decade, and represents the combined production rate of snags and down wood. The thinning treatments minimally affected the timing of the peak in mortality, but substantially affected the magnitude (Figure 4). The peak in mortality rates for trees

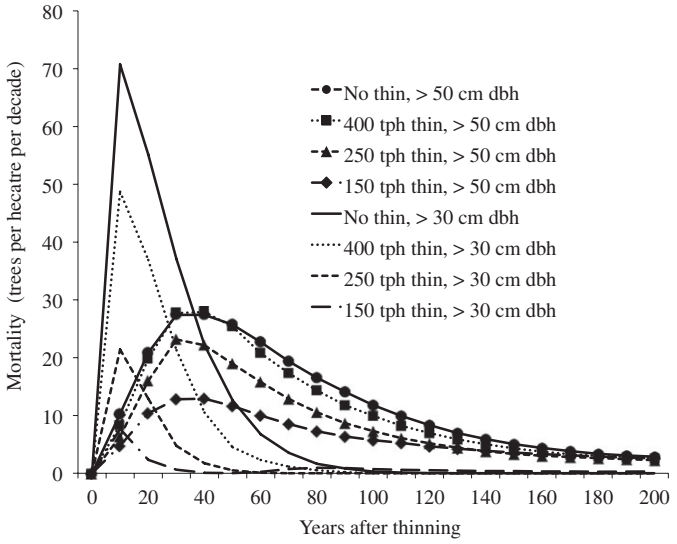


FIGURE 4. Graph Showing Projected Average Mortality Rates (number of trees dying per decade) of Trees >30 cm Diameter and Trees >50 cm Diameter, for each of the Four Simulated Treatments. The 10-year mortality rate of trees >100 cm diameter is low for all treatments throughout the length of the simulation and is not shown in the figure.

>30 cm diameter occurred about 10 years post-treatment and ranged from 8 to 71 trees/ha/decade, with the rate inversely proportional to the intensity of the thin. The peak mortality rate for trees >50 cm occurred about 30 years post-treatment and ranged from 13 to 28 trees/ha/decade, again with the rate inversely proportional to the intensity of the thin. Mortality rates for trees >100 cm were extremely low throughout the simulation (not shown on Figure 4).

The cumulative dead tree production varied considerably among each of the thinning treatments for the >30 cm and >50 cm size classes, while difference in cumulative mortality of trees >100 cm was minimal (Figures 5a and 5b). Over the course of the simulation, the most intensively thinned stands produced a third as many mortality trees >30 cm (145 *vs*. 461) and half as many mortality trees >50 cm (127 *vs*. 250) relative to the unthinned stands (Figures 5a and 5b). In contrast, the heaviest thin produced slightly more mortality trees >100 cm, a cumulative average production of 42 mortality trees >100 cm for the heaviest thin, relative to 37 mortality trees >100 cm for the unthinned stands (Figure 5a).

Relative to the no thin scenario, thinning reduced the mortality peak of boles in the 30-50 cm and 50-100 cm size classes that occurred 10-60 years post-treatment in the passively managed stands, with the reduction in mortality proportional to the intensity of the thin (Figure 4).

In summary, thinning minimally increased the production of large diameter deadwood >100 cm, while causing substantial losses in deadwood 30-

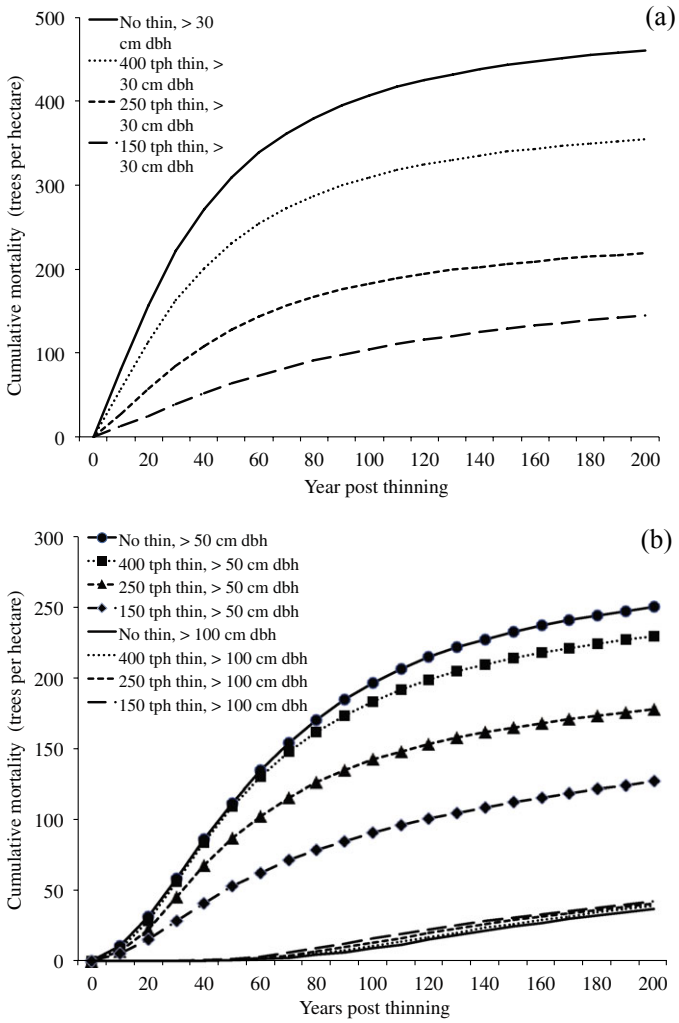


FIGURE 5. Graph Showing Cumulative Mortality over Time for Each of the Four Simulated Treatments. Cumulative mortality provides an index of the total production of deadwood over the course of the simulation and is useful to compare relative production rates of the different treatments for different size classes of wood. Cumulative production of dead trees >150 cm was close to zero for all treatments and is not shown in the figure.

50 cm and 50-100 cm diameter, with no acceleration in the production of these size classes (Figure 5). This suggests that the thinning regimes we examined are not an effective approach for increasing the abundance of ecologically functional deadwood. The no thin scenario produced substantially more deadwood across a wide range of sizes useful to a variety of vertebrate species (Table 1).

Live Trees

Relative to the no thin alternative, thinning initially accelerated the development of large diameter, live trees >100 cm (Figure 6). For example, 100 years post-treatment, the heavily thinned stand contained

34 trees/ha > 100 cm, *vs.* 18 trees/ha for the no thin treatment. However, from 100 to 200 years post-treatment, the number of >100 cm live trees begins to decline in the heavy thinning treatment, such that by year 200, it had the fewest trees >100 cm of all the treatments. Live trees >150 cm begin to show up in the stands 140-160 years post-treatment, but the densities of this size class are very low (9-11 trees/ha) in all the treatments 200 years post-treatment. Heavy thinning caused a 10-year acceleration in the development of live tree densities >50 cm relative to the unthinned stands (Figure 6). However, the higher initial tree densities in the unthinned stand ultimately enabled it to produce more live trees >50 cm than the thinned stands, beginning 30-60 years post-treatment. For trees >30 cm, density generally declined as the intensity of the thinning increased, and this trend was maintained throughout the treatment. The exception was that in the heavy thinning treatment, the growth of understory trees began to produce additional trees in this size class beginning around year 100 (Figure 7a). By year 200, the heavily thinned stand had a broad distribution of tree sizes from 20 to 160 cm, whereas the growth of understory trees in the other treatments was minimal and trees <60 cm diameter were generally absent (Figure 7b).

DISCUSSION

Consideration of the structural attributes that different species utilize and the effect that different restoration treatments have on the abundance of these structural attributes suggests that passive management may often be the treatment that will best enhance biological diversity in degraded riparian forests, but that in some cases thinning may be beneficial. We identified four quantifiable structural attributes of forested riparian ecosystems that are frequently associated with specific habitat needs of vertebrates. Of these structural attributes, three of them (trees that fall into streams, trees that fall onto forest floors and standing snags) are composed of large deadwood, and most species we examined utilize one or more of these structure types. This suggests that the key driver creating biologically diverse forested riparian ecosystems is a steady supply of large deadwood.

We provided examples, using a forest growth model, as to how different restoration efforts might affect the supply of large deadwood and large live

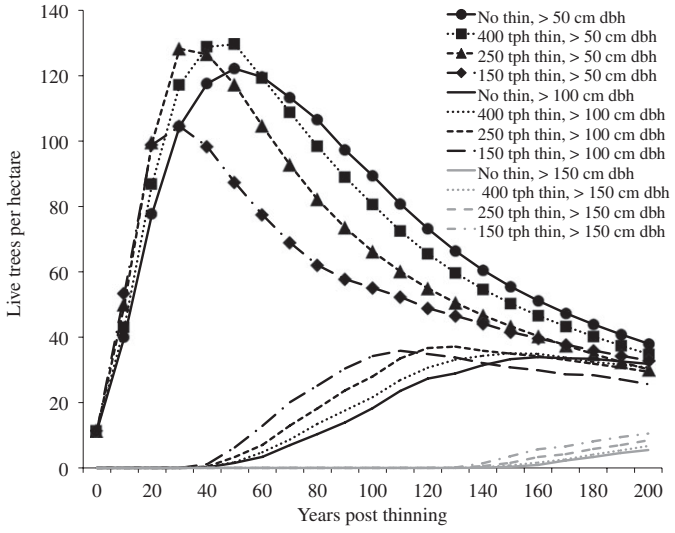


FIGURE 6. Graph Showing the Changes in the Abundance of Large Diameter Live Trees over Time for Each of the Four Simulated Treatments. Relative to deadwood production, the beneficial effect of thinning is more apparent when comparing live trees.

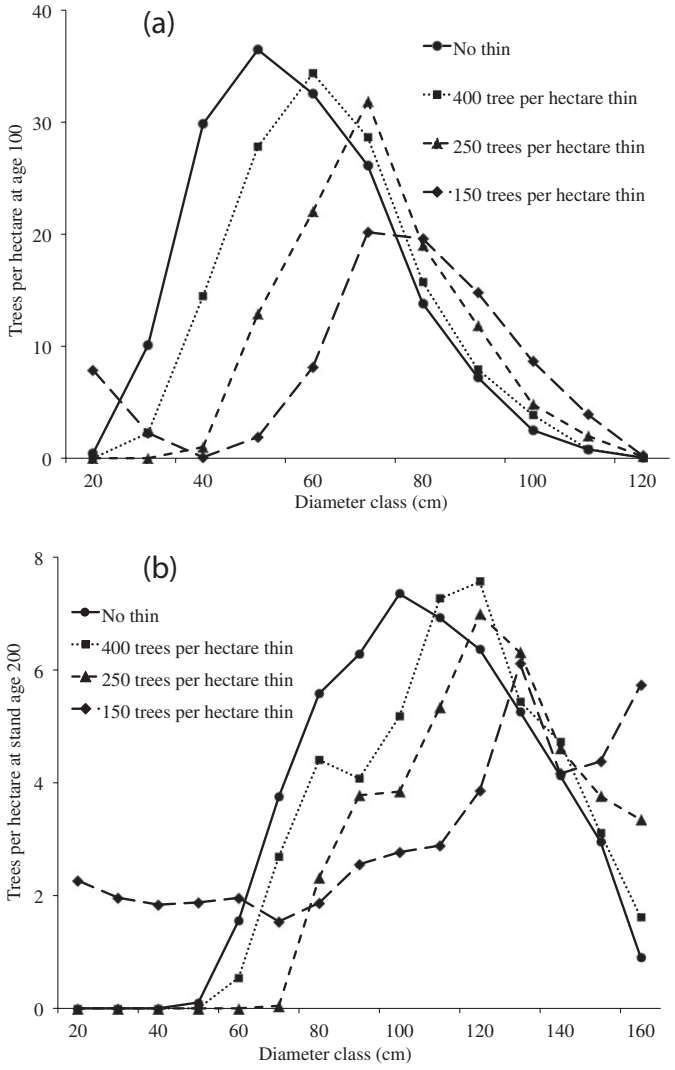


FIGURE 7. Graph Showing the Size Distribution of Live Trees at Age 100 and Age 200 for Each of the Four Simulated Treatments.

trees. Our results suggest that there are tradeoffs associated with both passive and active management, and that different treatments will result in substantial differences in forest structure that will persist over the long term. For the forest stands we examined, as thinning levels increase, forest development predictably trends toward a more open stand with a low number of overstory trees that attain very large sizes, an understory that develops more rapidly, and substantially reduced large diameter deadwood production (Figures 5-7). In contrast, unthinned stands produce abundant large diameter deadwood, but the growth rate of overstory trees and understory development is reduced.

Since different species have a variety of needs in terms of the size and abundance of large live trees and large deadwood (Table 1), we suggest that from a restoration perspective, there is no one "ideal" management regime, but that a range of passive and active management options should be considered for the purposes of creating biologically diverse riparian ecosystems, commensurate with the structural attributes needed by the species of concern. However, we note that for the scenarios examined, more large deadwood that is useful to vertebrates (Table 1) was produced across all size classes when the stands were left unthinned. This suggests that restoration thinning should generally be limited to situations where large deadwood is already abundant, or where the needs of the few species that need very large (>100 cm diameter) live trees outweighs the needs of the many species that utilize large deadwood.

In particular, for providing deadwood to streams, this suggests that for the purposes of facilitating the formation of complex wood jams to benefit the myriad species that utilize the diversity of habitat formed by such jams (e.g., salmonids), a passive management approach that allows for large deadwood production across a range of sizes may be most appropriate.

In contrast, the largest live trees were produced from the heaviest thinning treatment, but this treatment produced the least amount of large deadwood. Thus, such a treatment would be expected to benefit species that utilize very large live riparian trees, but not large deadwood (e.g., marbled murrelets). Examination of Table 1 suggests that deadwood >30 cm diameter creates habitat that is used by many species, but that deadwood >50 cm provides even more habitat benefits, and that maximizing the production of deadwood >50 cm diameter may be a suitable management target if the goal is to benefit the most vertebrates. There were far fewer species that preferred live trees or deadwood >100 cm, but larger diameter dead trees will take longer to decompose, extending the length of time that habitat benefits are provided.

From a restoration perspective, it may also be desirable to directly introduce wood to streams and riparian areas to ensure that there is adequate deadwood in the short term. Even unthinned riparian forests will provide deadwood to forests and streams at a relatively slow rate, and restoration of riparian and instream wood loads to levels that create complex habitat may take decades without active wood placement. Direct placement could also compensate for the loss of instream and riparian wood delivery that will occur if riparian stands are actively thinned.

While our results suggest that passive management will often lead to the most rapid development of large diameter trees and deadwood used by a wide range of species, this interpretation may be limited to the range of stand densities, ages, and forest types that we examined in our study (see Figure 1). Many degraded riparian forests throughout the Pacific Northwest and elsewhere contain stands with smaller and more densely crowded trees that may be dominated by species other than Douglas-fir. The purpose of this study was to assess what structural attributes are used by different species that utilize riparian forests and to provide a simple example of how different management approaches will emphasize the development of different structural attributes important to the maintenance of biological diversity. Future research should examine stands across a wider range of ages, densities, and forest types to develop a more comprehensive understanding as to the conditions where active management can help to restore species-rich riparian forest ecosystems.

Finally, while specific structural attributes of forest ecosystems have been correlated with certain species, it is uncertain how such species will respond to treatments designed to recreate these features. There is always the possibility that in our attempt to create a structural attribute we think is important, we eliminate another attribute that is equally important, but unrecognized. One example is that attempts to restore spotted owl habitat by heavily thinning to accelerate the development of large diameter nesting trees could actually delay spotted owl recovery by reducing production of the large down wood utilized by the species it preys upon (Forsman *et al.*, 1984; Carey, 1995; North *et al.*, 1999). Similarly, heavily thinning stands to accelerate the development of marbled murrelet nesting trees also create open stands with a dense understory that is ideal habitat for a number of corvid species that prey on marbled murrelet nest eggs (USFWS, 2010). Riparian thinning efforts to create long-term supplies of very large diameter instream wood that can initiate complex wood jam formation (e.g., key pieces) are also likely to reduce the supply of large diameter wood that will create pools (Beechie and Sibley, 1997; Beechie *et al.*,

2000; Fox and Bolton, 2007). Thus, we suggest that any efforts to actively restore riparian forests for the benefit of certain species should be treated as scientific experiments and proceed cautiously, skeptically, and with robust pre- and post-treatment data collection efforts. Hypothesized effects of thinning on riparian forest structure and the use of that structure by targeted species should be tested against empirical data.

CONCLUSIONS

The importance of large deadwood as habitat for many aquatic and terrestrial species has been extensively studied over the last three decades, yet there is little comprehensive understanding of how multiple aspects of forest structure contribute to maintaining biologically diverse aquatic, riparian, and upland ecosystems. Our analysis suggests that species rely on different sizes of the key structural attributes of large deadwood in streams, large deadwood on the forest floor, large snags, and large live trees. Different active and passive restoration treatments will have long-term effects on the abundance of these structural elements. For the forests we examined, passive management resulted in the most rapid development of deadwood 30-100 cm diameter, whereas heavy thinning most rapidly developed live trees >100 cm diameter. Other forest types in different climates may produce different results. In the example we provided, passive management created dense forests that produced large volumes of large diameter deadwood over extended time periods as overstory tree densities slowly declined. In contrast, heavy thinning immediately created an open forest that allowed a low-density stand of large diameter overstory trees and an understory of shade-tolerant species to more rapidly develop. Because these size classes of live and deadwood support different biological components of forest ecosystems, tradeoffs in the abundance and production rates of different large diameter live and deadwood size classes should be considered when weighing different management options. Light or medium restoration thins may be an option that provides some increase in diameter growth of live trees, while minimizing production losses of large diameter deadwood. Large deadwood and large live trees are not the only structural attributes needed to maintain biologically diverse riparian ecosystems, but the decline of numerous species has been attributed to the lack of these features. Management strategies that seek to create a range of large live and dead tree densities across the landscape will help to hedge against uncertain outcomes related to unanticipated disturbances, unexpected species needs, and unknown errors in model assumptions. Over the long term, careful monitoring of active and passive treatments can determine if restored riparian ecosystems are being used by the targeted species. Such monitoring will help guide management toward developing biologically diverse riparian ecosystems.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article that includes spreadsheets of the forest growth model inputs and outputs necessary to reproduce the results of this study.

ACKNOWLEDGMENTS

We thank Stu Johnson of the United States Forest Service for providing the field data used in this manuscript. We thank Phil Roni and Jon Ferguson of NOAA's Northwest Fisheries Science Center for their thoughtful reviews of the manuscript. Jeffrey Lockwood and Rob Markle of NOAA's Habitat Conservation Division provided initial input into the development of ideas that were later incorporated into the document. Funding for this project was provided by NOAA.

LITERATURE CITED

Amaranthus, M., J.M. Trappe, L. Bednar, and D. Arthur, 1994. Hypogeous Fungal Production in Mature Douglas-Fir Forest Fragments and Surrounding Plantations and Its Relation to Coarse Woody Debris and Animal Mycophagy. Canadian Journal of Forest Research 24:2157-2165.

Anthony, R.G., R.L. Knight, G.T. Allen, B.L. McClelland, and J.I. Hodges, 1982. Habitat Use by Nesting and Roosting Bald Eagles in the Pacific Northwest. US Fish and Wildlife Publications. Paper 34. *In*: Transactions of the 47th North American Wildlife and Natural Resource Conference, K. Sabol (Editor). US Fish and Wildlife Service, Washington, D.C., pp. 332-342.

Bauhus, J., K.J. Puettmann, and C. Messier, 2010. Silviculture for Old-Growth Attributes. Forest Ecology and Management 258:525-537.

Beatty, S.W., 1984. Influence of Microtopography and Canopy Species on Spatial Patterns of Forest Understory Plants. Ecology 65:1406-1419.

Beechie, T., G.R. Pess, P. Kennard, R. Bilby, and S. Bolton, 2000. Modeling Recovery Rates and Pathways for Woody Debris Recruitment in Northwestern Washington Streams. North American Journal of Fisheries Management 20:436-452.

Beechie, T. and T.H. Sibley, 1997. Relationships between Channel Characteristics, Woody Debris and Fish Habitat in Northwestern Washington Streams. Transactions of the American Fisheries Society 126:217-229.

Berglund, H., M. Edman, and L. Ericson, 2005. Temporal Variation of Wood-Fungi Diversity in Boreal Old-Growth Forests: Implications for Monitoring. Ecological Applications 15:970-982.

Bible, K.J., 2001. Long Term Patterns of Douglas-Fir and Western Hemlock Mortality in the Western Cascade Mountains of Washington and Oregon. Ph.D. Dissertation, University of Washington, Seattle, Washington, D.C.

Bilby, R.E., 1981. Role of Organic Debris Dams in Regulating the Export of Dissolved and Particulate Matter from a Forested Watershed. Ecology 62:1234-1243.

Bilby, R.E. and G.E. Likens, 1980. Importance of Organic Debris Dams in the Structure and Function of Stream Ecosystems. Ecology 61:1107-1113.

Bilby, R.E. and J.W. Ward, 1989. Changes in Characteristics and Function of Woody Debris with Increasing Size of Streams in Western Washington. Transactions of the American Fisheries Society 118:368-378.

BLM, 2011. Hills Camp Thinning Project Upper Willamette Resource Area Environmental Assessment. Bureau of Land Management, Eugene District, Eugene, Oregon.

Bragg, D.C., 2000. Simulating Catastrophic and Individualistic Large Woody Debris Recruitment for a Small Riparian System. Ecology 81:1383-1394.

Brigham, R.M., M.J. Vonhof, R. Barclay, and J.C. Gwilliam, 1997. Roosting Behavior and Roost-Site Preferences of Forest-Dwelling California Bats (Myotis californicum). Journal of Mammology 78:1231-1239.

Bull, E.L., J.J. Akenson, and M.G. Henjum, 2000. Black Bear Dens in Trees and Logs in Northwestern Oregon. Northwestern Naturalist 81:148-153.

Bull, E.L. and T.W. Heater, 2000. Resting and Denning Sites of American Martens in Northeastern Oregon. Northwest Science 74:179-185.

Bunnell, F.L. and I. Houde, 2010. Down Wood and Biodiversity – Implications to Forest Practices. Environmental Reviews 18:397-421.

Bunnell, F.L., I. Houde, B. Johnston, and E. Wind, 2002. How Dead Trees Sustain Live Organisms in Western Forests. USDA Forest Service General Technical Report PSW-GTR-181, pp. 291-318.

Bunnell, F.L., L.L. Kremsater, and E. Wind, 1999. Managing to Sustain Vertebrate Richness in Forests of the Pacific Northwest: Relationships Within Stands. Environmental Reviews 7:97-146.

Bunnell, F.L., T. Spribille, I. Houde, T. Goward, and C. Bjork, 2008. Lichen on Down Wood in Logged and Unlogged Forest Stands. Canadian Journal of Forest Research 38:1033-1041.

Bury, R.B. and P.S. Corn, 1988. Douglas-Fir Forests in the Oregon and Washington Cascades: Relation of the Herpetofauna to Stand Age and Moisture. U.S. Forest Service General Technical Report PNW-GTR-RM-166, pp. 11-22.

Butts, S.R. and W.C. McComb, 2000. Associations of Forest-Floor Vertebrates with Coarse Woody Debris in Managed Forests of Western Oregon. Journal of Wildlife Management 64:95-104.

Carey, A.B., 1995. Sciurids in Pacific Northwest Managed and Old-Growth Forests. Ecological Applications 5:648-661.

Carey, A.B., 2000. Effects of New Forest Management Strategies on Squirrel Populations. Ecological Applications 10:248-257.

Carey, A.B., J.L. Kershner, B. Biswell, and L. Dominquez, 1999. Ecological Scale and Forest Development: Squirrels, Dietary Fungi, and Vascular Plants in Managed and Unmanaged Forests. Wildlife Monographs 142:1-71.

Cluer, B. and C. Thorne, 2014. A Stream Ecosystem Model Integrating Habitat and Ecosystem Benefits. River Research and Applications 30:135-154.

Coleman, D.C. and W.B. Whitman, 2005. Linking Species Richness, Biodiversity and Ecosystem Function in Soil Systems. Pedobiologia 49:479-497.

Comfort, E.J., S.D. Roberts, and C.A. Harrington, 2010. Midcanopy Growth Following Thinning in Young-Growth Conifer Forests on the Olympic Peninsula Western Washington. Forest Ecology and Management 259:1606-1614.

Crookston, N.L. and G.E. Dixon, 2005. The Forest Vegetation Simulator: A Review of Its Structure, Content and Applications. Computers and Electronics in Agriculture 49:60-80.

Davis, H., 1996. Characteristics and Selection of Winter Dens by Black Bears in Coastal British Columbia. Thesis, Department of Biological Sciences, Simon Fraser University, British Columbia.

Davis, L.R., K.J. Puettmann, and G.F. Tucker, 2006. Overstory Response to Alternative Thinning Treatments in Young Douglas-Fir Forests of Western Oregon. Northwest Science 81:1-14.

Forsman, E.D., E.C. Meslow, and H.M. Wight, 1984. Distribution and Biology of the Spotted Owl in Oregon. Journal of Wildlife Management 87:3-64.

Fox, M. and S. Bolton, 2007. A Regional and Geomorphic Reference for Quantities and Volumes of Instream Wood in Unmanaged Forested Basins of Washington State. North American Journal of Fisheries Management 27:342-359.

Gregory, S.V., K. Boyer, and A. Gurnell (Editors), 2003. The Ecology and Management of Wood in the World Rivers. American Fisheries Society, Bethesda, Maryland.

Hagar, J., 2009. Young Stand Thinning and Diversity Study: Response of Songbird Community One Decade Post-Treatment. Open File Report 2009-1253. United States Geological Survey, Renton, Virginia.

Halpern, C.B. and T.A. Spies, 1995. Plant Species Diversity in Natural and Managed Forests of the Pacific Northwest. Ecological Applications 5:913-934.

Hamer, T.E. and S.K. Nelson, 1995. Characteristics of Marbled Murrelet Nest Trees and Nesting Stands. USDA Forest Service General Technical Report PSW-152, pp. 69-82.

Hann, D.W., A.S. Hester, and C.L. Olsen, 2009. ORGANON User's Manual: Edition 8.4. Department of Forest Resources, Oregon State University, Corvallis, Oregon.

Harmon, M.E. and J.F. Franklin, 1989. Tree Seedlings on Logs in Picea-Tsuga Forests of Oregon and Washington. Ecology 70:48-59.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromackm, Jr., and K.W. Cummins, 1986. Ecology of Coarse Woody Debris in Temperate Ecosystems. Advances in Ecological Research 15:133-302.

Huff, M., M.G. Raphael, S.L. Miller, S.K. Nelson, and J. Baldwin. 2006. Status and Trends of Populations and Nesting Habitat for the Marbled Murrelet. USDA Forest Service General Technical Report PNW-GTR-650, pp. 1-149.

Kluber, M.R., D.H. Olson, and K.J. Puettmann, 2009. Downed Wood Microclimates and Their Potential Impact on Plethodontid Salamander Habitat in the Oregon Coast Range. Northwest Science 83:25-34.

Long, C.J. and C. Whitlock, 2002. Fire and Vegetation History from the Coastal Rain Forest of the Western Oregon Coast Range. Quaternary Research 58:215-225.

Mannan, R.W., C.E. Meslow, and H.M. Wight, 1980. Use of Snags by Birds in Douglas-Fir Forests, Western Oregon. Journal of Wildlife Management 44:787-797.

Marcot, B.G., J.L. Ohmann, K.L. Mellen-McLean, and K.L. Waddell, 2010. Synthesis of Regional Wildlife and Vegetation Field Studies of Guide Management of Standing and Down Trees. Forest Science 56:391-404.

Meyer, C.B. and S.L. Miller, 2002. Use of Fragmented Landscapes by Marbled Murrelets for Nesting in Southern Oregon. Conservation Biology 16:755-766.

Meyer, C.B., S.L. Miller, and C.J. Ralph, 2002. Multi-Scale Landscape and Seascape Patterns Associated with Marbled Murrelet Nesting Areas on the U.S. West Coast. Landscape Ecology 17:95-115.

Michel, A.K. and S. Winter, 2009. Tree Microhabitat Structure as Indicators of Biodiversity in Douglas-Fir Forests of Different

Stand Ages and Management Histories in the Pacific Northwest, USA. Forest Ecology and Management 257:1453-1464.

Mitchell, S.J. and J. Rodney, 2001. Windthrow Assessment and Management in British Columbia. Proceedings of the Windthrow Researchers Workshop held January 31-February 1, 2001 in Richmond, British Columbia, University of British Columbia, Vancouver, British Columbia.

Montgomery, D.R., T.B. Abbe, J.M. Buffington, N.P. Peterson, K.M. Schmidt, and J.D. Stock, 1996. Distribution of Bedrock and Alluvial Channels in Forested Mountain Drainage Basins. Nature 381:587-589.

Moore, R.D., D.L. Spittlehouse, and A. Story, 2005. Riparian Microclimate and Stream Temperature Response to Forest Harvesting: A Review. Journal of the American Water Resources Association 41:813-834.

Muir, P.S., T.R. Rambo, R.W. Kimmerer, and D.B. Keon, 2006. Influence of Overstory Removal on Growth of Epiphytic Mosses and Lichens in Western Oregon. Ecological Applications 16:1207-1221.

Munger, T.T., 1940. The Cycle from Douglas-Fir to Hemlock. Ecology 21:451-459.

Munger, T.T., 1946. Watching a Douglas-Fir Forest for Thirty Five Years. Journal of Forestry 44:705-708.

Naiman, R.J., H. Decamps, and M. Pollock, 1993. The Role of Riparian Corridors in Maintaining Regional Biodiversity. Ecological Applications 3:209-212.

Naslund, N.L., K.L. Kuletz, M.B. Cody, and D.K. Marks, 1995. Tree and Habitat Characteristics and Reproductive Success at Marbled Murrelet Tree Nests in Alaska. Northwestern Naturalist 76:12-25.

Nehlsen, W., J.E. Williams, and J.A. Lichatowich, 1991. Pacific Salmon at the Crossroads: Stocks at Risk from California, Oregon, Idaho, and Washington. Fisheries 16:4-21.

Norden, B., M. Ryberg, and F. Gotmark, 2004. Relative Importance of Coarse and Fine Woody Debris for the Diversity of Wood-Inhabitating Fungi in Temperate Broadleaf Forests. Biological Conservation 117:1-10.

North, M.P., J.F. Franklin, A.B. Carey, E.D. Forsman, and T. Hamer, 1999. Forest Stand Structure of the Northern Spotted Owl's Foraging Habitat. Forest Science 45:520-527.

Ormsbee, P.C. and W.C. McComb, 1998. Selection of Day Roosts by Female Long-Legged Myotis in the Central Oregon Cascade Range. Journal of Wildlife Management 62:596-603.

Pabst, R.J., M.N. Goslin, S.L. Garman, and T.A. Spies, 2008. Calibrating and Testing a Gap Model for Simulating Forest Management in the Oregon Coast Range. Forest Ecology and Management 256:958-972.

Pollock, M.M., T.J. Beechie, and H. Imaki, 2012. Using Reference Conditions in Ecosystem Restoration; An Example for Riparian Conifer Forests in the Pacific Northwest. Ecosphere 3:1-23.

Pollock, M.M., R.J. Naiman, and T.A. Hanley, 1998. Predicting Plant Species Richness in Forested and Emergent Wetlands – A Test of Biodiversity Theory. Ecology 79:94-105.

Puettmann, K.J., K.D. Coates, and C. Messier, 2009. A Critique of Silviculture: Managing for Complexity. Island Press, Washington, D.C.

Raphael, M.G., D. Evans-Mack, and B.A. Cooper, 2002. Landscape Relationships between Abundance of Marbled Murrelets and Distribution of Nesting Habitat. Condor 104:331-342.

Ripple, W.J., S.K. Nelson, and E.M. Glenn, 2003. Forest Landscape Patterns Around Marbled Murrelet Nest Sites in the Oregon Coast Range. Northwestern Naturalist 84:80-89.

Rodway, M.S. and H.M. Regehr, 2000. Measuring Marbled Murrelet Activity in Valley Bottom Habitat, Bias Due to Station Placement. Journal of Field Ornithology 71(3):415-422.

Ruel, J.-C., D. Pin, and K. Cooper, 2001. Windthrow in Riparian Buffer Strips: Effect of Wind Exposure, Thinning and Strip Width. Forest Ecology and Management 143:105-113.

Ruggiero, L.F., E. Pearson, and S.E. Henry, 1998. Characteristics of American Marten Den Sites in Wyoming. Journal of Wildlife Management 62:663-673.

Sala, O.E., 2000. Biodiversity: Global Biodiversity Scenarios for the Year 2100. Science 287:1770-1774.

Soulliere, G.J., 1988. Density of Suitable Wood Duck Nest Cavities in a Northern Hardwood Forest. The Journal of Wildlife Management 52:86-89.

Spies, T.A., 1989. Gap Characteristics and Vegetation Response in Coniferous Forests of the Pacific Northwest. Ecology 70:543-545.

Stromberg, J., M. Briggs, C. Gourley, M. Scott, and P. Shafroth, 2004. Human Alterations of Riparian Ecosystems. *In*: Riparian Areas of the Southwestern United States: Hydrology, Ecology and Management, M.B. Baker, Jr., P.F. Ffolliott, L.F. DeBano, and D.G. Neary (Editors). CRC Press, Boca Raton, Florida, pp. 101-126.

Swenson, J.E., 1981. Osprey Nest Site Characteristics in Yellowstone National Park. Journal of Field Ornithology 52:67-69.

USDA and USDI, 1994. Record of Decision for Amendments to Forest Service and Bureau of Land Management Planning Documents within the Range of the Northern Spotted Owl. Standards and Guidelines of Habitat for Late-Successional and Old-Growth Forest Related Species within the Range of the Northern Spotted Owl. USGPO 1994 - 589-111/00001 Region No. 10. United States Government Printing Office, Washington, D.C.

USFS (United States Forest Service), 2010a. Bear Springs Plantation Thinning Environmental Assessment. United States Forest Service, Mt. Hood National Forest, Sandy, Oregon.

USFS (United States Forest Service), 2010b. East Alsea Landscape Management Project Biological Assessment. United States Forest Service, Siuslaw National Forest, Central Coast Range District, Corvallis, Oregon.

USFS (United States Forest Service), 2010c. Forest Vegetation Simulator. Forest Management Service Center, Fort Collins, Colorado. http://www.fs.fed.us/fmsc/fvs/, *accessed* April, 2014.

USFWS (U.S. Fish and Wildlife Service), 2004. Evaluation Report for the 5-Year Status Review of the Marbled Murrelet in Washington, Oregon and California. U.S. Fish and Wildlife Service, Portland, Oregon.

USFWS (U.S. Fish and Wildlife Service), 2010. Draft Revised Recovery Plan for the Northern Spotted Owl. U.S. Fish and Wildlife Service, Portland, Oregon.

Van Pelt, R. and J.F. Franklin, 1999. Response of Understory Trees to Experimental Gaps in Old-Growth Douglas-Fir Forests. Ecological Applications 9:504-512.

Walter, R.C. and D.J. Merritts, 2008. Natural Streams and the Legacy of Water-Powered Mills. Science 319:299-304.

Weller, T.J. and C.J. Zabel, 2001. Characteristics of Fringed Myotis Day Roosts in Northern California. Journal of Wildlife Management 65:489-497.

WFPB (Washington Forest Practices), 1995. Rules-WAC 222, Board Manual (Including Standard Methodology for Conducting Watershed Analysis) & Forest Practices Act RCW 76.09. Department of Natural Resources, Olympia, Washington.

Wilhere, G.F., 2001. Simulation of Snag Dynamics in an Industrial Douglas-Fir Forest. Forest Ecology and Management 174:521-539.

Zielinski, W.J., R.L. Truex, G.A. Schmidt, F.V. Schlexer, K.N. Schmidt, and R.H. Barrett, 2004. Habitat Selection by Fishers in California. Journal of Wildlife Management 68:472-492.

View publication stats

Forest Ecology and Management 291 (2013) 268–277

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Post-fire management regimes affect carbon sequestration and storage in a Sierra Nevada mixed conifer forest

Elizabeth M. Powers [a,*], John D. Marshall [a], Jianwei Zhang [b], Liang Wei [c]

[a] Department of Forest Ecology and Biogeosciences, University of Idaho, P.O. Box 441133, Moscow, ID 83844, USA
[b] USDA, Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA
[c] Department of Forest Ecology and Biogeosciences, University of Idaho, CNR Room 203, Moscow, ID 83844, USA

ARTICLE INFO

Article history:
Received 9 February 2012
Received in revised form 25 July 2012
Accepted 26 July 2012

Keywords:
Carbon flux
Carbon storage
Forest management
Fire
Climate change

ABSTRACT

Forests mitigate climate change by sequestering CO_2 from the atmosphere and accumulating it in biomass storage pools. However, in dry conifer forests, fire occasionally returns large quantities of CO_2 to the atmosphere. Both the total amount of carbon stored and its susceptibility to loss may be altered by post-fire land management strategies. Forest managers face a great challenge when asked to manage these lands for C sequestration and simultaneously reduce fire hazard. The objective of our study was to understand how differing post-fire management strategies affect C sequestration and the size of storage pools in the 10 years after a wildfire in a Sierra Nevada mixed-conifer forest. Post-fire management regimes included: (1) salvage-logged, planted, and intensively managed plantation (IM); (2) salvage-logged and planted (SP); (3) no salvage (NS); and (4) green canopy (GC), where fire burned through, but 95% of the overstory trees survived. Carbon sequestration and storage were estimated from measurements of individual ecosystem carbon pools. These pools included: aboveground trees, saplings, snags, stumps, and understory, coarse wood and fine wood, duff, and soil. We found total ecosystem carbon storage was 282 ± 15 Mg ha^{-1} of C in the NS treatment, 206 ± 31 Mg ha^{-1} in the GC, 137 ± 13 Mg ha^{-1} in the SP, and 101 ± 15 Mg ha^{-1} in the IM treatment. There were no significant treatment differences in C storage among the pools that would constitute labile/fine fuels, but there were differences in recalcitrant (coarse fuel) C pools. The greatest C storage in recalcitrant C pools was 258 ± 10 Mg ha^{-1} in the NS and 197 ± 30 Mg ha^{-1} in the GC treatments. Post-fire carbon sequestration rates were 1.6 ± 0.7 Mg ha^{-1} - year^{-1} of C in the GC, 0.7 ± 0.3 Mg ha^{-1} year^{-1} in the SP, 0.5 ± 0.1 Mg ha^{-1} year^{-1} in the NS, and 0.5 ± 0.1 Mg ha^{-1} year^{-1} in the IM treatments, but these differences were not statistically significant. Tree carbon sequestration rates were highest in the GC treatment and lowest in the NS treatment. Overall, our results suggest that a mature green-canopy stand provides most benefit in terms of C sequestration, wildfire resilience, and other ecosystem services at a point 10 years after severe wildfire. For forests that suffer high fire mortality, unsalvaged (NS) stands will retain the most carbon onsite.

Published by Elsevier B.V.

1. Introduction

Forests play an important role in the global C cycle because they sequester large quantities of carbon into storage as biomass. Here we will refer to "sequestration" as the rate of annual transfer between atmosphere and biosphere; "storage" will refer to the size of the carbon pool at a point in time. Summed over the land area of the US, forests sequester 148–204 Tg year^{-1} of C (Birdsey et al., 2006), which would offset 10–19% of the annual fossil fuel emissions in the US (Birdsey et al., 2006; Woodbury et al., 2007; Ryan et al., 2010) However, both storage amount and sequestration vary with climate, ecosystem type, disturbance regime, and land use and management practices (Bonan, 2008). Many of these characteristics are changing. For example, the US sequestration rate has increased by 33% from the 1990s to 2000s as a result of increased forest area and recovery from past disturbance, management, and environmental change (Pan et al., 2011).

Several forest management strategies have been proposed to mitigate C emissions. Silvicultural practices seek to increase the density of C in existing forests by promoting carbon sequestration (Canadell and Raupach, 2008). These strategies include afforestation, reforestation, and other silviculture practices (Fahey et al., 2009; Stephens et al., 2009a,b). Afforestation and reforestation increase the amount of land area covered by forest and the amount of carbon stored in biomass.

Climate mitigation efforts may also be achieved by reducing carbon losses from decomposition, which tends to increase carbon

* Corresponding author. Tel.: +1 612 269 0369; fax: +1 208 885 6564.
E-mail addresses: epowers@vandals.uidaho.edu (E.M. Powers), jdm@uidaho.edu (J.D. Marshall), jianweizhang@fs.fed.us (J. Zhang), liangwei@vandals.uidaho.edu (L. Wei).

0378-1127/$ - see front matter Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.foreco.2012.07.038

storage. Carbon storage can be increased through management that favors specific carbon pools that decompose less rapidly (Gaudinski et al., 2000; Kirschbaum, 2000). We will refer to these pools as "recalcitrant." For example, recalcitrant pools include large-diameter trees, coarse wood, and organic matter in mineral soil. In comparison, "labile" C, which decomposes more rapidly, is found in foliage, litter, and understory. Promoting carbon storage in recalcitrant C pools may help managers achieve mitigation goals.

A third way to increase carbon storage is to reduce wildfire occurrence and severity. Managers may achieve these reductions by implementing fuel reduction treatments. Such treatments may seek to reduce surface fuels, increase the height to live crown, decrease crown density, and retain large trees of fire-resistant species (Agee and Skinner, 2005). Fuel reduction may be achieved through prescribed fire, understory removal, tree thinning, whole-tree harvest, or a combination of these approaches (Fule et al., 2001; Peterson et al., 2005; Stephens et al., 2009a,b). These treatments shift carbon storage from pools that favor ignition and increase severity to pools that resist ignition and reduce severity. These pools largely overlap with the ones we have previously termed labile and recalcitrant, because pools that decompose slowly are also less likely to combust. In this study, we will include the following pools as labile/fine fuels: duff, fine wood, and understory. Recalcitrant pools will include coarse wood, stumps, snags, trees, and the portion of soil below the duff layer.

Management of fire-prone forests thus presents a unique challenge. Managers must trade off the promotion of carbon storage against the reduction of fire risk. Managing for carbon storage may increase forest or understory biomass, which may increase fuels (Dore et al., 2008), perhaps propagating crown fires (Agee and Skinner, 2005). On the other hand managing to reduce fire risk often requires a reduction in C storage as fuel loads are reduced (Mitchell et al., 2009). For example, several of our sites have intense post-fire shrub growth (*Ceanothus cordulatus*). This research was initiated in part because, for these shrubs, we did not know the tradeoff between carbon sequestration and their contribution to the labile/fine fuel pool. More generally, we sought to quantify all the major carbon pools and sequestration rates in areas that had been managed differently after fire. The specific objectives of this study were to (1) determine the effects of post-fire management on forest C sequestration, (2) determine how the distribution of C pools varies across management treatments, and (3) compare among treatments the tradeoff between the benefits of C sequestration and the risks of labile/fine fuel accumulation.

2. Materials and methods

2.1. Study site

The study was conducted on the Storrie Fire, which was started at Storrie, CA, USA on August 17, 2000. The fire quickly burned northward through the Sierran mixed-conifer forests of the Plumas and Lassen National Forests in Plumas County, CA. It burned about 21,000 ha on national forest land and 1300 ha on private forest land.

Climate is characterized by hot and dry summers and cold and wet winters. Based on 90-year weather records in Chester, CA, which is located 25 km north of the study plots, annual average maximum temperature was 16.8 °C and minimum temperature was −0.4 °C. Daily extreme high and low temperatures were 40.0 °C and −26.7 °C, respectively. Annual precipitation was 813 mm, with approximately 90% occurring as snow between November and April.

Soils at the study site are loamy, mixed, mesic Ultic Haploxeralfs. They fall within either the Holland family or Holland–Skalan family with volcanic parent materials. The depth to parent material is at least 1.0 m and slope angles range from 0% to 50%. Before the fire, the vegetation was a typical mixed conifer forest dominated by *Abies concolor*, *Abies magnifica*, *Calocedrus decurrens*, *Quercus kelloggii*, *Pinus ponderosa*, *Pinus lambertiana*, and *Pseudotsuga menziesii*; the understory was dominated by *Arctostaphylos*, *Castanopsis*, *Ceanothus*, and *Purshia.* The site index of the tallest trees in this mixed-conifer forest is 23 m at 50 years. The plots are located near latitude 40°5′N and 121°16′W.

2.2. Experimental treatments

The study plots were established with four differing post-fire forest management regimes as our treatments. We selected these treatment areas based on the location of existing forest cover created by the fire and post-fire management regimes. We were able to locate three 300-ha blocks on soils classified as loamy, mixed, mesic Ultic Haploxeralfs; each block included the four treatments. Live tree basal area was between 0 m^2 ha^{-1} on the salvage-logged treatments and 41 ± 6 m^2 ha^{-1} on the green canopy (control) treatment (Table 1). The green canopy experienced a low severity burn with little mortality; the post-fire managed treatments all experienced a high severity burn with nearly 100% tree mortality.

The intensively managed (IM) treatment was established on existing plantations managed by W.M. Beaty and Associates (Redding, California). Following the fire in August of 2000, salvage logging commenced immediately and was completed by the fall of 2001. Total sawlogs and biomass removal averaged 68.8 Mg ha^{-1} C (based on the company's timber sales records). Site preparation began in 2001 and the soil was mechanically altered by ripping. Approximately 740 one-year-old seedlings per hectare were planted between 2001 and 2004. The plantations consisted of either pure *P. ponderosa* or mixed conifer species including *P. ponderosa*, *P. lambertiana*, *P. menziesii*, *A. concolor*, and *C. decurrens*. Competing understory vegetation was controlled with herbicide applied twice within the first 5 years. Our treatment plots were located in pure ponderosa pine plantations planted in 2002 and 2003.

The salvage and planted (SP) treatment plots were selected at three plantations established by the US Forest Service in 2004. After the fire, the Forest Service proposed to salvage and plant some relatively flat areas, but the project was withheld due to an appeal of the project and subsequent reversal of the decision. Three years later, the Forest Service was able to salvage 62.5 Mg ha^{-1} C of equivalent wood materials from four areas for a total of 42 ha (based on records in Lassen National Forest). The salvaged area was planted with *P. ponderosa* at 1000 trees ha^{-1} in 2004. The competing vegetation was removed from circles of 1.5 m radius for the largest 50% of the planted seedlings in 2005. The soil was not mechanically altered by ripping.

The no salvage (NS) treatment plots were naturally regenerating burned stands. These plots were not managed following the fire. They burned at such high severity that the fire killed all of the trees on the plots; the resulting snags were not removed from the site. Snags, down wood, and a dense stand of thorny shrubs

Table 1
Stand characteristics across forest management treatment. Tree parameters included live trees and saplings at least 1.37 m tall.

	Stand characteristic across treatments			
Parameter	GC	NS	SP	IM
Tree basal area (m^2 ha^{-1})	41 ± 6		0.4 ± 0.1	3.8 ± 1.0
Ave. stem diameter (cm)	35 ± 7		3.2 ± 0.3	6.9 ± 0.8
Tree density (stems ha^{-1})	300 ± 59		360 ± 79	840 ± 120
Snag basal area (m^2 ha^{-1})	5.7 ± 1.3	34 ± 5		0.9 ± 0.4

Table 2
Species specific allometric equations used to calculate aboveground tree carbon storage and aboveground tree carbon sequestration. Allometric equation symbols are DBH (diameter at breast height), D (ground level diameter), and variables a, b, and c are constants. Units are biomass units and independent variable units, respectively.

Species	Allometric equation	a	b	c	Component	Units	Source
Abies concolor	$y = a * (D)^2 * H + c$	677.6747		0.03725	AB	kg, m	Pacific Southwest Research Station – Redding, unpublished data
Abies concolor	$\ln(y) = a + b * \ln(\text{DBH})$	4.36982	2.5043		AB	g, cm	Westman (1987)
Abies concolor	$y = a * e^{(b*\text{height})}$	0.0153	0.0369		AB	kg, cm	Pacific Southwest Research Station – Redding, unpublished data
Calocedrus decurrens	$y = a * D^b$	54.932	2.3719		AB	g, cm	Pacific Southwest Research Station – Redding, unpublished data
Calocedrus decurrens	$\ln(y) = a + b * \ln(\text{DBH})$	−11.7031	2.7818		ST and B	Mg, cm	Pacific Southwest Research Station – Redding, unpublished data
Pinus lambertiana	$y = a * (D)^2 * H + c$	474.865		0.03495	AB	kg, m	Pacific Southwest Research Station – Redding, unpublished data
Pinus lambertiana	$y = a * (\text{DBH})^2 + c * (\text{DBH})$	0.1212		0.8268	AB	kg, cm	Pacific Southwest Research Station – Redding, unpublished data
Pinus lambertiana	$y = a * e^{(b*\text{height})}$	0.0165	0.0319		AB	kg, cm	Pacific Southwest Research Station – Redding, unpublished data
Pinus ponderosa	$y = a * (D)^2 * H + c$	278.1443		0.40039	AB	kg, m	Pacific Southwest Research Station – Redding, unpublished data
Pinus ponderosa	$y = a * (\text{DBH})^b$	0.0599	2.4711		AB	kg, cm	Pacific Southwest Research Station – Redding, unpublished data
Pinus ponderosa	$y = a * e^{(b*\text{height})}$	0.1625	0.0147		AB	kg, cm	Pacific Southwest Research Station – Redding, unpublished data
Pseudotsuga menziesii	$y = a * (D)^b$	69.8758	1.62976		AB	g, cm	Brown (1978)
Pseudotsuga menziesii	$y = a * (\text{DBH})^2 + c * (\text{DBH})$	0.1215		1.137	AB	kg, cm	Brown (1978)
Quercus kelloggii	$y = a * (\text{DBH})^b$	0.0945	2.503		AB	kg, cm	Ter-Mikaelian and Korzkhun (1997) and Wiant et al. (1977)

occupied the plots by the time the experimental measurements began.

The green canopy (GC) plots were comprised of mixed conifer stands that experienced a low intensity fire. Following the fire, the dominant and co-dominant trees experienced low or no mortality; we assumed that the understory was consumed by the fire. The stands may have been thinned in the past, but there are no records of such pre-fuel treatment activity. This regime has been considered the managers' model of fire-adapted structure in this forest type. Photographs of the treatments can be obtained upon request to the authors.

Each treatment plot was approximately 2090 m^2 (ca. 150 ft by 150 ft). The plot corners were determined using a rangefinder and compass. We calculated the exact area (S) of each plot as follows:

$$S = 0.5 \times a \times b \times \sin\alpha + 0.5 \times c \times d \times \sin\beta \quad (1)$$

where a, b, c, d were the lengths of the four sides of the plot, α was the angle between a and b, and β was the angle between c and d. We used the exact plot size to calculate C storage and sequestration. Each plot contained five subplots, each 9.29 m^2 (100 ft^2) in area, which were used for some components of forest carbon storage and sequestration. The subplot and plot level data were summed to determine total ecosystem carbon storage and sequestration, as described below.

2.3. Aboveground tree carbon

We estimated the carbon content of all trees in each ~2020 m^2 treatment plot. Total aboveground tree biomass was calculated using species-specific allometric equations (Table 2) that predict aboveground tree biomass from tree diameter at breast height (DBH: 1.37 m above ground line). These allometric equations describe the biomass of live trees above the height of a short stump (~15 cm). Although stump mass of the green trees would have added slightly to the total biomass in the GC treatment, the biomass of these short stumps was neglected in this analysis. We used separate calculations to determine the aboveground portion of C in tall stumps and snags. Additional allometric equations were used to predict aboveground biomass for trees shorter than 1.37 m using tree diameter at ground level and/or tree height. We measured every single tree on each replicate, regardless of size. We assumed that the carbon content of tree biomass was 50% (Table 3) (Woodbury et al., 2007; Campbell et al., 2009) to convert biomass to carbon content and then scaled the tree carbon content to a per hectare basis (Mg ha^{-1} of C).

2.4. Understory carbon

Understory carbon content was defined as the carbon stored in aboveground understory biomass (Mg ha^{-1} of C), which included all annual and perennial plants. It was measured by destructively sampling all non-tree aboveground biomass in three 9.29 m^2 subplots per treatment plot. We measured the fresh weight in the field and subsampled to determine the water content. Subsamples were dried at 60 °C until they reached constant mass, and then weighed. Understory field biomass was converted to carbon content by subtracting the water content from the field fresh weight and assuming that the dry weight of understory biomass was 50% C (Thornton et al., 2002).

2.5. Snag carbon

We measured the carbon content for all snags within each treatment plot. Snags were defined as any standing dead tree at least 1.3 m in height. Snag carbon (Mg ha^{-1} of C) was calculated as:

$$\text{SN} = V \times D \times C \quad (2)$$

where V was volume, D was density, and C was the carbon concentration of the snag. Volume was estimated from an allometric equation that predicts volume from snag diameter measured 1.37 m from the forest floor (Zhang et al., 2005). The volume of the snags with broken tops was estimated as if they were cylinders. We estimated the density of snags by felling and sub-sampling cookies

Table 3
Carbon concentration of ecosystem components used to convert biomass to carbon.

Component	Carbon (%)	Source
Tree	50	Woodbury et al. (2007) and Hurteau and North (2010)
Snag	50	Hurteau and North (2010)
Stump	50	Janisch and Harmon (2002)
Understory	50	Thornton et al. (2002)
Coarse wood	50	Harmon (2008) and Hurteau and North (2010)
Fine wood	50	Hurteau and North (2010)
Duff	40	Campbell et al. (2009)
Soil coarse fraction	29.2–47.8	This study
Mineral soil	1.7–7.5	This study

Table 4
Specific gravity of snag and coarse wood for each decay class. The parameters were used convert coarse wood and snag biomass to carbon.

Wood component	Specific gravity
Decay class 1	0.38
Decay class 2	0.32
Decay class 3	0.23
Snag	0.41

*This study.

from snags of three size classes. Cookie subsamples were dried at 60 °C until they reached constant weight. Density was determined from the dry mass of the subsample and volume as determined by the volume displacement of water (Table 4). After weighing, samples were sprayed with carburetor sealant to minimize water uptake. They were then forced underwater and the apparent increase in mass was used as an estimate of water displacement (Williamson and Wiemann, 2010) and thus volume.

2.6. Stump carbon

The carbon content of aboveground stump biomass was estimated on three subplots per treatment plot. Stumps were defined as the aboveground tree bole biomass remaining after trees were harvested. Stumps were assumed to be cylindrical and stump volume was determined from field measurements of stump diameter and height. Stump carbon content was calculated as:

$$\mathrm{ST} = \pi \times \left(\frac{D_1}{2}\right)^2 \times H \times D_2 \times C \quad (3)$$

where D_1 was the diameter, H was height, D_2 was density, and C was the carbon concentration. We assumed that the carbon concentration of stumps is 50% (Janisch and Harmon, 2002). We assigned a decay class from 1 to 3. Decay class 1 was defined as stumps with greater than 70% of the biomass remaining. Decay class 2 had 30–70% of the biomass remaining. Decay class 3 had up to 30% of the biomass remaining and was characterized by cubical fragments and crumbling chunks. We took four subsamples from each of the decay classes to determine density following the same methods as described in Section 2.5 above (Table 4).

2.7. Coarse wood

We measured the carbon content of all coarse wood (CW) in three subplots per treatment plot. CW was defined as any downed woody debris over 5 cm in diameter (Mattson et al., 1987). The carbon content of CW was calculated as:

$$\mathrm{CW} = \pi \times \left(\frac{D_1}{2}\right)^2 \times L \times D_2 \times C \quad (4)$$

where D_1 was midpoint diameter, L was length within the plot, D_2 was the density of wood determined for each decay class, and C was the carbon concentration. We assumed that the carbon concentration of CW is 50% (Harmon, 2008). We measured the length and diameter of each piece of CW in the 9.29 m^2 subplots. As above, we assigned a decay class from 1 to 3 to determine the density.

2.8. Fine wood

Fine wood was collected on three subplots per treatment plot using a 2500 cm^2 duff sampler. FW was defined as plant biomass 1–5 cm in diameter. FW samples were dried in the oven at 60 °C until the samples reached constant mass and then weighed. To convert FW biomass to carbon, we assumed a carbon concentration of 50% (Prichard et al., 2000).

2.9. Duff

Duff was collected on three subplots per treatment plot using a 2500 cm^2 duff sampler. Duff was defined as plant biomass less than 1 cm in diameter. Samples were oven-dried at 60 °C until they reached constant mass and then weighed. Duff biomass was converted to carbon by assuming that the carbon concentration of duff was 40% (Campbell et al., 2009).

2.10. Soil carbon

Three soil samples per treatment plot were collected to determine soil carbon storage at 0–10 cm, 10–20 cm, and 20–30 cm depths. The samples were collected with a soil auger at a randomly selected corner of each of three subplots on each plot. Soil samples were oven dried at 60 °C until they reached constant mass and then separated into rock, coarse fragment (CF), and mineral soil components using a 2 mm mesh sieve. CF was defined as any organic material that would not pass a 2-mm mesh sieve (Page-Dumroese and Jurgensen, 2006). The dry weight of each component was determined and an Elemental Analyzer (CE Instruments, Milan, Italy) connected to a Delta^{plus} isotope ratio mass spectrometer (Finnigan-MAT, Bremen, Germany) was used to determine the carbon concentration for a subset of coarse fraction and mineral soil samples. One set of bulk density samples per treatment plot was taken using a 52.5-mm diameter slide hammer. Bulk density samples were taken at 1–6 cm, 11–16 cm, and 21–26 cm depths. These samples were assumed to represent 0–10, 10–20, and 20–30 cm depths, respectively. The soil coarse fraction and mineral soil carbon pools were estimated from the dry mass and bulk density of soil samples: the product of dry mass carbon concentration, divided by the bulk density at each depth.

$$\text{Soil C pool} = \frac{M}{V} \times D \times \frac{C}{100} \quad (5)$$

where Soil C pool (g cm^{-2} of C) represented either soil coarse fraction (SCF) or mineral soil C in a 10-cm soil layer, M was the component mass (g), V was the soil corer volume (cm^{-3}), D was the soil depth (10 cm), and C was the carbon concentration (%) of the component. The resultant volumetric C content was summed over the appropriate depths, and then scaled up to Mg ha^{-1}.

2.11. Total ecosystem carbon storage

Total ecosystem carbon storage was estimated by summing the individual carbon pools on each treatment plot. Total ecosystem carbon storage (TEC) was defined as:

$$TEC = TC + UC + SN + ST + CW + FW + D + SCF + MS \quad (6)$$

where TEC was the sum of carbon content of individual ecosystem carbon pools (Mg ha^{-1} of C), TC was aboveground live tree, UC was aboveground understory, SN was snag, ST was stump, CW was coarse wood, FW was fine wood, D was duff, SCF was soil coarse fraction, and MS was mineral soil.

2.12. Aboveground carbon sequestration

For mature trees in the GC treatment, aboveground carbon sequestration was estimated for total carbon accumulated since the fire. Aboveground carbon sequestration (CS) was defined as:

$$CS = TS + US \quad (7)$$

(in Mg ha^{-1}year^{-1} of C) where TS was aboveground tree carbon sequestration, US was aboveground understory carbon sequestration. Aboveground tree carbon sequestration (TS) was calculated as the average annual change in live aboveground tree carbon (TC) for individual trees (Jenkins et al., 2001).

$$TS_m = \frac{(TC)_{t_1} - (TC)_{t_0}}{(t_1 - t_0)} \quad (8)$$

where TS_m was tree carbon sequestration of mature trees on the GC treatment, TC was the aboveground tree carbon (Mg tree^{-1} of C) and $t_1 - t_0$ was the 10 year increment (Hudiberg et al., 2009) between 2001 and 2010. We calculated the average annual change in diameter from the 10 year tree ring width between 2001 and 2010 because we wanted to represent the growth of trees as it recovered from disturbance. We expected that growth patterns in the first few years immediately following the fire and management installation would be low as the trees recovered from the initial disturbance, so the average annual growth would be more representative of the tree response in the 10 years following the fire. TC was calculated using the same species-specific allometric equations that were used to calculate aboveground tree carbon from the tree bole diameter (D) measurements (Table 2). The 2010 diameter, $D_{(t1)}$, was measured in the field as described in the section labeled aboveground tree carbon.

The 2001 diameter, $D_{(t0)}$, was determined from radial tree cores. The radial tree core increment was determined by sampling tree cores from three GC treatment plots. We selected 30 trees from each plot to represent the range of tree size and species. We measured the diameter and took two tree core samples at perpendicular directions at 1.37 m from the forest floor. We also measured the 10-year radial increments (or fresh length, L_w) of the 2001–2010 rings using a caliper to 0.1 mm in the field. The cores were dried and the total dry length (L_d) of the 2001 to 2010 tree rings was measured using a caliper. The shrinkage rate (S) was determined using samples that had been measured outdoors as follows:

$$S = \frac{L_w - L_d}{L_w} \quad (9)$$

The shrinkage was determined to be 3.02%. The 10 year radial increment (r) was calculated using the dry tree ring length measurements for tree ring lengths that were not measured in the field:

$$r = L_w = \frac{L_d}{(1 - S)} \quad (10)$$

Finally, the 2001 diameter on the subsampled trees, $D_{(t0)}$, was calculated as:

$$D_{(t0)} = D_{(t1)} - [2 \times k \times r] \quad (11)$$

where k was the bark correction factor (Wykoff et al., 1982).

In order to estimate the annual tree carbon sequestration for all of the trees in each plot, we developed a regression equation using the 2010 diameter measurements and tree rings from the subsampled trees to predict 2001 tree diameter from the 2010 measured diameter:

$$D_{(t0)} = -4.172 + 0.998 \times D_{(t1)} \quad (12)$$

where the $R^2 = 0.996$.

We used a separate TS calculation for the seedlings planted on the IM and SP treatments because they were planted up to 4 years after the fire:

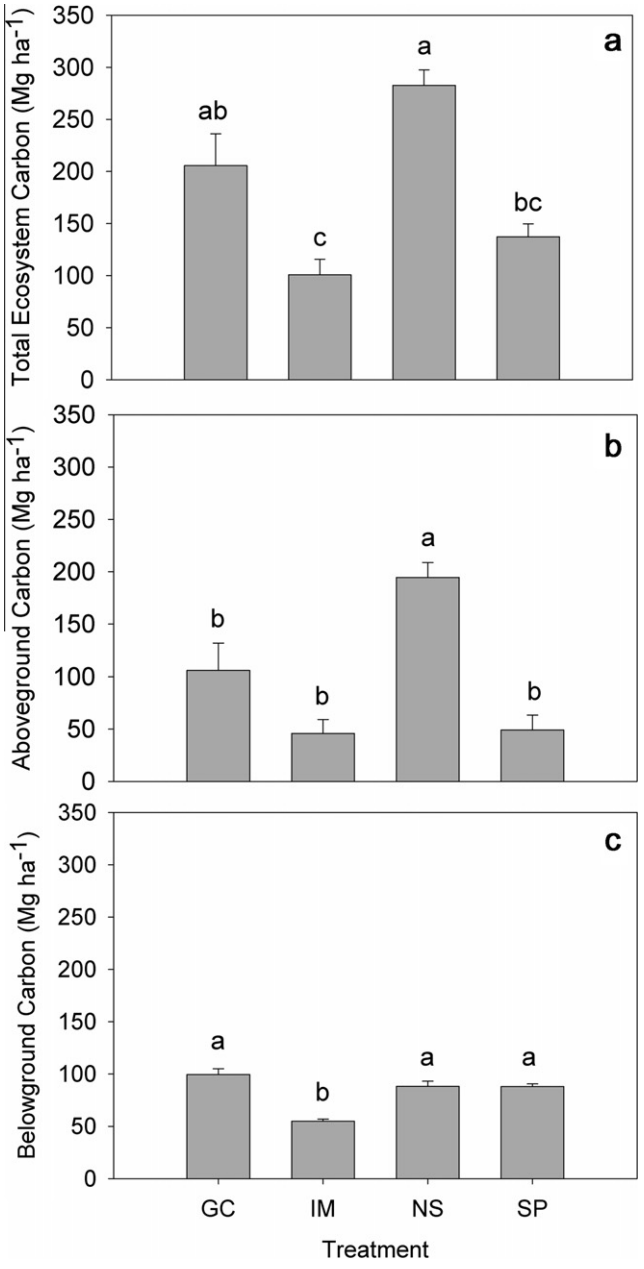


Fig. 1. Carbon storage across management treatment (Mg ha^{-1}) for (a) total ecosystem carbon (aboveground and belowground C storage); (b) total aboveground C (tree, sapling, snag, understory, FW, CW); (c) soil carbon (soil coarse fraction and MS C from 0 to 30 cm depth). Forest management treatments include: green canopy (GC), intensive management (IM), no salvage (NS), and salvage and planted (SP). Bars that are not connected by the same letter are significantly different ($\alpha = 0.05$).

Table 5
Aboveground carbon storage (Mg ha^{-1} of C) for each component across forest management treatments. Letters not connected by the same letter horizontally are significantly different ($\alpha = 0.05$).

Component	Carbon pool (Mg ha^{-1})			
	GC	IM	NS	SP
Tree	81 ± 30*a*	4.1 ± 1.2*b*	0*b*	0.4 ± 0.1*b*
Snag	6.5 ± 1.8*a*	0.5 ± 0.2*a*	82 ± 14*b*	0*a*
Stump	0.6 ± 0.4*a*	11 ± 3*a*	8.2 ± 4.9*a*	2.8 ± 0.7*a*
Understory	1.3 ± 0.6*a*	0.2 ± 0.1*a*	5.2 ± 1.3*a*	5.6 ± 2.4*a*
Coarse wood	9.9 ± 5.7*a*	19 ± 11*a*	81 ± 8*b*	23 ± 9*a*
Fine wood	1.4 ± 0.2*a*	9.5 ± 1.2*a*	13 ± 3*a*	13 ± 5*a*
Duff	5.5 ± 0.2*a*	1.8 ± 0.5*a*	5.7 ± 2.6*a*	4.6 ± 0.9*a*

$$TS_s = \frac{TC_{(t1)}}{(t_1 - t_0)} \quad (13)$$

where TS_s was seedling tree carbon sequestration (Mg ha^{-1} year^{-1}), $TC_{(t1)}$ was the seedling carbon (Mg ha^{-1}) in 2010, t_1 was the year 2010, and t_0 was the year of the start of the growth interval. On the IM and SP treatments, t_0 was the year when the seedlings were planted (see Section 2.2). The individual TS estimates from seedlings and trees were summed on each plot and scaled to an area basis to determine annual tree carbon sequestration.

Aboveground understory carbon sequestration was determined as:

$$US = \frac{UC}{(t_{2010} - t_{2001})} \quad (14)$$

where US was understory carbon sequestration (Mg ha^{-1} year^{-1}), UC was understory carbon storage (Mg ha^{-1}), and t was the year, on the GC, IM, and NS treatments. On the SP treatment, we accounted for the partial understory removal in 2005. We estimated the proportion of the plot that fell within the treated area, which was comprised of circles of 1.5 m radius around the largest 50% of the planted trees:

$$US = p \times \frac{UC}{(t_{2010} - t_{2001})} + (1 - p) \times \frac{UC}{(t_{2010} - t_{2001})} \quad (15)$$

where t was the year, and p was the proportion of plot area with radial understory removal:

$$p = \pi r^2 \times \frac{t}{a} \times 0.5 \quad (16)$$

where r was the1.5 m radius, t was the number of trees per plot, and a was the plot area (m^2).

2.13. Data analysis

Treatment differences in TEC, aboveground C storage, and soil C storage were evaluated using the Tukey–Kramer honest significant difference (HSD) test to make multiple comparisons among treatment means. The HSD was also used to determine treatment differences in less combustible coarse fuels, fine fuels, and individual C storage pools. Statistical analysis was performed using JMP 9 statistical software (SAS, Cary, NC, USA).

To scale plot level estimates of TEC to a land area basis, carbon pool estimates were required for each plot. Due to errors in sample labeling and loss, we were left with 14 missing soil C data points. We used the average of the plot measurements to fill in these missing data. This allowed us to sum each individual ecosystem component of TEC for each replicate. We also excluded one of the coarse wood plots on the NS treatment because satellite imagery (Google earth, http://earth.google.com) showed an anomalously high density of coarse wood when this plot was compared to the surrounding landscape.

3. Results

3.1. Carbon storage across forest management regimes

Total ecosystem carbon storage differed among post-fire management regimes. Total ecosystem carbon storage was 283 ± 15 Mg ha^{-1} in the no salvage (NS) and 206 ± 31 Mg ha^{-1} in the green canopy (GC) treatment (Fig. 1a). These values were significantly higher than those in the plots that were salvaged. The salvage planted (SP) and intensively managed (IM) treatments had values of 137 ± 13 Mg ha^{-1} and 101 ± 15 Mg ha^{-1}, respectively. There were also management differences in aboveground and soil carbon storage (Fig. 1b and c). NS stored significantly more carbon aboveground (194 ± 14 Mg ha^{-1}) than all the other treatments (Fig. 1b); aboveground storage was 106 ± 26 Mg ha^{-1} on the GC, 49 ± 14 Mg ha^{-1} on the SP, and 46 ± 13 Mg ha^{-1} on the IM. The IM treatment stored the least C in the soil (55 ± 2 Mg ha^{-1}); this was significantly lower than the other treatments. The other treatments held 100 ± 6 Mg ha^{-1} in the GC, 88 ± 5 Mg ha^{-1} in NS, and 88 ± 2 Mg ha^{-1} in the SP treatment.

3.2. Distribution of component C storage among treatments

The distribution of carbon among aboveground pools also varied with post-fire management. The largest pool in GC was live tree biomass, with 81 ± 30 Mg ha^{-1} of C (Table 5). The largest pool in IM and SP was coarse wood, which stored 19 ± 11 Mg ha^{-1} and 23 ± 9 Mg ha^{-1}, respectively. The NS treatment stored nearly equal amounts in coarse wood and snag biomass, with 81 ± 7 Mg ha^{-1} and 82 ± 14 Mg ha^{-1}, respectively.

The distribution of carbon among belowground pools was less variable among treatments compared to the aboveground components. The greatest differences in soil C storage were in the top 0–10 cm of soil. In this layer the IM stored 22 ± 1 Mg ha^{-1} in the sieved mineral soil and 1.8 ± 0.8 Mg ha^{-1} in the soil coarse fraction (Table 6). In contrast, the GC stored 47 ± 6 Mg ha^{-1} in the sieved mineral soil from this layer and 1.2 ± 0.7 Mg ha^{-1} in the soil coarse fraction. There were no post-fire management differences in the mineral or soil coarse fraction carbon storage at 10–20 cm and 20–30 cm depths.

There were also shifts in the storage of carbon between labile/fine-fuel and recalcitrant carbon pools with fire and post-fire management. For example, the SP treatment removed all the carbon sequestered in snags and the IM treatment removed over 99% of the snag C compared to the NS treatment. In the NS treatment, fire shifted the carbon stored in large-diameter trees to the snag C pool. The shift in carbon storage among individual ecosystem C pools resulted in treatment differences in carbon storage in fire resistant C pools (Fig. 2a). The NS stored 258 ± 10 Mg ha^{-1} and the IM stored 89 ± 15 Mg ha^{-1} in recalcitrant C pools. There were no significant management differences in labile/fine fuel C storage (Fig. 2b) or individual components of labile/fine fuels, which include the understory, fine wood or duff C pools (Table 5).

3.3. Carbon sequestration

Post-fire management affected components of carbon sequestration, but not total carbon sequestration. Total aboveground carbon sequestration was 1.6 ± 0.7 Mg ha^{-1} year^{-1} of C on the green canopy, 0.7 ± 0.3 Mg ha^{-1} year^{-1} on the SP, 0.5 ± 0.1 Mg ha^{-1} year^{-1} on the NS, and 0.5 ± 0.1 Mg ha^{-1} year^{-1} on the IM treatment (Fig. 3a). There were no treatment differences in understory carbon sequestration. Understory carbon sequestration was 0.1 ± 0.1 Mg ha^{-1} year^{-1} of C on the green canopy, 0.7 ± 0.3 Mg ha^{-1} year^{-1} on the SP, 0.5 ± 0.1 Mg ha^{-1} year^{-1} on the NS, and

Table 6
Components of belowground carbon storage with soil depth and forest management treatments. Values that are not connected by the same letter horizontally are significantly different ($\alpha = 0.05$).

Component	Carbon pool (Mg ha^{-1})			
	GC	NS	SP	IM
Soil coarse fraction				
0–10 cm	1.2 ± 0.7*a*	3.7 ± 0.4*a*	2.0*a*	1.8 ± 0.8*a*
10–20 cm	7.1 ± 2.7*a*	1.9*a*	6.7 ± 0.6*a*	1.1 ± 0.2*a*
20–30 cm	1.3*a*	4.3 ± 2.2*a*	0.9 ± 0.3*a*	0.2 ± 0*a*
Mineral soil				
0–10 cm	47 ± 6*a*	36 ± 3*ab*	35*ab*	22 ± 1*b*
10–20 cm	26 ± 2*a*	26 ± 1*a*	22 ± 1*ab*	16 ± 1*b*
20–30 cm	17*a*	16 ± 2*a*	21 ± 2*a*	14 ± 1*a*

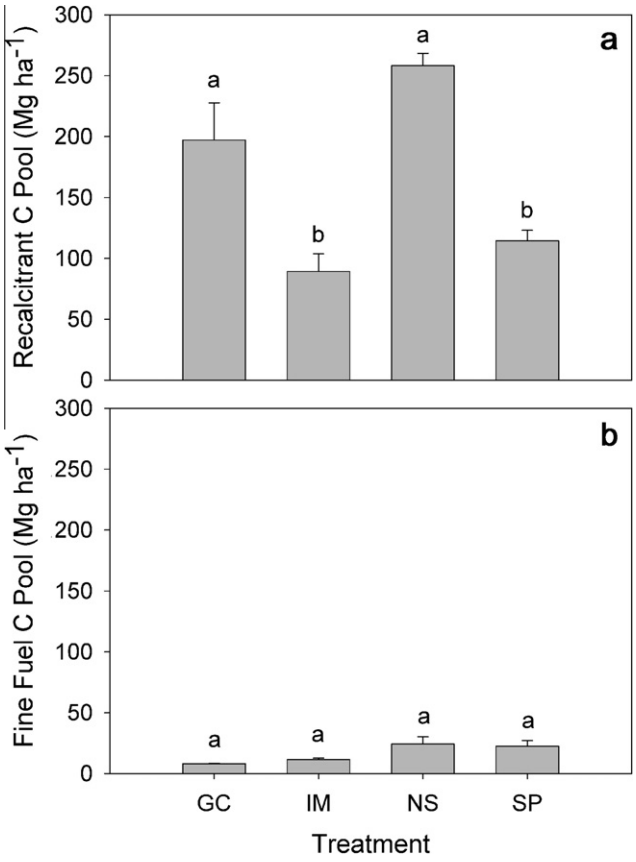


Fig. 2. Ecosystem carbon storage in (a) recalcitrant C pools including tree, snag, stump, coarse wood, and all soil carbon and (b) fine fuels including understory, fine wood, and duff. Forest management treatments include: green canopy (GC), intensive management (IM), no salvage (NS), and salvage and planted (SP). Bars that are not connected by the same letter are significantly different ($\alpha = 0.05$).

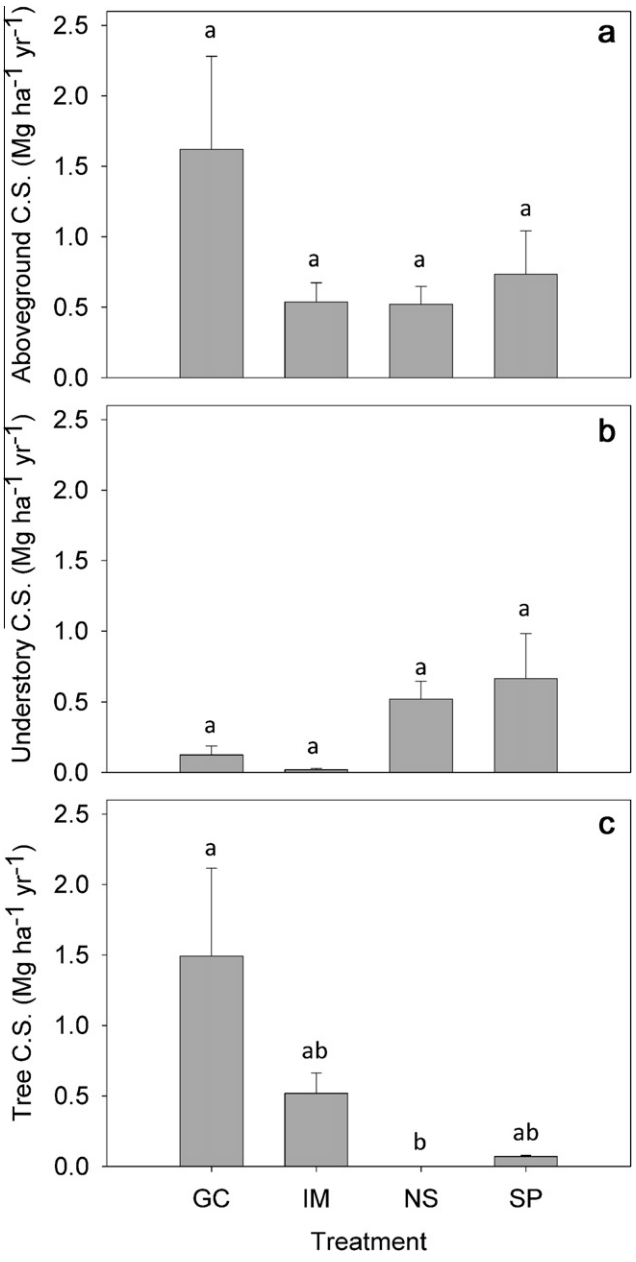


Fig. 3. Carbon sequestration (CS) across forest management treatment averaged over 10 years following fire, (a) total aboveground carbon sequestration (tree and understory), (b) aboveground understory carbon sequestration, and (c) aboveground tree carbon sequestration. Forest management treatments include: green canopy (GC), intensive management (IM), no salvage (NS), and salvage and planted (SP). Bars that are not connected by the same letter are significantly different ($\alpha = 0.05$).

0.02 ± 0.02 Mg ha^{-1} year^{-1} on the IM treatment (Fig. 3b). Aboveground tree carbon sequestration was significantly greater on the GC than the NS treatment; values were 1.5 ± 0.6 Mg ha^{-1} year^{-1} on the GC, 0 Mg ha^{-1} year^{-1} on the NS, 0.07 ± 0.0 Mg ha^{-1} year^{-1} on the SP, and 0.5 ± 0.1 Mg ha^{-1} year^{-1} on the IM (Fig. 3c).

4. Discussion

4.1. Carbon storage and sequestration among treatments

Post-fire management affected total C storage and the distribution of C among ecosystem pools. Of the burned and treated sites, the NS treatment had the highest total C storage due to the large snag and coarse wood pools. The least total ecosystem C was stored in IM and SP treatments due to the reduction of the tree C by the fire and snag C by the logging. The removal of sawlogs and biomass from post-fire salvage logging averaged 68.8 Mg ha^{-1} of C on the IM and 62.5 Mg ha^{-1} of equivalent wood materials on the SP. In addition, soil C was reduced in the 0–10 cm layer on the IM treatment. The IM removed 44. 7 Mg ha^{-1} of soil C from 0 to 30 cm depth compared to the GC (Fig. 1c). Of the 44.7 Mg ha^{-1} removed on the IM, approximately half, 22 Mg ha^{-1}, was lost in the top 0–10 cm of mineral soil (Table 6).

Soil C pools are often incompletely measured or ignored in estimates of carbon storage although soil carbon has been estimated to

represent approximately 40% of terrestrial carbon (Dixon et al., 1994; Kindermann et al., 2008). In our study, soil C contributed between 31% and 64% to total ecosystem carbon storage. Our estimates agree with a previous model of C dynamics throughout the state of California, which estimated that approximately half of total C was in the soil (Turner et al., 1995). The potential change in storage following disturbance is variable (Johnson, 1992). We observed a 45% decrease in total soil C storage in the IM treatment compared to the GC. These reductions were attributed to a decrease in the mineral soil fraction. Two meta-analyses (Johnson, 1992; Johnson and Curtis, 2001) show similar reductions in soil C storage, however the responses were dependent upon disturbance severity and management. For example, soil C storage generally increased after sawlog harvest, decreased following whole tree harvest or prescribed fire, and increased after wildfire (Johnson and Curtis, 2001; Powers et al., 2005). A more recent meta-analysis concluded that harvesting generally reduced soil C by 8%, with the reductions occurring primarily in the forest floor (organic horizon) and not the deeper mineral soil layers (Nave et al., 2010). Other studies observed stable to slight increases in mineral soil C following harvest, however the responses also varied with management intensity and ecosystem type (Sanchez et al., 2006).

Snags also stored a large proportion of total ecosystem carbon in the NS treatment. On the SP and IM treatments, carbon storage had been substantially reduced because the fire-killed trees had been removed during salvage-logging. Snag C and soil C represent large and variable carbon storage pools that should be included in carbon budget estimates.

Carbon sequestration was expected to differ among treatments. However, post-fire management did not affect rates of total aboveground carbon sequestration 10 years after fire. We expected to observe higher total carbon sequestration on the GC treatment resulting from greater stand level tree carbon sequestration rates. In fact, we did observe greater tree carbon sequestration rates on the GC treatment compared to the NS, which had no trees. In contrast, the higher aboveground C in the GC treatment was not different from the IM and SP. This lack of difference may have resulted from the high variability among plots.

It is important to recognize that this storage occurred in the 10 years immediately after the fire. After 10 years, stands have not recovered from disturbance in terms of either site occupation (Pretzsch, 2009) or C sequestration (Fig. 3). We expect that stand sequestration rates will reach GC rates at a later successional stage. The amount of time it takes for the seedlings to recover from disturbance depends upon disturbance type and severity, species composition, post-fire management, and stand density. Intensive management will accelerate this process. For example, it took only 36 years for an intensively managed plantation to carry as much aboveground carbon as pre-fire stands that were approximately 70 years old (Zhang et al., 2008). This leads us to speculate that the C losses on the IM treatment would be offset by the acceleration of stand establishment. It would require a modeling exercise to determine whether and when the offset would occur.

Differences in pre-fire conditions could have influenced our measurements of post-fire C. The study was initiated after the fire, so it was not possible to determine pre-fire carbon stocks. However, our study plots were chosen in similar landscapes with similar soils to minimize pre-fire differences. Further, if we compare live tree basal area on the green canopy treatments to snag basal area on the no salvage treatment, the snag basal area is only a little lower (41 vs. 34 m^2/ha in Table 1). We would not expect them to be exactly the same because the fire may have consumed some of the trees or they may have fallen following fire. Nonetheless, the similarity in these values supports our assumption that the sites were similar before they were treated.

4.2. Error analysis

Sources of error in the carbon measurements include inaccurate and incomplete measurements. One possible source of inaccuracy was the use of inappropriate allometric equations. We minimized inaccuracy by using species-, and where possible, region-specific allometric equations. However, sometimes this was impossible. For example, for *Q. kelloggii*, we applied allometric equations developed for *Quercus velutina* Lam. located in West Virginia. Where possible, we also applied different allometric equations, developed from saplings, to predict C storage in saplings. However, we were forced to use an allometric equation developed for *A. concolor* saplings to estimate C for four individual *P. menziesii* saplings. Error may also have resulted from our snag C estimates, which were derived by assuming that snags are cylinders (Kueppers et al., 2004). This may not be accurate because although broken snags approximate cylinders, they do taper with height and some snags had branches remaining. Future studies could reduce these errors by generating allometric equations for large trees of all species and improving estimates of snag C.

Rates of decomposition were accounted for in our estimates of carbon pools by assigning a decay class to snags and stumps, which we related to wood density and used to reduce our volume to mass conversions. When the sequestration rates were calculated from these pools, the influence of decomposition had thus already been accounted for. Whether this was sufficient is not known. We explored the possibility of further accounting for this flux and concluded that it was too variable to include in the current analysis. Decomposition rates would vary among species, among pools, and probably among treatments given the variable temperature and moisture conditions induced by the treatments. Future work will be needed to address this issue more quantitatively on these sites.

Finally, errors due to incomplete measurements were mostly belowground. We did not, for example, include the carbon in coarse roots or the belowground portions of stumps and snags. We explored the use of coarse-root allometric equations (Jenkins et al., 2003) to live trees and snags and found that coarse root C would increase TEC by 0.4–7% depending upon treatment. We did not include these estimates because the equations were not species–specific. Worse, the coarse roots had probably decayed since the fire and we did not measure the decline in their density; moreover, we would expect that decay rates would differ among treatments. Given these limitations, we decided not to try to estimate coarse root C. Our soil C estimates would also have been more accurate if it had not been necessary to fill in data for the missing samples. Finally, our soil sampling was limited to three soil samples per replicate, which would increase the likelihood of a type II error. We recognize that soil C is often variable (Page-Dumroese et al., 2006) and that we would have benefited from more replication.

4.3. Managing for carbon sequestration and storage

Managing forests for carbon storage and sequestration has become an increasingly important priority to help offset anthropogenic CO_2 emissions. Forest carbon management strategies may include maximizing total ecosystem carbon storage, retaining carbon in recalcitrant pools, or promoting carbon sequestration. The GC and NS treatments had the highest total carbon storage. They also stored the highest proportion of total carbon in recalcitrant C pools. This is important because recalcitrant pools such as large diameter trees, soil, and snags retain C for longer periods of time than labile pools.

This study underlines the importance of soil carbon storage. Previous studies have shown that the reduction of soil C following

forest management is not ubiquitous; the effects vary with time since disturbance, soil type, and forest management (Black and Harden, 1995; Breshears and Allen, 2002; Page-Dumroese and Jurgensen, 2006; Boerner et al., 2008). Because this site underwent mechanical site preparation, some of the reduction may have been due to the mixing of the deep soil materials into the surface horizons. However, the reductions occurred in the 0–20 cm depth without an increase in the 20–30 cm depth, so it is unlikely that downward mixing of organic matter was sufficient to explain the reduction.

4.4. Managing for carbon sequestration and fire

Managing for carbon sequestration may increase fire hazard. Although carbon storage is often favored by climate mitigation efforts, fire hazard reduction often seeks to reduce fuel accumulation by lowering forest carbon density. Managing for both climate mitigation and fire hazard reduction may be achieved by managing to favor recalcitrant carbon storage pools and minimize storage in labile/fine fuels. As noted earlier, recalcitrant pools include large diameter trees, snags, coarse wood, and soil. Labile/fine fuels include understory, fine wood, and duff.

Reducing C storage in labile/fine fuels may be achieved by controlling understory C that burns readily and may propagate crown fires. In this study, the contribution of understory C is relatively low compared to total ecosystem carbon storage, so loss of the understory would have little effect on carbon sequestration. We therefore recommend thinning understory C as a means to reduce labile fuel loading while maximizing C storage. Post-fire strategies favoring recalcitrant carbon may reduce fuels that contribute to increased fire risk and do not contribute a large proportion of C to long term storage. Recalcitrant C is also favored by reducing soil disturbance (Lal, 2004; Page-Dumroese and Jurgensen, 2006).

A complete accounting for C storage would consider forest products (Johnson et al., 2005; Mitchell et al., 2009). For example, partial or complete removal of snags from the forest with post-fire planting could theoretically increase overall long-term carbon storage by promoting forest regeneration and storage of C in recalcitrant forest products offsite. Accounting for off-site storage is beyond the scope of our study. The objectives of our study were to determine C storage and sequestration in previously burned forests, not a full carbon accounting in forest products. An accurate accounting for the carbon removed from the site is complex and would require additional information about the C storage in sawlogs, the post-harvest use, and an accounting of the C required for processing and shipment.

While this study provides management opportunities to balance carbon sequestration efforts with fire, these opportunities should consider management implications besides fire hazard and carbon sequestration. Post-fire salvage should consider the effects on ecosystem function in terms of vegetation regeneration, animal and plant diversity, hydrology, erosion, and nutrient cycling (Serrano-Ortiz et al., 2011; Donato et al., 2006; Castro et al., 2010). For example, fuel reduction treatments that remove shrub cover should consider the ecological significance of *C. cordulatus* as a nitrogen fixer. The presence of nitrogen-fixing shrubs could influence soil C and N dynamics (Boerner et al., 2008) because a significant proportion of N lost from fire disturbance may be offset by nitrogen fixation (Agee, 1993). It remains uncertain how much plant available nitrogen *C. cordulatus* may be adding to the soil and what are its effects on soil fertility and total plant productivity. Managers must also balance management goals with the cost of implementing post-fire treatments at the landscape and regional scale. These management considerations are becoming increasingly important as various lines of evidence suggest that frequency, extent, and – in some cases – the severity of fire is increasing across the western US (Miller et al., 2009; Dillon et al., 2011).

5. Conclusion

Forest managers are faced with complex decisions about how best to manage forest systems for carbon sequestration, fire risk, forest products, and ecosystem processes. Differing management strategies may be implemented depending upon management goals. The results of our study suggest that in fire-prone ecosystems, the green canopy forest and no salvage logging treatments store the most carbon 10 years after a wildfire. Long-term management goals should account for how stand structural changes may shift the distribution of carbon between labile/fine fuels and recalcitrant pools as the stands continue to recover.

To manage for carbon sequestration while still reducing fire hazard, management efforts should maximize carbon storage and carbon sequestration rates in large diameter live trees and other recalcitrant pools, including soils and dead trees, if possible. They should minimize carbon storage in saplings, understory, and surface fuels. The results of our case study provide managers with important background information to make decisions about how to mitigate climate change and reduce future fire risk in a fire-prone Sierra Nevada forest ecosystem.

Acknowledgments

We would like to acknowledge Martin Ritchie and Travis Springer from the Pacific Southwest Research Station, Redding, CA, John Zarlengo from the Almanor Ranger District, Lassen National Forest, CA, and Bob Rynearson from W.M. Beaty and Associates for their contributions. This study was made possible with funding from the USDA Forest Service Lassen National Forest.

References

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC.
Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211, 83–96.
Birdsey, R. et al., 2006. Forest carbon management in the United States: 1600–2100. Journal of Environmental Quality 35, 1461–1469.
Black, T.A., Harden, J.W., 1995. Effect of timber harvest on soil carbon storage at Blodgett experimental forest, California. Canadian Journal of Forest Research 25, 1385–1396.
Boerner, R.E.J. et al., 2008. Fire, thinning, and the carbon economy: effects of fire and fire surrogate treatments on estimated carbon storage and sequestration rate. Forest Ecology and Management 255, 3081–3097.
Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320, 1444–1449.
Breshears, D.D., Allen, C.D., 2002. The importance of rapid, disturbance-induced losses in carbon management and sequestration. Global Ecology and Biogeography 11, 1–5.
Brown, J.K., 1978. Weight and density of crowns of Rocky Mountain conifers. U.S. Forest Service Research Paper INT-197, 56.
Campbell, J. et al., 2009. Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada. Forest Ecology and Management 257, 453–463.
Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. Science 320, 1456–1457.
Castro, J. et al., 2010. Experimental test of postfire management in pine forests: impact of salvage logging versus partial cutting and nonintervention on bird–species assemblages. Conservation Biology 24, 810–819.
Dillon, G.K., et al., 2011. Both Topography and Climate Affected Forest and Woodland Burn Severity in Two Regions of the Western US, 1984 to 2006. Ecosphere 2 (art. 130).
Dixon, R.K. et al., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–190.
Donato, D.C. et al., 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science 311, 352.
Dore, S. et al., 2008. Long-term impact of a stand-replacing fire on ecosystem CO_2 exchange of a ponderosa pine forest. Global Change Biology 14, 1801–1820.
Fahey, T.J. et al., 2009. Forest carbon storage: ecology, management, and policy. Frontiers in Ecology and the Environment 8, 245–252.

Fule, P.Z., et al., 2001. Potential fire behavior is reduced following forest restoration treatments. In: Vance, R.K., Edminster, C.B., Covington, W.W., Blake, J.A. (Eds.), Ponderosa Pine Ecosystems Restoration and Conservation: Steps Towards Stewardship. USDA Forest Service Rocky Mountain Research Station, pp. 28–35.
Gaudinski, J.B. et al., 2000. Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. Biogeochemistry 51, 33–69.
Harmon, M.E.W., Christopher, W., Fasth Becky, Sexton Jay, 2008. Woody detritus density and density reduction factors for tree species in the United States: a synthesis. In: U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, p. 84.
Hudiberg, T. et al., 2009. Carbon dynamics of Oregon and northern California forests and potential land-based carbon storage. Ecological Applications 19, 163–180.
Hurteau, M.D., North, M., 2010. Carbon recovery rates following different wildfire risk mitigation treatments. Forest Ecology and Management 260, 930–937.
Janisch, J.E., Harmon, M.E., 2002. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. Tree Physiology 22, 77–89.
Jenkins, J.C. et al., 2001. Biomass and NPP estimation for the Mid-Atlantic Region (USA) using plot-level forest inventory data. Ecological Applications 11, 1174–1193.
Jenkins, J.C. et al., 2003. National-scale biomass estimators for United States tree species. Forest Science 49, 12–35.
Johnson, D.W., 1992. Effects of forest management on soil carbon storage. Water, Air, & Soil Pollution 64, 83–120.
Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta analysis. Forest Ecology and Management 140, 227–238.
Johnson, L. et al., 2005. Life-cycle impacts of forest resource activities in the Pacific Northwest and southeast United States. Wood and Fiber Science 37, 30–46.
Kindermann, G.E. et al., 2008. A global forest growing stock, biomass and carbon map based on FAO statistic. Silva Fennica 42, 387–396.
Kirschbaum, M.U.F., 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? Biogeochemistry 48, 21–51.
Kueppers, L. et al., 2004. Dead wood biomass and turnover time, measured by radiocarbon, along a subalpine elevation gradient. Oecologia 141, 641–651.
Lal, R., 2004. Soil carbon sequestration to mitigate climate change. Geoderma 123, 1–22.
Mattson, K.G. et al., 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. Canadian Journal of Forest Research 17, 712–721.
Miller, J. et al., 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. Ecosystems 12, 16–32.
Mitchell, S.R. et al., 2009. Forest fuel reduction alters fire severity and long-term carbon storage in three Pacific Northwest ecosystems. Ecological Applications 19, 643–655.
Nave, L.E. et al., 2010. Harvest impacts on soil carbon storage in temperate forests. Forest Ecology and Management 259, 857–866.
Page-Dumroese, D.S., Jurgensen, M.F., 2006. Soil carbon and nitrogen pools in mid- to late-successional forest stands of the northwestern United States: potential impact of fire. Canadian Journal of Forest Research 36, 2270–2284.
Page-Dumroese, D.S. et al., 2006. Soil physical property changes at the North American long-term soil productivity study sites: 1 and 5 years after compaction. Canadian Journal of Forest Research 36, 551–564.
Pan, Y. et al., 2011. A large and persistent carbon sink in the world forests. Science 333, 988–993.
Peterson, D.L., et al., 2005. Forest Structure and Fire Hazard in Dry Forests of the Western United States, p. 30.
Powers, R.F. et al., 2005. The North American long-term soil productivity experiment: findings from the first decade of research. Forest Ecology and Management 220, 31–50.
Pretzsch, H., 2009. Forest Dynamics, Growth and Yield. Springer.
Prichard, S.J. et al., 2000. Carbon distribution in subalpine forests and meadows of the Olympic Mountains, Washington. Soil Science Society of America Journal 64, 1834–1845.
Ryan, M.G., et al., 2010. A synthesis of the science on forests and carbon for US forests. Issues in Ecology, 1–16.
Sanchez, F.G. et al., 2006. Effects of organic matter removal and soil compaction on fifth-year mineral soil carbon and nitrogen contents for sites across the United States and Canada. Canadian Journal of Forest Research 36, 565–576.
Serrano-Ortiz, P. et al., 2011. Post-fire salvage logging reduces carbon sequestration in Mediterranean coniferous forest. Forest Ecology and Management 262, 2287–2296.
Stephens, S.L. et al., 2009a. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. Ecological Applications 19, 305–320.
Stephens, S.L.M., Hartsough, Jason J., Moghaddas, Bruce R., Clinton, Emily E.Y., Nicholas, E., 2009b. Fuel treatment effects on stand-level carbon pools, treatment-related emissions, and fire risk in a Sierra Nevada mixed-conifer forest. Canadian Journal of Forest Research 39, 1538–1547.
Ter-Mikaelian, M.T., Korzkhun, M.D., 1997. Biomass equations for sixty-five North American tree species. Forest Ecology and Management 97 (1), 1–24.
Thornton, P.E. et al., 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. Agricultural and Forest Meteorology 113, 185–222.
Turner, D.P. et al., 1995. A carbon budget for forests of the conterminous United States. Ecological Applications 5, 421–436.
Westman, W.E., 1987. Above ground biomass, surface area, and production relations of red fir (Abies magnified) and white fir (*A. concolor*). Canadian Journal of Forest Research 17, 311–319.
Wiant, H.V.J. et al., 1977. Tables and procedures for estimating weights of some Appalachian hardwoods. West Virginia University, Agricultural Experiment Station.
Williamson, G.B., Wiemann, M.C., 2010. Measuring wood specific gravity correctly. American Journal of Botany 97, 519–524.
Woodbury, P.B. et al., 2007. Carbon sequestration in the US forest sector from 1990 to 2010. Forest Ecology and Management 241, 14–27.
Wykoff, W.R., et al., 1982. User's Guide to the Stand Prognosis Model. In: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, p. 112.
Zhang, J. et al., 2005. Long-term effects of thinning and fertilization on growth of red fir in northeastern California. Canadian Journal of Forest Research 35, 1285–1293.
Zhang, J. et al., 2008. Reforestation after the fountain fire in Northern California: an untold success story. Journal of Forestry 106, 425–430.

Forest Ecology and Management 450 (2019) 117405

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Traditional knowledge of fire use by the Confederated Tribes of Warm Springs in the eastside Cascades of Oregon

Michelle M. Steen-Adams[a,*], Susan Charnley[a], Rebecca J. McLain[b], Mark D.O. Adams[a], Kendra L. Wendel[a]

[a] USDA Forest Service, Pacific Northwest Research Station, 620 SW Main St., Suite 502, Portland, OR 97205, United States
[b] Portland State University, Institute for Sustainable Solutions, 1600 SW 4th Avenue, Suite 110, Portland, OR 97201, United States

ABSTRACT

We examined traditional knowledge of fire use by the Ichishikin (Sahaptin), Kitsht Wasco (Wasco), and Numu (Northern Paiute) peoples (now Confederated Tribes of Warm Springs, CTWS) in the eastside Cascades of Oregon to generate insights for restoring conifer forest landscapes and enhancing culturally-valued resources. We examined qualitative and geospatial data derived from oral history interviews, participatory GIS focus groups, archival records, and historical forest surveys to characterize cultural fire regimes (CFRs) –an element of historical fire regimes– of moist mixed conifer (MMC), dry mixed conifer (DMC), and shrub-grassland (SG) zones. Our ethnohistorical evidence indicated a pronounced cultural fire regime in the MMC zone, but not in the two drier zones. The CFR of the MMC zone was characterized by frequent (few-year recurrence), low-severity burns distributed in a shifting pattern. This regime helped to maintain forest openings created by previous ignitions, resulting from lightning or possibly human-set, that had burned large areas. The CFR was influenced by the CTWS traditional knowledge system, which consisted of four elements: fire use and associated resource tending practices, tribal ecological principles, the seasonal round (the migratory pattern to fulfill resource needs), and culture. Thinleaf huckleberry (*Vaccinium membranaceum*), a cultural keystone species, occurs primarily in the MMC zone and was a principle focus of traditional fire use of the CTWS peoples. Fire was deployed to maintain shrub productivity and site access for harvesting. Cessation of fire use by ~1940 has caused a decline in huckleberry productivity throughout much of the historical harvest zone. Our findings about CFR scale show how a nested, multi-level framework (patch- and landscape-levels) may be employed to reintroduce fire and thereby promote forest restoration and enhance culturally-valued resources. Our findings also highlight the utility of engaging the communities that hold traditional knowledge in the forest management and planning process.

1. Introduction

Millions of hectares of forest in the eastside Cascades of Oregon and Washington have accumulated excessive fuel and undergone stand structural alteration over the past century, priming them for uncharacteristically severe wildfire and insect outbreak (Stine et al., 2014). Public land management agencies and American Indian tribes seek to restore resilience to natural disturbances in these altered forest landscapes given climate change and human development stressors (Lake and Long, 2014; Hessburg et al., 2015). Investigations of historical fire regimes have revealed knowledge to guide forest restoration in Pacific Northwest forests (Cissel et al., 1999; Hessburg et al., 2005; Stine et al., 2014). Historical fire regime metrics including frequency, severity, and patch size, can point to ecological targets for restoration. To date, there is limited understanding of the influence of traditional fire use on historical fire regimes and forest structure of specific ecological zones within a landscape (however, see Boyd, 1999; Turner and Peacock, 2005; Lake, 2007; Turner et al., 2011).

There is growing recognition that American Indians influenced historical fire regimes and forest landscape structure during the Holocene (e.g., Anderson and Moratto, 1996; Agee, 1993; Crawford et al., 2015; Lake et al., 2017). Fire use varied geographically (Crawford et al., 2015), sparking scientific debate about the magnitude of this influence (Denevan, 1992; Vale, 2002). Despite such debate, investigations of traditional fire use have generated restoration applications, such as restoration conceptual models and prescribed fire strategies (Kimmerer and Lake, 2001; Anderson and Barbour, 2003; Senos et al., 2006). In addition, for American Indian tribes, knowledge of fire use can guide restoration practice to promote diverse landscape values, including community identity, intergenerational cohesion, economic benefits, and ecological functions (Lake and Long, 2014; Long et al., 2015; LeCompte, 2018).

Here we focus on the "cultural fire regime" (CFR), meaning the characteristic pattern of managing fuels and ignitions of a particular plant community that a society uses to promote desired natural resources and ecological conditions (Bonnicksen et al., 1999; Lewis and Anderson, 2002; Senos et al., 2006; Lake, 2007; Lake et al., 2017). In combination, the pattern of natural ignitions (e.g., lightning-ignited fires) and that of the

* Corresponding author.
E-mail addresses: michelle.steen-adams@usda.gov (M.M. Steen-Adams), susan.charnley@usda.gov (S. Charnley), mclainrj@pdx.edu (R.J. McLain), mark.adams1@usda.gov (M.D.O. Adams), kendra.wendel@usda.gov (K.L. Wendel).

https://doi.org/10.1016/j.foreco.2019.06.002
Received 20 January 2019; Received in revised form 25 May 2019; Accepted 1 June 2019
0378-1127/ © 2019 Elsevier B.V. All rights reserved.

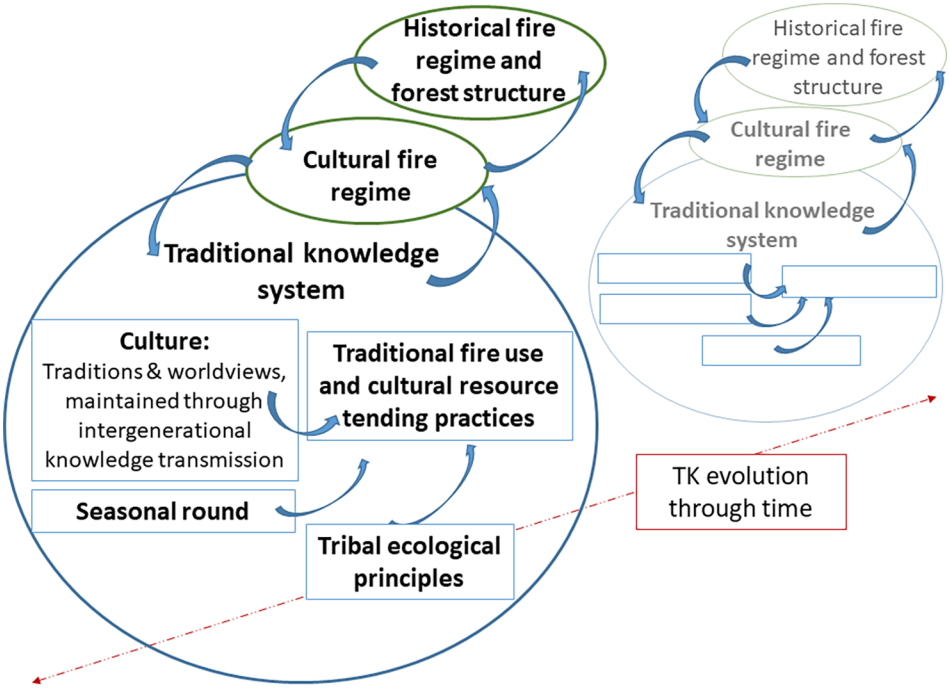


Fig. 1. Conceptual diagram of the traditional knowledge system in relation to the cultural fire regime.

CFR constituted an ecosystem's historical fire regime (Agee 1993; Lake, 2007). This said, the CFR is not necessarily in conjunction with natural fires, e.g., in the eastern U.S., where lightning ignitions are rare (Bonnicksen et al., 1999). CFRs are not well understood, particularly CFR variability across ecological zones, such as those of the eastside Cascades of Oregon (Senos et al., 2006; Lake, 2007; Lake et al., 2017). CFRs are distinct from natural fire regimes in several respects: (1) seasonality; (2) frequency; (3) severity and effects; (4) spatial scale and burn site; (5) ignition strategies; and (6) controls on fire spread, e.g., development of fuel breaks, appropriate timing of fire use (Bonnicksen et al., 1999; Kimmerer and Lake, 2001; Lake, 2007; Lake et al., 2017).

The CFR was structured by the traditional knowledge system of the inhabitant tribal group. In this paper, we use the term traditional knowledge to refer to the body of place-specific knowledge, practices, and beliefs that a society has developed over time to bring about desired ecological conditions, structure, and function (Berkes et al., 1995; Turner et al., 2000). The fire use practices that tribes historically applied to the eastside Cascades landscape were one element of a multi-themed traditional knowledge system (Turner et al., 2000): (1) traditional fire use and associated resource tending practices; (2) tribal ecological principles (understandings about the effects of tending practices on resource productivity and site access); (3) the seasonal round (the migratory pattern to fulfill resource needs); and (4) culture (traditions, ceremonies, and worldviews maintained through intergenerational communication) (Fig. 1). The traditional knowledge system, CFRs, and historical landscape structure were linked through a coevolutionary process of knowledge accumulation and adaptation in response to ecological change (Durham, 1991).

Our focus here is on the CFRs maintained by the Confederated Tribes of Warm Springs (CTWS). The CTWS are three tribal groups who historically inhabited and / or migratorily occupied sites in the eastside Cascades: the Ichishikin- (or Sahaptin) speaking tribes, including the Warm Springs, Tenino, and Dog River bands; the Kitsht Wasco (Wasco); and the Numu (Northern Paiute) peoples (Murdock, 1980; Hunn, 1990; Aguilar, 2005).[1] Our primary research goal was to generate knowledge about traditional fire use and CFRs in the three main ecological zones of the eastside Cascades—the moist mixed conifer (MMC), dry mixed conifer (DMC), and shrub-grassland (SG) zones—and thereby generate applications to forest restoration. Second, we aimed to expand understanding of the CTWS traditional knowledge system and its influence on CFRs. We examined two questions:

(1) How did the CTWS peoples traditionally use fire in the MMC, DMC, and SG zones, and thereby create and maintain CFRs?
(2) How was the CTWS traditional knowledge system structured, and how did fire use fit into this system?

One approach to understanding a society's traditional fire use is to examine which resources it relies on for subsistence and other purposes, including its cultural keystone species – the particular species that "form the contextual underpinnings of a culture" by fulfilling both a key material resource need, and an iconic cultural role as reflected in important ceremonies or narratives (Garibaldi and Turner, 2004; see also, Turner et al., 2011; Long et al., 2015). Western red cedar (*Thuja plicata*) is a cultural keystone species of Northwest coastal peoples of North America, for instance. Keystone species are often intensively managed, as guided by traditional practices and rules. For the CTWS, thinleaf huckleberry (*Vaccinium membranaceum)* (elsewhere, big-leaf huckleberry (Helliwell, 1987), big huckleberry (Minore, 1984; Anzinger, 2002), mountain huckleberry (Richards and Alexander, 2006)) — one of six huckleberry species that grow on the Warm Springs Reservation (Marsh et al., 1987) — is a cultural keystone species because of its importance as a traditional food, for food gatherers, for an annual ceremonial feast, and for wildlife hunted as game (Hunn, 1990; Aguilar, 2005). One CTWS management objective is enhancement of this species, due to its cultural importance (CTWSRO, 1992; Jimenez, 2002). In the broader scope, treaty rights and U.S. government trust responsibility to American Indians (i.e., federal legal obligations to tribes) direct that the area's tribes continue to have access to this species, including on off-reservation sites (primarily on US Forest Service lands), as they have had historically (Goschke 2016; see also, Pitt, 2015). Legal scholarship has advanced the case for co-management of the resource to maintain and/ or restore huckleberry field size and productivity

[1] However historically the Numu people occupied areas outside of the eastside Cascades, in southeastern Oregon (CTWS, 2016).

(Goschke, 2016). We found that traditional knowledge about thinleaf huckleberry (French, 1965; Anzinger, 2002), provided insight into the CFRs of the eastside Cascades.

Lacking in the literature are landscape-level, geographically-explicit analyses of CFR variability across multiple ecological zones of a landscape. This is because much of the research to date has examined fire use of individual ecological zones, resulting in knowledge about CFRs that has been assembled from disparate studies. This situation yields a fragmentary, geographically imprecise understanding of CFR variability across the ecological zones of a tribe's seasonal round and landscape. Moreover, landscape ecological data (e.g., spatial extent, patch size) relevant to our current understanding of historical fire regimes are lacking. Another area that is not well understood is the structure of traditional knowledge systems that maintained CFRs. We address these gaps by conducting a geographical analysis of CTWS burning practices across three ecological zones of the eastside Cascades, and examining the traditional knowledge system in which these practices were rooted. Knowledge about historical fire use may highlight priority zones where reintroducing traditional knowledge-based restoration strategies may have the most impact.

After describing the study area, we review the literature pertaining to historical natural resource use by the CTWS, and traditional fire use in the eastside Cascades. We then describe the mix of qualitative and geospatial methods used in this study. Our presentation of results associated with the research questions is followed by a discussion of their contributions to the literature and application to forest restoration, particularly thinleaf huckleberry restoration. We conclude by summarizing our key findings.

1.1. Study landscape and community

The Greater Warm Springs Reservation Area (GWSRA), the study landscape, spans MMC, DMC, and SG zones in the eastside Cascades (Fig. 2). We primarily employed ecological subregions (ESRs), (Hessburg et al., 2000) to delineate the three zones. In addition, in response to emergent data about resource sites, we expanded the initial MMC zone to include the area along the Cascades crest (Kuchler, 1964; USDA Forest Service ECOMAP Team, 2017).

The GWSRA consists of the Warm Springs Reservation and adjacent forest and shrub-grassland areas within which the CTWS tribes traditionally harvested culturally-valued resources (Hunn, 1990; Aguilar, 2005), including “cultural foods” – foods harvested or gathered by tribal members that have social and historical significance—as defined by the tribes’ Integrated Resources Management Plan (CTWSRO, 1992). The CTWS lands currently include the Warm Springs Reservation (259,000 ha), and treaty-ceded lands (approximately 4 million ha) where the CTWS have reserved rights (WSGVCRD, n.d.). Reserved rights sites in this study were limited to those that lie within the eastside Cascades and adjoining Cascades crest. The Ichishikin-speaking (Sahaptin) people fulfilled their food, household, and cultural needs by harvesting plant and wildlife resources found in the eastside Cascades (Hunn, 1990). The Kitsht Wasco (Wasco) also developed traditional knowledge about the area, as did the Numu (Northern Paiute), who were resettled to the Warm Springs Reservation in 1879 (Aguilar, 2005; CTWS, 2016). After reservation establishment (1855), the knowledge systems of the three tribal groups intermingled (tribal elder informants, personal communication).

2. Seasonal rounds, traditional fire use, and cultural fire regimes of the eastside Cascades

2.1. Seasonal rounds of the CTWS

At the landscape-level, the seasonal round of American Indians set the fundamental migratory spatial and temporal pattern of fire use (Turner et al., 2000), and in turn CFRs (Lake et al., 2017). “Seasonal round” means the pattern of annual migration across an area’s ecological zones to secure the variety of food and household goods that fulfill social-economic and cultural needs. Traditional fire use, as a seasonal round practice, was applied on a consistent return interval at the landscape-level (Hunn, 1990; Senos et al., 2006; Turner et al., 2011). Fire use was also applied at smaller, nested scales, specifically the habitat-scale (e.g., creating canopy openings to maintain productivity of species associated with a specific seral stage), and the population-scale (e.g., practices to maintain a particular patch) (Turner et al., 2000). Fire use was one of a variety of horticultural techniques American Indians used to maintain the composition, distribution, and spatial extent of plant communities (Anderson and Moratto, 1996; Bonnicksen et al., 1999). Others included tree girdling, pruning plants of unproductive branches, and weeding. In combination, these techniques encouraged site conditions that promoted culturally-valued resources.

Since at least 9000 years ago, when fishing settlements were inhabited near present-day The Dalles, Oregon along the Columbia River (Hunn, 1990), eastside Cascades tribes sustained themselves through a migratory seasonal round of gathering and fishing, supplemented by hunting. In addition to their dependence on the abundant salmon runs of the Columbia River system, tribes tended and gathered hundreds (or more) of forest plant species, spanning four plant categories: trees, shrubs, forbs and ferns, and grasses and grass-like plants (Marsh et al., 1987; Helliwell, 1987). The sequence of resource ripening and availability, influenced by phenological, wildlife ecological, and other seasonal factors, as well as annual climatic variability, structured the burning and tending pattern. Each of the three CTWS tribes had its own seasonal round, as structured by their territory and the distribution of culturally-valued resources (Murdock, 1980; Hunn, 1990; Aguilar, 2005).

For the Ichishkin- (Sahaptin) speaking bands, such as the Warm Springs band, dietary staples consisted of roots, especially of the *Lomatium* genus (Hunn and French, 1981), and fish, particularly salmon (Hunn, 1990). Beginning in the early spring, harvesters dug the roots and stems of plants that occur on low elevation, dry sites, particularly on dry rocky hillsides and flats, especially bitterroot (*Lewisia rediviva*), Canby’s biscuitroot (*Lomatium canbyi*), and Indian celery (*Lomatium grayi*). The round proceeded upslope as spring progressed (Hunn, 1990; Aguilar, 2005). Harvest of montane roots such as western springbeauty (*Claytonia lanceolatata* pursh) began soon after snowmelt (French, 1965). During the summer, the harvest focused on foothill species, including chokecherry (*Prunus virginiana*) and serviceberry *(Amelanchier alnifolia)*. In summer and early fall, the harvest transitioned to higher elevation forest sites, often based from encampments (French, 1965; Murdock, 1980; Hunn, 1990; Williams, 2000). For dietary and cultural reasons, thinleaf huckleberry (“We woo no Wash”), the focus of an annual ceremonial feast, was particularly important (Hunn, 1990; Pitt, 2015). The Sahaptin social-economic system also featured fibrous plants, which were used to make mats, clothing, and baskets for food gathering (Hunn, 1990).

The Wasco resided along a stretch of the Columbia River that was prime for trading, near The Dalles (Aguilar, 2005; CTWS, 2016). Celilo Village, located near the now-submerged Celilo Falls, was a main settlement. This Chinookan tribe developed a culture that resembled the Northwest Coast people. The Wasco seasonal round focused on fish (trout, pike, sturgeon, salmon, smelt, and eels)—the staple food and a trade good—, which was supplemented by roots, berries, game, and materials for household goods (Knudson, 1980; Aguilar, 2005). Gathered foods included wild potatoes, onions, hazelnuts, acorns, and huckleberries. Baskets were made of bark or grass; spoons, ladles and bowls were carved of wood.

The Numu (Northern Paiute) people inhabited the western part of the Great Basin (Fowler, 2000). Their territory extended from northern California and western Nevada into south-central and southeastern Oregon, particularly the area between the eastern Cascades and the southern Blue Mountains (Voegelin, 1955; Zucker, 1983; Couture et al.,

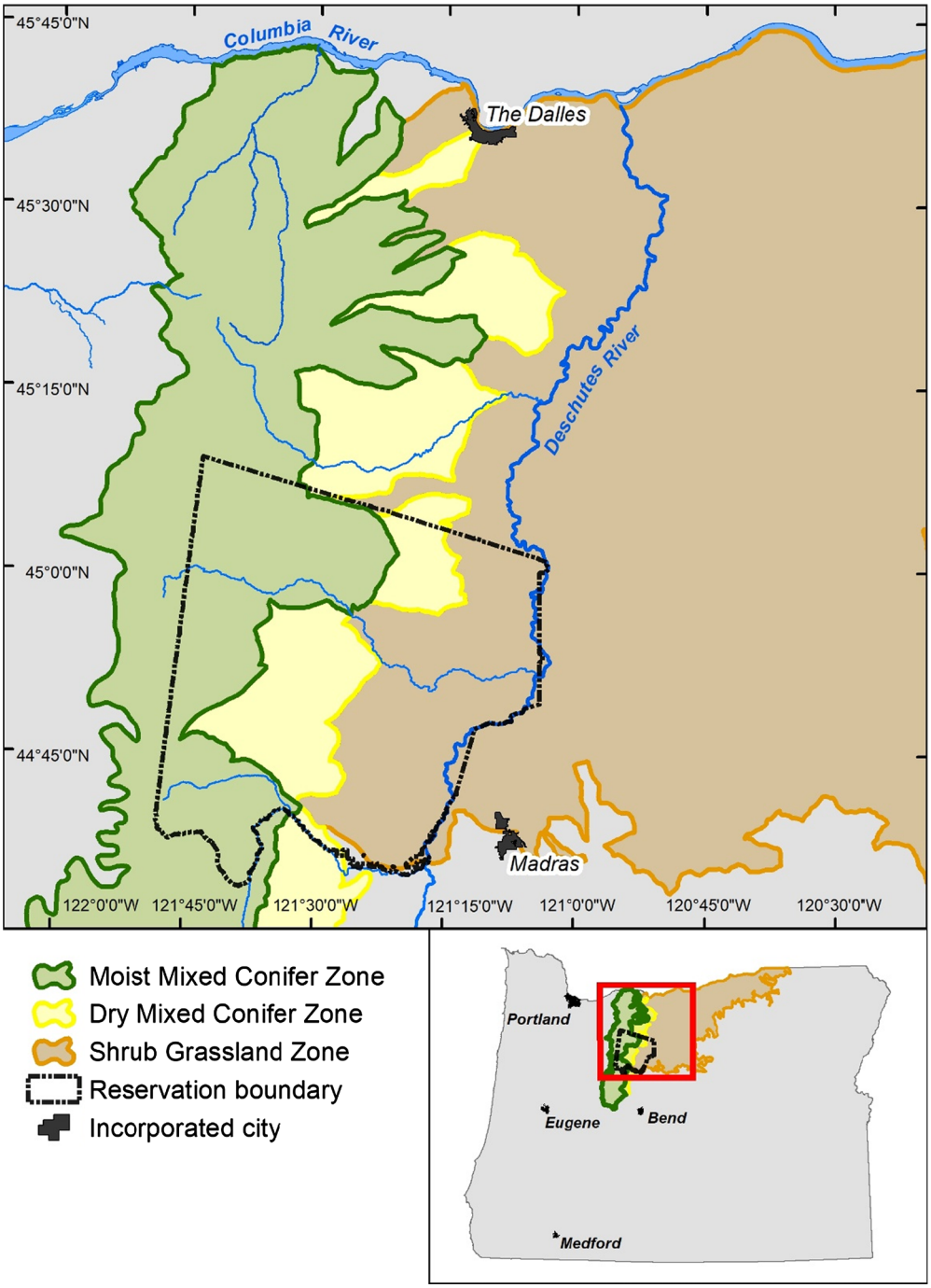


Fig. 2. Greater Warm Springs Reservation Area of the eastside Cascades of Oregon. Ecological zones are delineated mainly from ecological subregions (ESRs, Hessburg et al., 2000), with supplementation of potential natural vegetation geography (USDA Forest Service ECOMAP Team, 2017). MMC zone: ESR 4, ESR 5, and Cascades Crest (Kuchler). DMC zone: ESR 11, ESR 41, and ESR 46. SG zone: ESR 7, ESR 9, ESR 10, and ESR 45.

1986). The Numu seasonal round was adapted to the arid, drought-prone, sparsely vegetated Great Basin environment through its expansive area and "broad-spectrum" hunting and gathering (Fowler, 2000) of a large diversity of plants and animals. The family foraging group resided in temporary camps that moved in response to resource availability. Key plant resources included seed-bearing grasses for consumption, including Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Agropryon spicatum*) (Marsh et al., 1987), and at least for tribes of northern California, grasses for basketry construction and herbs for cordage (Anderson and Moratto, 1996; see also, Fowler, 2000).

2.2. Cultural fire regimes of the eastside Cascades of Oregon

In the U.S. Pacific Northwest, CFRs fall into three broad categories, generally spanning a west-to-east geography (Agee, 1993; see also Kimmerer and Lake, 2001). (1) West of the Cascade Range, the Kalapuya Indians frequently burned prairies, e.g., the Willamette Valley, and adjacent dry Douglas-fir forest. (2) In drier coastal and montane areas, including the eastside Cascades, tribal burning maintained meadow openings to promote desired plant resources and game. (3) In the inland Pacific Northwest, tribes broadcast burned grasslands and shrub-steppe regions (Shinn, 1980). Fire use varied ecologically and culturally (Boyd, 1999). In the wet conifer zone of the northern

Table 1
Ecological characteristics of ecological zones of the Greater Warm Springs Study Area, in the eastside Cascades of Oregon.

	Moist mixed conifer zone	Dry mixed conifer zone	Shrub-grassland zone
Key forest/woodland species	Grand fir (*Abies grandis*) White fir (*Abies concolor*) Douglas fir (*Pseudotsuga menziesii*) Western hemlock (*Tsuga heterophylla)* Lodgepole pine (*Pinus contorta*)	Ponderosa pine (*Pinus ponderosa*) Douglas fir (*Pseudotsuga menziesii*)	Western juniper (*Juniperus occidentalis*)
Elevation (m)[1]	820–2100	640–1100	300–700
Physiography	Deep U-shaped valleys, steep to gentle slopes, dissected ridges	Gentle to moderate slopes	Low-elevation plateau, level to gentle slopes, broken by steep V-shaped valleys
Historical fire regime	Variable regimes[2]: Mixed-severity fire/Frequent to moderately frequent intervals (< 20–50 years) Mixed severity, 50–100 year-interval High severity fire (rare)	Variable regimes[3]: PP: Low severity/1–10 year interval DF-OR: Mixed severity/ 10–25 year interval (approximately)	Variable regimes[4]: Grasslands: Low severity/very frequent (< 10 year) Shrublands: Mixed- and high-severity (25–35 year- (occasionally 50 year-) interval

[1] Marsh et al. (1987). Elevation data are approximate. Elevation ranges of zones are not mutually exclusive, due to variability in aspect and other ecological factors.

[2] "Mixed-severity": both low- and high-severity patches occur. Sources: Perry et al. (2011); Stine et al. (2014). "Low severity" = < 20% overstory trees or basal area affected. "Mixed severity" = 20–70% overstory trees or basal area affected.

[3] Sources: Hessburg et al. (2007); Perry et al. (2011); Stine et al. (2014). PP = ponderosa pine; DF-OR = Douglas fir-Oregon.

[4] The confidence of the estimated fire return interval is lower for this ecological zone than forest zones, due to limited fire scar data. Fire interval estimate based primarily on shrub and grassland species, which were historically predominant in the GWSRA; present-day prevalence of western juniper has expanded since the mid-19th century (Miller, 2005). Sources: Morgan et al. (1996); Baker and Shinneman (2004); Stine et al. (2014).

Cascades, fires were typically large and severe, potentially displacing tribes and damaging valued resources, suggesting less prevalent burning, if at all (Agee, 1993). There is evidence of Indian burning in the Oregon coast range, however (Zybach, 2003). The traditional fire use and CFRs of the eastside Oregon Cascades, where the CTWS reside today, lie within this regional context. Below, we present what is known about fire use and CFRs of the MMC, DMC, and SG zones. Table 1 presents the historical fire regimes and related ecological characteristics of these zones.

2.2.1. Moist mixed conifer zone

The CFR of the MMC zone of the eastside Cascades was characterized by small patch, low-severity burns, which maintained meadows and glades (Hunn, 1990; Agee, 1993; Williams, 2000; see also, Kimmerer and Lake, 2001). These openings dotted the matrix and edges of the true fir, Douglas fir, and other conifer communities (Agee, 1993). These openings improved the productivity of berry-producing shrub fields, including thinleaf huckleberry, grouseberry (*V. scoparium*) and blueberry (*V. caepitosum*) (Hunn, 1990; French, 1999), and increased populations of game species, such as deer and elk (Agee, 1993; Williams, 2000). Similarly, on mountain slopes of British Columbia, Canada, tribes burned to enhance berry-producing shrubs (e.g., thinleaf huckleberry, blackcap raspberry [*Rubus leucodermis*]), starch-rich roots (e.g., avalanche lily, *Erythronium grandiflorum*), and nuts (e.g., hazelnut, *Corylus cornuta*) (Gottesfeld, 1994; Turner, 1999; Turner et al., 2011).

Two factors, burn frequency and timing, controlled burn patch size and severity. Ignitions were applied to berry patches every several years. This interval is the sweet spot in which there is adequate fuel to carry a light surface burn, yet not so much fuel that the fire burns hot and creates a large patch. One Oregon Cascades settler observed, "The Indian method was to burn the old burns about every three years or as soon as there was growth enough to make a good fire" (Pioneer of 1847, in Williams, 2000:15). In general however, the burn interval may have been longer than that noted in the settler's account, due to the > 7-year period required for abundant berry production (Minore, 1984; Anzinger, 2002). Burns were timed to coincide with early autumn rain events, or in the early summer before forest fuels became dry, which moderated flammability (Hunn, 1990; Williams, 2000).

2.2.2. Dry mixed conifer zone

Forest characteristics relevant to the historical fire regime of the DMC zone are the historical presence of grasses; a well-developed understory vegetation component; and in ponderosa pine-dominant forests, a diverse age class structure due to susceptibility of older and/or scorched trees to native bark beetle-caused mortality (*Dendroctonus ponderosae; D. brevicomus*) (Agee, 1993). A frequent (approx. 10–25 year), low-severity historical fire regime promoted these vegetation and forest structural characteristics (Agee, 1993; Hessburg et al., 2007; Stine et al., 2014). Evidence of traditional fire use in the DMC zone in the eastside Cascades is sparse. For the northern Rockies however, there is suggestive evidence of widespread Indian burning of DMC forests and grasslands (Barrett and Arno, 1982).

2.2.3. Shrub-grassland zone

Tribal groups may have applied broadcast, low-severity fire to the SG zone, though the paucity of historical ecological records (e.g., fire scars) limits the certainty of conclusions (Agee, 1993). Immediately to east of the SG zone of this study, in the east-central rangelands of Oregon, the Paiute burned in late summer and early fall (Shinn, 1980). For instance, in September 1826, a Hudson's Bay Company explorer traveling east of the Deschutes River noted recently burned-over land, consistent with practices elsewhere, such as the Snake River (Shinn, 1980; Agee, 1993). In less remote places, there is suggestive evidence that tribes broadcast burned large areas frequently (perhaps even annually) (Shinn, 1980). Fire use frequency probably varied widely in association with human population density, as well as social-cultural motivations, specifically signal fires, insect gathering, and hunting (Agee, 1993).

3. Materials and methods

3.1. Approach

To answer our research questions we undertook three main steps. First, we identified culturally-valued resources for the Warm Springs Reservation and located their occurrence by ecological zone. Second, we investigated whether and how fire was used to manage these resources. We sought to understand fire use within the context of the CTWS traditional knowledge system. Third, we sought evidence of how CFRs affected historical fire regimes.

As noted, a major challenge of conducting research on CFRs is the fragmentary record and sparse geospatial data regarding traditional fire use by specific tribes (Turner, 1999; Williams, 2000). We addressed this challenge by developing an anthropological-landscape ecological GIS

framework and a traditional knowledge database. We constructed the integrative GIS framework in steps. (1) We delineated the seasonal round area of the CTWS peoples, based on secondary literature (e.g., French, 1965; Murdock, 1980; Hunn, 1990). (2) We divided this area into its constituent ecological zones (MMC, DMC, SG) constructed from biophysically modeled ecological subregions (Hessburg et al., 2000) and potential natural vegetation (Kuchler, 1964; USDA Forest Service ECOMAP Team, 2017). (3) Historical resource use sites and migration features (trails, settlements) were entered into the GIS. (4) We analyzed the elements of the traditional knowledge database by ecological zone. This approach revealed insights into geographical variation of traditional fire use and CFRs.

3.2. Materials and data processing

3.2.1. Qualitative analysis of traditional knowledge

We constructed a traditional knowledge database, featuring qualitative data, from three sources: oral history interviews, a participatory GIS (PGIS)-based workshop, and archival records (McBride et al., 2017). Where needed, CTWS ethnobotanical and forest ecological sources served as a data cross-reference (e.g., French, 1965; Marsh et al., 1987; Helliwell, 1987; Jimenez, 2002). The oral history interviews (n = 14), conducted with key informants in 2014–2015, employed a semi-structured protocol (Patton, 2002). Interview guide topics were traditional fire use of various ecological zones and influences on fire use. The PGIS workshop, conducted in November 2017, generated focus group-based oral histories (3 focus groups, 32 participants) and geographical data about the interview guide topics. Standard PGIS techniques consist of participant mapping of features relevant to community knowledge and/or values (Besser et al., 2014; McBride et al., 2016). We developed a novel PGIS technique that was adapted to the CTWS community. We supplemented maps with ethnohistorical photographs that depicted activities, places, and people familiar to CTWS participants. We also used base map features that included historical village sites and trail networks derived from a federal survey conducted in 1922–1926, and botanical zones containing culturally-important resources derived from primary and secondary sources (Marsh et al., 1987; Helliwell, 1987; Jimenez, 2002; UWLSC, 2008). These photographs and base map features elicited interactive oral histories associated with each ecological zone. To protect sensitive cultural data, all place-specific data were aggregated by ecological zone. We also extracted data from archival resources (ethnographic records, survey maps) collected from the David H. and Kathrine S. French Papers and the Eugene Hunn Papers, held by the University of Washington and Reed College.

Interviews and the PGIS workshop were recorded and the recordings transcribed. We analyzed the qualitative data using a coding scheme developed through a grounded theory approach (Patton, 2002). We identified emergent themes from the data, which we related to *a priori* themes from the literature. This process generated the four traditional knowledge system elements (Fig. 1) that structured the coding scheme and was applied to the transcribed data. Inter-coder reliability procedures consisted of examining data examples as a team to assess and refine the coding scheme.

3.2.2. Geographical characterization of traditional fire use and burn land-cover

Geographical characterization of traditional fire use and burn land-cover was derived from the Cascade Range Forest Reserve inventory conducted by the U.S. Geological Survey, in 1901 (Langille et al., 1903); ethnohistorical slide imagery of cultural food harvest sites, 1952–1954 (UWLSC, 2008); and oral history interviews. We also quantified the historical village site and trail network data from the PGIS base maps by ecological zone to improve understanding of where human activity was concentrated.

Historical burn land-cover polygons, acquired from the Cascade Range Forest Reserve inventory, were processed using ArcMap 10.3.1. The purpose was to develop baseline data of historical burn geography as a potential influence on subsequent fire use, regardless of ignition source (lightning vs. anthropogenic). We derived data for two variables, burn land-cover area and patch size, from this inventory. Limitations are noted: (i) DMC forest burns are potentially under-represented because surveyors tended to focus on high-severity fire (Langille et al., 1903); (ii) paucity of ignition source information (natural vs. anthropogenic); and (iii) an absence of data for the SG zone, which was outside the inventory area.

The ecological conditions of cultural food sites were derived from the ethnohistorical imagery of D.H. and K.S. French. These anthropologists conducted field work on the CTWS peoples in the mid-20th century, particularly 1949–1956 (UWLSC, 2008). Site locations of the images were identified and entered into the project GIS using U.S. Geographical Survey (USGS) 7.5 min topo-quadrangle maps in consultation with forest managers (CTWS Branch of Natural Resources, Mt. Hood National Forest) and tribal informants.

Spatial data about fire use were gleaned from the PGIS workshop-based oral histories (conducted in 2017) and oral history interviews (2014–2015). Our interview protocol elicited information about the location, timing, severity, and patch size of anthropogenic fire. We elicited data about reference forest structure conditions using imagery from two sources: historical photographs of the study area showing forest type and successional stage, and stand simulations of forest type and successional stage, constructed from Visual Nature Studio software (USDA Forest Service, n.d.).

4. Results

4.1. CFRs among ecological zones of the GWSRA

Evidence from the oral history interviews, participatory GIS, archival data, and spatial analysis revealed that the CTWS peoples deployed fire to increase the ecological productivity of, and access to, certain disturbance-dependent culturally-valued resources in the east-side Cascades. However, fire use varied among ecological zones (Table 2). We found evidence of traditional fire use in the MMC zone, and an absence of such evidence in the DMC and SG zones, which we interpreted to mean that the CTWS peoples maintained a CFR in the MMC zone only. Diverse cultural foods of the seasonal round were tended historically in all three zones (Fig. 3). The ecological utility of burning apparently varied, however, which contributed to fire use variability among ecological zones. In addition, analysis of the historical travel network revealed that trail length was concentrated in the MMC zone (59.0%), compared to the DMC zone (31.8%) and SG zone (9.2%). Settlements were primarily located in the SG zone (80%) and DMC zone (20%). The dense trail network into MMC forests from lower-elevation SG zone settlements supported an overall picture of migratory burning and tending in this zone (e.g., based from encampments).

In the MMC zone, the CFR consisted of low severity, frequent (every few years), small-scale ignitions applied to existing huckleberry shrub sites according to most, but not all, informants. The main reasons to burn were to clear away competing vegetation from the thinleaf huckleberry shrubs and maintain access. If left unchecked, competing vegetation would likely have reduced huckleberry productivity owing to the combination of moist growing conditions and fire recurrence interval variability. Besides burning, other practices to maintain productivity were harvesting and girdling trees, which maintained canopy openings, and possibly weeding out competing shrubs.

In the DMC zone, culturally-important resources included roots (e.g., wild carrot (“saw-wickt”, *Peridérida gairdneri*)); bulbs (e.g., blue camas (“wa-ka-mo”, *Camassia quamash*), which occurred in meadows); and chokecherry, a berry-producing shrub. Thinleaf huckleberry also occurred in the DMC zone of the GWSRA, though with lower productivity than in the MMC zone (Jimenez, 2002; USDA Forest Service,

Table 2
Cultural fire regime and traditional knowledge across ecological zones of the Greater Warm Springs Study Area.

	Moist mixed conifer zone	Dry mixed conifer zone	Shrub-grassland zone
Cultural fire regime	Low severity, frequent ignitions applied to specific plant resources	Fire use not reported	Fire use not reported; natural ignitions perceived as beneficial
Tribal ecological principles	Burning promotes ecological functions that maintain huckleberry productivity (control of competing vegetation and insects, soil replenishment) and resource access	None reported	Fire replenishes productivity of edible roots
Key resources	– Bear grass – Mountain ash berries – Pine nuts[1] – Thin-leaf huckleberry – Western red cedar	– Black lichen – Blue camas – Chokecherry – Thin-leaf huckleberry[2] – Wild carrot	– Biscuitroot – Bitterroot – Desert parsley – Indian celery
Cultural relevance	Huckleberry feast ceremony	None reported	Root feast ceremony
Seasonal round mode[3]	Large, extended family group, long duration	None reported	Individual/small group, short duration
Trail distribution (% length in zone)	59.0	31.8	9.2
Village distribution (% in zone)	0.0	20.0	80.0

[1] White bark pine (*Pinus albicaulis*) may be the species of the pine nuts historically gathered in the MMC zone, as indicated by several sources: Keane, R.E., Tomback, D.F., Aubry, C.A., Bower, A.D., Campbell, E.M., Cripps, C.L., Jenkins, M.B., Mahalovich, M.F., Manning, M., McKinney, S.T. and Murray, M.P., 2012, A range-wide restoration strategy for whitebark pine (Pinus albicaulis), Gen. Tech. Rep. RMRS-GTR-279, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO,108 pp.; US Forest Service, 1977, Draft Environmental Statement, Badger-Jordan Planning Unit of Mt. Hood National Forest, Portland, OR, 219 pp.; Hayes, H.E. and Pague, B.S. 1891. Biennial Report of the Oregon Weather Bureau, Frank C. Baker, State Printer, Salem, Oregon; Lang, F.A. 2019. Whitebark pine, The Oregon Encyclopedia, https://oregonencyclopedia.org/articles/whitebark_pine/#.XQk0dYhKh9N, last accessed 6/17/19.

[2] Occurrence is occasional in this zone (Marsh et al., 1987).

[3] Sources: Zucker (1983); ethnohistorical records, D.H. and K.S. French papers, Special Collections, University of Washington.

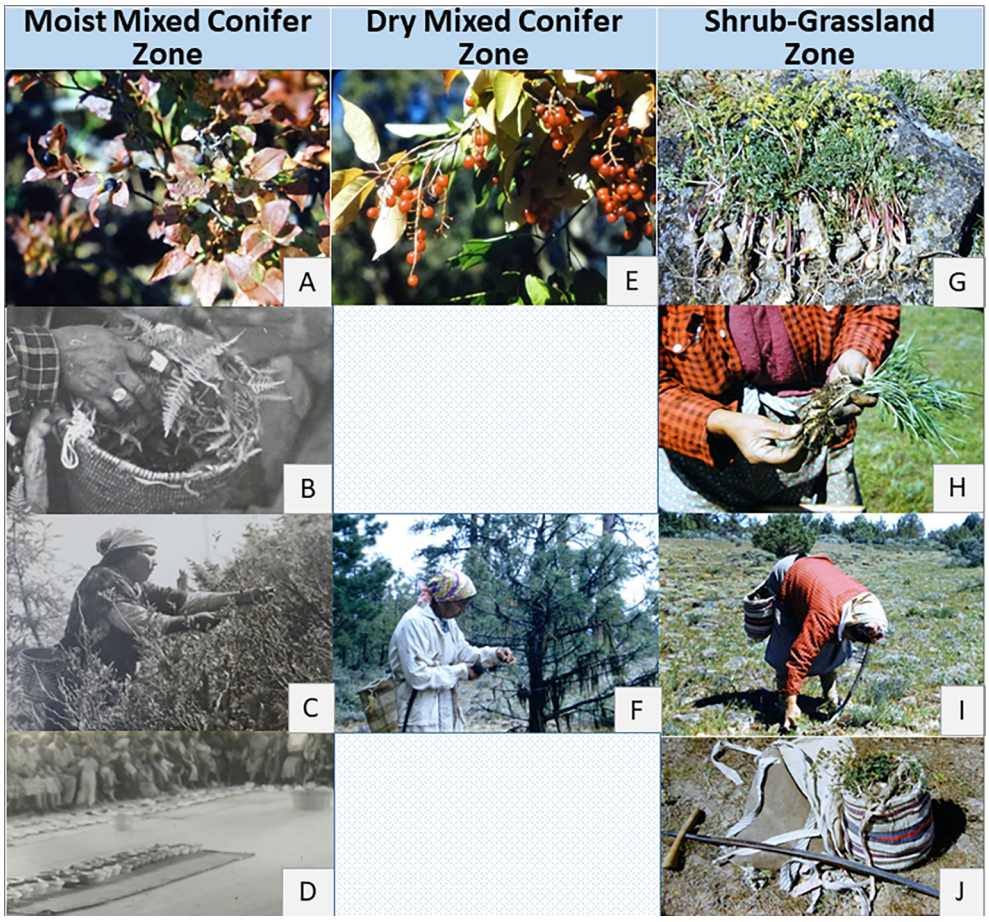


Fig. 3. Example resources maintained by traditional knowledge in ecological zones of the Greater Warm Springs Study Area. Moist mixed conifer zone: big-leaf huckleberry, Mt. Hood area (A); harvest, preserved with fern fronds (B, UW negative 38663); huckleberry picking (C, UW negative 38875); huckleberry feast ceremony (D). Dry mixed conifer zone: chokecherries, Shitike Creek area, Warm Springs Reservation (E); "kunc", a confection derived from black lichen (F). Shrub-grassland zone: biscuit root (G, H, I, J). Image dates: 1951–1955. Images are derived from the University of Washington Libraries, Special Collections, David H. and Kathrine S. French papers, Accession 5496-001, Box 54. (Slide images not assigned a UW negative number unless otherwise stated.)

Table 3
Historical (1901) burn land-cover pattern in the eastside Cascades of Oregon, Greater Warm Springs Study Area.

Ecological zone	Ecological subregion (ESR)[1]	Percentage of area in burn land-cover	Burn land-cover patch, mean (ha)
Moist mixed conifer zone	All ESRs of zone	12.3	406.7
	Ecological subregion 4	16.6	280.0
	Ecological subregion 5	9.9	363.3
	Cascades Crest (Kuchler)[2]	12.8	738.2
Dry mixed conifer zone	All ESRs of zone	1.7	107.0
	Ecological subregion 11	2.4	60.6
	Ecological subregion 41	2.6	223.0
	Ecological subregion 46	0.0	0.0
Shrub-grassland zone	n.a.	no data	no data

[1] Names corresponding with ESR numbers are of the form: ESR number = Bailey's ecoregion – Dominant Precipitation Class(es) – Dominant Potential Vegetation Group(s) – Dominant Solar Radiation Class(es) (Hessburg et al., 2000). 4 = M242C – Wet – Warm – MFCF – Low Solar; 5 = M242C – Moist – Warm – MF/CF – Mod Solar; 11 = 200/300 – Dry Moist – Warm – MF/DF – Mod Solar; 41 = M242C – Moist – Warm – MF/DF/CF – High Solar; 46 = M242C – Moist – Warm – DF – High Solar. M242C = Eastern Cascades Section. 200/300 = Okanogan Highlands - Eastern Cascades Sections.

[2] The area of this ecological unit lies outside the geographical extent of the ESR framework (Hessburg et al., 2000). Thus, this unit is derived from the potential natural vegetation framework (Kuchler, 1964; USDA Forest Service ECOMAP Team, 2017).

2010). Our informants reported an absence of burning in this drier zone—a surprising result, given evidence elsewhere that demonstrates burning to promote geophytes (Anderson, 1997, Anderson and Lake, 2016). Lower precipitation and a comparatively frequent natural fire return interval may have constituted an ecological combination that posed less need for fire use in the eastside Cascades.

Edible roots were (and are) the primary cultural food of the SG zone. Staple roots included biscuitroot ("coush", *Lomatium cous*) and bitterroot ("Piyati", *Lewisia rediviva*). The cultural importance of these starch-rich foods was manifested in the root feast, an annual ceremony. These foods were tended through digging practices of the seasonal round. Apparently, fire was not employed by the CTWS to promote resource productivity in this zone, according to tribal informants. However, informants noted increased resource productivity in the years after a natural fire burned over gathering sites; such ignitions were spoken of as a positive event. In this arid zone, the need to control competing vegetation and improve resource access may have been minimal.

Our analysis of historical burn land-cover data provided a landscape-scale context for assessing the role of CFRs in historical fire regimes. The burn area distribution was disproportionately high in the MMC zone (12.3% of zone area) compared to the DMC zone (1.7% of zone area); (SG: no data), (Table 3, Fig. 4). Variability in burn severity, persistence, and cumulative fire scar area may have contributed to the magnitude of difference in burn area among zones, however. The forest inventory (Langille et al., 1903) indicates that burn openings were prevalent in the MMC zone, regardless of initial ignition source (e.g., lightning, settler burns), which traditional fire use appears to have subsequently maintained. Within the MMC zone, burn land-cover was prevalent in the ecological subregions where huckleberry fields were maintained, particularly the Cascades Crest Forest (12.8%). Burn patch size was comparatively large in the MMC zone (406.7 ha) relative to the DMC zone (107.0 ha).

The CFR of MMC forests contributed to the maintenance of openings in mid- and high-elevation montane sites according to ethnohistorical slide imagery and oral history data (Fig. 5). The CTWS applied frequent, low-severity burns on an as-needed basis to maintain openings apparently initially created by large conflagrations. Ignitions were applied to targeted shrub patches, thereby tending to maintain and/ or expand existing openings, estimated at tens to hundreds of hectares (based on historical inventory data), rather than create new openings. This practice resulted in a shifting anthropogenic disturbance pattern across an area that spanned an estimated 220,000 ha across 24 cultural food resource sites on the mid- and upper-elevations of mountain slopes (Mt. Hood, Mt. Jefferson) and buttes of the eastside Cascades and Cascades crest.

4.2. Traditional fire use of thinleaf huckleberry in the CTWS traditional knowledge system

Traditional fire use by the CTWS focused on thinleaf huckleberry. Further analysis revealed that fire use was maintained by a traditional knowledge system composed of four interconnected elements: (i) resource tending practices; (ii) tribal ecological principles; (iii) the seasonal round; and (iv) culture (see Appendix A).

4.2.1. Resource tending practices

Most informants were told by their elders, or had seen as a child, that burning was intentionally used to manage huckleberries. However, one participant reported that tribal members relied on lightning-ignited fires, yet indicated that humans promoted ignitions by preparing site conditions, such as concentrating flammable material (e.g., conifer needles), then praying for lightning strikes. Ignition sites occurred in the MMC zone on Mount Hood and Mount Jefferson, particularly along the Cascades crest. Huckleberry patches were described as having sparsely distributed, small-diameter, short trees, a dense field structure of huckleberry shrubs, and few other understory plants. Huckleberries were also harvested at lower elevation DMC sites. However, informants reported that fire was not used to manage berry patches in the DMC zone. Fire does not appear to have been used extensively, if at all, to manage other resources, such as edible roots, lichen, and medicinal plants in this zone. This said, one interviewee reported that the Paiute used fire to manage roots and possibly oak in lower elevations east of the reservation. All other informants reported that fire was not used to manage roots, although several had observed an increase in root productivity on some sites after burn exposure.

Participants described a rotational system in which different areas were burned each year. One informant reported a 7-year rotation interval. Fires were typically set in the fall at the end of the berry season when temperatures were lower, at precipitation onset, thereby promoting low-severity burns. Occasionally fires were set in late spring but not in the summer because they would be too difficult to control. Small (e.g., < 1 ha), low-intensity burns were designed to control competing underbrush (e.g., snowbrush (*Ceanothus velutinus*)) while not damaging the berry bushes. Fire control practices consisted of clearing flammable material (needles, small branches) from the target area and stationing fire guards. Rather than burn one large area simultaneously, a series of micro-fires (~1 m in diameter) were set. Several informants reported that rituals and prayers were used to bring rain to control the burns.

Fire specialists determined when ecological conditions were appropriate for burning. Fire specialists were older males who had been trained from an early age and had accrued knowledge to determine

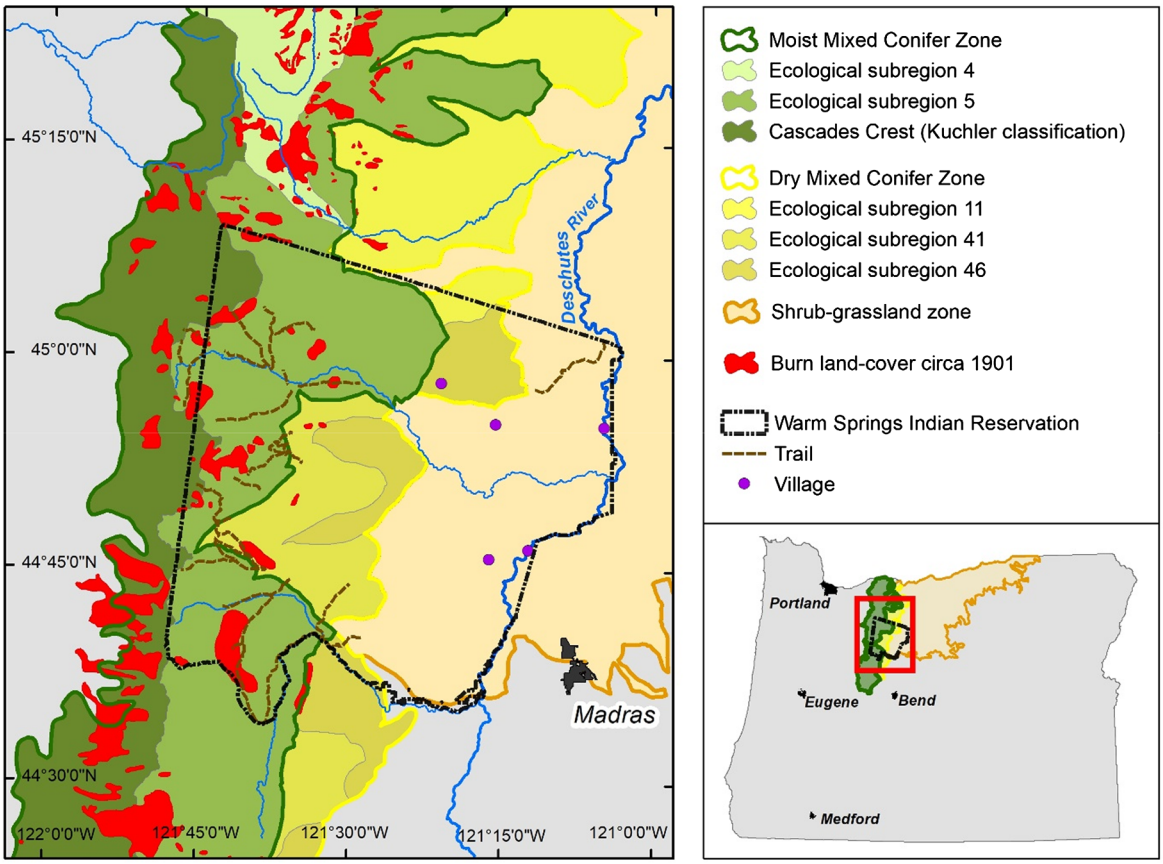


Fig. 4. Historical (1901) landscape pattern of burn land-cover, Greater Warm Springs Study Area. Land-cover data: Langille et al. 1903. Trail and village data: federal survey of Warm Springs Reservation, 1922–1926. For ecological zone details, see Table 3.

when weather conditions were conducive to controlled burns. Internal regulation of fire use by the community has been observed elsewhere (Huffman 2013). Huckleberry resource management was a collective endeavor rather than an individually-organized practice, as described by tribal informants.

4.2.2. Tribal ecological principles

Controlled burns were based on a set of tribal ecological principles and aimed to fulfill several purposes: insect control, reduction of understory vegetation and downed debris, control of tree encroachment, huckleberry patch expansion, stimulation of new plant growth, and soil fertility replenishment. Burn practices were designed to produce stand structure conditions that promoted huckleberry productivity, consistent with previous findings (French, 1999). Target conditions included open sites with scatterings of small diameter trees within the berry fields, relatively little underbrush, few downed logs, and large, densely concentrated huckleberry bushes. Removal of competing understory vegetation improved ecological productivity (e.g., of berries) and facilitated traversing of the fields by harvesters. These cultural site characteristics are also important to beargrass (*Xerophyllum tenax*), which sometimes occurs intermixed with huckleberry shrubs (Hummel and Lake, 2014).

4.2.3. Seasonal round

Fire use was integrated into the seasonal round. In late summer and early fall, tribal members traveled from villages, primarily located in the low elevation SG zone up into the MMC zone to access high country berry fields, deer and elk hunting grounds, and other resources. Base camps near the berry fields, where multiple extended families camped, functioned as an important social structure of the seasonal round. Women and children did most of the berry picking; men handled the packhorses and hunted for deer and elk. The volume of annual huckleberry harvest was substantial (2.5–8 gallons (estimated)/harvester/day).

4.2.4. Culture

The use of fire for huckleberry management was strongly associated with CTWS culture, particularly prayers and rituals. The huckleberry feast, held in early August, was (and remains) an important annual ritual in honor of the huckleberries. A number of participants attributed the poor present-day condition of berry fields to failure by tribal members to properly honor the huckleberries. They highlighted the importance of treating the plants that sustain the tribes with respect; otherwise, ecological productivity would be reduced.

Community cohesion embodied in the intergenerational and interfamilial gifting of huckleberries was a primary tending motivation. A rite of passage for CTWS adolescent girls—a counterpart to a hunting rite for adolescent boys—was a girl's first harvest, which culminated in gifting.[2] Similarly, the huckleberry feast functioned as a ceremonial expression of the longhouse religion, and included ritualized food songs, speeches, and reciprocal gifting. The ceremony brought together the community in sacred thanksgiving.

A worldview of human-nature interdependence also governed fire use and associated practices among the CTWS: if people take care of nature, nature will provide. Linked to this worldview is the belief that plants will reduce productivity if people neglect to tend them. Harvesting berries and edible roots was viewed also as benefitting and thereby honoring these cultural foods.

[2] University of Washington Libraries, Special Collections, David H. and Kathrine S. French papers, Accession 5496-001, Box 16.



Fig. 5. Historical reference conditions of sites traditionally tended for big-leaf huckleberry, in the moist mixed conifer zone, Greater Warm Springs Study Area. Fire use was applied into the late 1920s-/early 1940s. Mt. Hood area resource site, 1953, depicting upslope and downslope views (A, B). Multorpor Mountain berry picking area, western slope, 1952; Multorpor Mountain is a small volcanic cone on the southern slope of Mt. Hood (C, UW negative 38660). Mt. Hood area from Multorpor Mountain berry picking area, 1952 (D, UW negative 38662). *Wasquapam satas*, loosely translated as "site where the Wasco harvest", Warm Springs Reservation, 1954 (E, F). Images are derived from the University of Washington Libraries, Special Collections, David H. and Kathrine S. French Papers, Accession 5496-001, Box 54. (Slide images not assigned a UW negative number unless otherwise stated.)

The intergenerational transmission of traditional knowledge was largely field-based and informal, with children expected to learn by watching and imitating their elders. For specialized knowledge such as fire prayers and practices, knowledge was passed on to someone who was recognized by the elders as having a gift for being a "seer". The longhouse ceremonies, such as the huckleberry feast, were key occasions during which cultural knowledge was transmitted to tribal youth.

4.3. Social and ecological ramifications of the disruption of traditional fire use

Traditional fire use on the GWSRA continued on some sites into the late 1920s/early 1940s, according to most tribal participants, although one informant observed that burning had stopped by the late 1800 s. It may be that burning continued into the 20th century on sites where enforcement was limited. The cessation of traditional burning was due in part to the emergence of fire suppression policies of forest land management agencies, as occurred for the Karuk of northern California (Norgaard, 2014), and the Klamath (Turner, 2011). One example policy may have been the US Forest Service – state Cooperative Forest Fire Prevention Campaign of the early 1940s to protect wartime timber supply (Williams, 2009). Another potential factor in fire use disruption may have been escaped burns. One participant noted a large fire that took place in 1938 near Mount Hood—attributed to tribal members burning their huckleberry fields—as a key turning point in burning prohibition. This fire burned the same year that a fire (40,000 ha) occurred in the SG zone of the Warm Springs Reservation (Logan, 1982). Finally, fire use cessation was attributed to the younger generation of men not acquiring the necessary knowledge or skills during the post-World War II era, when they began shifting into new occupations. This combination of change in forest policy, social conditions, and fire events may have increased pressure on CTWS members to curtail burning practices.

The disruption of traditional fire use has contributed to an array of social ramifications (Table 4). One, tribal youth reportedly have experienced a loss of traditional knowledge of burning techniques, a diminished interest in food gathering, and an erosion of tribal language fluency. In response, the Warm Springs community—as one of thirteen tribes operating within the U.S. Fire Learning Network—has worked to recover and rejuvenate this traditional knowledge, including tribal languages, by engaging tribal youth in traditional burning practices (Huffman, 2013). Two, the overall community has reportedly experienced a weakening of traditional beliefs, the traditional relationship with the natural world, and community cohesion.

Fire use disruption also brought about ecological change (Table 4). All of the study participants described the present-day montane huckleberry fields where they had picked as youth as "overgrown," resulting in decreased patch area and productivity, and impeding access due to dense undergrowth. Key ecological changes included an increase in competing vegetation and tree size, resulting in more shade, smaller berry shrubs, and smaller patches. An implication of the understory vegetation accumulation is an increase in fuel loading and potential fire risk and severity if and when wildfires burn after a long absence. Additionally, informants reported the incursion of "non-traditional" plants and willows and more downed wood, further inhibiting access.

Table 4
Social and ecological changes and ramifications of disruption of traditional fire use.

Category	Changes	Ramifications
Social	Loss of ecological knowledge of traditional fire use practices and gathering site locations	– Diminished interest among youth in traditional food gathering and tending – Reduced fluency of language associated with traditional food gathering
	Weakening of traditional beliefs	– Huckleberry plants no longer honored; consequently, the resource is making itself less available for harvest, as perceived by traditional food gatherers – Harvest for huckleberry feast sometimes occurs outside the tribes' traditional territory – Huckleberry fields neglected, due to lack of harvest (harvest perceived by traditional gatherers as a fundamental mechanism of resource tending) – Some tribal members sell huckleberries –a departure from the traditional view that surplus berries should be given to elders and others who aren't physically able to gather them
	Weakening of community cohesion	– Fewer tribal members respect traditional beliefs, behaviors, and spiritual practices
Ecological	Forest encroachment into huckleberry patches	– Decline in huckleberry productivity and area
	Increased density of understory species other than huckleberry plants	– Increased competition for sunlight and soil nutrients, decreased size and productivity of berry bushes, and impeded access to and within berry fields
	Increased fuel loading of downed woody debris	– Impeded access to and within berry fields – Increased fire risk and susceptibility to higher severity, more damaging fires, especially under extreme conditions (e.g., summer drought)

5. Discussion

5.1. Fire use in the eastside Cascades in relation to CTWS traditional knowledge

Our analysis revealed that the distribution of fire use across ecological zones of the eastside Cascades was maintained by the CTWS traditional knowledge system, which was comprised of four interrelated elements: resource tending practices, tribal ecological principles, the seasonal round, and culture. These findings expand upon the existing understanding that fire use is a part of the traditional knowledge system (Turner et al., 2000; Lewis and Anderson, 2002; Stewart, 2009; Huffman, 2013; Lake and Long, 2014) in that we relate fire use to a landscape ecological framework. The seasonal round provided valuable insight into the spatial and temporal pattern of fire use. This factor is associated with data about the biogeographical distribution of culturally-valued plant resources, and by extension the spatial pattern of practices to enhance and access such resources. In addition, the seasonal round denoted data about an array of factors influential to fire use (e.g., encampment duration, encampment group size, harvest volume, preservation techniques). For instance during dry, windy periods, the escaped embers of fires set to dry and preserve the harvest may have augmented intentional burning (Minore et al., 1979). Finally, an aspect of the seasonal round that provided insight into the spatial pattern of fire use was quantification of the trail network. We found that the zone with the highest density of trails, indicating prevalent tribal activity, was associated with fire use. Similarly in the western Klamath Mountains, a relationship has been detected between the spatial patterns of the trail network and settlements and traditional fire use (Lake, 2013). These findings demonstrate how the seasonal round —a type of cultural geographical variable— can reveal historical linkages between tribal societies and landscapes, thereby guiding current restoration.

Our data also highlighted the role of culture in fire use pattern. Culture includes the traditions (e.g., ritualized ceremonies) and social roles (fire specialists; determinants of the start of the huckleberry harvest) through which fire use and other tending knowledge was maintained over generations. For instance, huckleberry traditional knowledge was stewarded by small, designated groups of men and women; in time, these groups transmitted this knowledge to the next generation through a deliberate process of designating specific tribal youth to learn and steward the traditional knowledge. Huckleberry ("We woo no Wash") drew together the tribal community through intergenerational and interfamilial gift-giving, the longhouse religion, as well as gathering by family groups at seasonal encampments, making it a cultural keystone species. When considered in light of previous studies (Berkes et al., 1995; French, 1999; Turner, 1999; Stewart, 2009; Long et al., 2015), we conclude that CTWS traditional burning in MMC forests of the eastside Cascades was purposeful, systematically deployed, intergenerationally maintained, guided by a highly valued knowledge system, and understood as a spiritual obligation and a stewardship responsibility.

Our results also highlight the ramifications of the disruption of traditional fire use on the CTWS community and resources, as has been documented elsewhere in the Pacific Northwest (Turner, 1999; Senos et al., 2006; LeCompte, 2018, and the Inland Northwest (Carroll et al., 2010)). By the late 1920s/early 1940s—about eight decades after the 1855 Treaty with the Tribes of Middle Oregon and roughly contemporaneous with the onset of commercial forestry on the Warm Springs Reservation (Logan, 1982) –fire use had been largely discontinued. Traditional knowledge must be applied if it is to persist and flourish (Charnley et al., 2007; Huffman, 2013; Lake et al., 2017). We found that traditional knowledge has a community basis. An implication of this finding is that unless the community is engaged, traditional knowledge risks deterioration (LeCompte, 2018).

5.2. CFRs of eastside Cascades ecological zones

Our analysis of the MMC zone of the eastside Cascades revealed a CFR characterized by a shifting rotation of frequent, low-severity, small-scale burns at targeted huckleberry patch sites. These results correspond with those of montane areas elsewhere in the Pacific Northwest, including of the Stl'atl'imx (Lillooet) peoples of the Pemberton Valley, B.C., Canada who deployed fire to tend berries and montane roots (*Erythronium, Lilium*) (Turner, 1999), and the Gitksan and Wet-suwet'en peoples of northwestern B.C., who tended mid-elevation *Vaccinium* berry patches (Gottesfeld, 1994). Oral histories have produced evidence of a several-year, rotational fire use pattern in montane areas of B.C. and ecological reasoning that corresponds with the results of this study: "when it got [too] bushy" (Turner, 1999:189), individuals burned one hillside area, then redirected harvesting to an unburnt area. In combination, these findings provide evidence that tribal peoples maintained a CFR in MMC forests of the Pacific Northwest.

Our findings also provide insight into how the CFR of MMC forests may have influenced the zone's historical fire regime and landscape structure. Our results correspond with the evolving picture of MMC zone dynamics that large fires accounted for the most area burned, yet small and medium fires were the most numerous (Stine et al., 2014). The CTWS apparently contributed to fire frequency by applying frequent, low-severity burns on an as-needed basis to maintain openings initially created by large conflagrations, as indicated in the 1901 forest inventory. This finding also expands upon previous research (French,

1999) by identifying geographical evidence that sites traditionally maintained for huckleberry tended to occur on or near large burn scars. This result suggests that the CFR may have contributed to the variability of the mixed severity fire regime, as occurs in the Pacific Northwest (Perry et al., 2011). That is, CTWS ignitions may have intermixed frequent, low-severity fire with the comparatively infrequent, natural ignitions that initially created large openings. The resulting patchwork of burn openings and fuels distribution may have increased historical forest resilience to wildfire (Stine et al., 2014; Hessburg et al., 2015).

At the landscape level, our results show evidence of variability in the eastside Cascades CFRs. We found that traditional fire use was pronounced in mid- to high-elevation MMC forests, but unpronounced for the DMC and SG zones. This result suggests that the CTWS varied ignitions in response to the practical need and appropriateness in different ecological zones and associated natural fire regimes. For certain roots harvested by the CTWS in the SG zone, our results differ from existing studies. For geophyte food plants such as Indian carrot, CTWS informants reported that fire was not purposefully applied, although natural ignitions were perceived to be beneficial. This result contrasts with that of many Sierra Nevada tribes (e.g., Sierra Miwok , North Fork Mono, and others), who reported burning, along with tilling, to promote this species (Anderson, 1997; Anderson and Lake, 2016). For the CTWS, this species tends to grow on low elevation meadows (Marsh et al., 1987), which may be slightly drier and less prone to competing vegetation than those of the Sierra Nevada. Similarly, the absence of CTWS fire use to promote camas contrasts with that reported for the Salish of southern Vancouver Island (Turner, 1999; Turner and Peacock, 2005). Camas harvested by the CTWS tends to grow in meadows (Marsh et al., 1987), whereas that harvested by the Salish occurred on Gerry Oak savannah within the Western Hemlock Biogeoclimatic zone, which is thought to be prone to afforestation. These contrasting findings may be due to regional differences in fire utility. We conclude that fire use variability in the eastside Cascades was driven by its relative ecological appropriateness for maintaining culturally-important resources, as has been shown in Pacific coastal North America (Turner et al., 2011).

5.3. Applications

5.3.1. Applications to thinleaf huckleberry enhancement and forest restoration

Our analysis revealed that the cessation of fire use (by the 1920s-1940s) contributed to reduced productivity and trail navigability of thinleaf huckleberry patches, despite the persistence of this understory shrub (USDA Forest Service, 2010). Informants cite two main causes of this ecological change. First, little sunlight reaches the shrub patches, due to canopy closure and encroachment by trees and competing undesired shrubs—a finding that corresponds with other studies of the eastside Cascades (Senos et al., 2006; USDA Forest Service, 2010; LeCompte, 2018), and B.C., Canada (Turner, 1999). Second, on commercial forest management units, trampling by equipment, vehicles, and yarding can damage shrub patches in the short-term; in addition, logging appears to promote weedy annuals and biennials (Anzinger, 2002). However, foresters note that these impacts subside over time. Soil moisture loss is a compounding factor on sites prone to evaporation and drainage (CTWS Branch of Natural Resources, personal communication). These findings highlight the need for huckleberry restoration prescriptions.

In response, natural resource managers of the GWSRA have adopted huckleberry enhancement prescriptions (Jimenez, 2002; USDA Forest Service, 2010). These prescriptions address objectives to enhance cultural foods for use by tribal members while fulfilling forest stand growth and yield targets, as directed by the agency's forest plan (CTWSRO, 1992). Huckleberry treatments strive to balance appropriate levels of sunlight and shade by retaining a partial overstory (canopy closure target: 30–50% (CTWS personal communication)). CTWS managers are implementing a variety of treatments, which range from commercial thin (70–110 trees per acre (tpa)), to "landscape" intermediate thin (50–70 tpa), to shelterwood (15–25 tpa), and "shelterwood – light" (10–15 tpa) on selected commercial harvest units in the MMC zone (management groups: grand fir; western hemlock-beargrass; mountain hemlock-lodgepole pine, and Pacific silver fir). These harvest modifications constitute an initial transition away from the intensive timber management of the 1960s-1970s, which featured even-aged harvests (clear-cut and plantation) (Logan, 1982). Such harvest modifications are notable, given the constraints posed by long-term management plan harvest commitments (CTWSRO, 1992; CTWSRO, 2012), forest operations, and restoration funding limitations. Managers report that huckleberry treatments allow sunlight to reach understory vegetation and reduce soil water loss, resulting in improved huckleberry productivity. In addition, a snowpack logging prescription (snowpack minimum: 0.9 m to 1.5 m) protects understory vegetation. Finally, CTWS managers have adopted road-edge vegetation retention, which reduces the deposition of detrimental roadbed dust onto huckleberry shrubs.

Although silviculture proxy fire treatments reportedly promote the objectives of forest growth and resource enhancement, such proxy treatments fall short of replicating the ecological benefits of traditional fire use. At the Big Huckleberry Summit (2007), Muckleshoot, Nisqually, Umatilla, and Warm Springs participants reported that fire performs many ecological functions, including nutrient cycling, reinvigoration of plant sprouting, and control of detrimental insects and diseases (LeCompte, 2018). This finding highlights the utility of fire reintroduction on sites where silvicultural objectives allow.

Our results about CFR scale suggest how a nested, multi-level framework, spanning patch- ("landscapes within landscapes") and landscape-levels (Hessburg et al., 2015:1089; see also, Stine et al., 2014) may be employed to reintroduce fire. At the finer-scale, our analysis revealed that the CTWS historically used fire in a rotational pattern to maintain patch openings in the MMC zone (Fig. 5). This finding suggests that one approach to restoration is a multi-stage fire reintroduction process. First, low severity fire initially could expand (or create) forest openings. Second, on-going, shifting application of frequent fire or proxy treatments around the management unit could maintain openings.

At the landscape-level, our analysis revealed that the spatial extent of the CFR (~220,000 ha) spanned an area that currently includes multiple ownerships—the Warm Springs Reservation and the Mt. Hood National Forest. This finding suggests that coordinated planning across ownerships is important to manager capacity to restore forest resilience and enhance cultural food resources. Incident management teams could allow wildfire use in areas that promote desired resources, provided that they do not pose a threat to life and property (Wildland Fire Decision Support System, 2018). However, many reservations, as well as private owners, have tended to favor fire suppression to protect timber resources, due to an array of social-economic and cultural constraints (Steen-Adams et al., 2017). Thus, efforts toward landscape-level, coordinated restoration may require dialogue both within tribal communities and across tribal and nontribal communities about acceptable trade-offs of reintroducing traditional fire as a management tool.

5.3.2. Applications to community engagement

Our research has applications for engaging communities who hold traditional knowledge. Our team's interactions with the CTWS revealed protocols that can promote productive collaboration between forest scientists, tribal communities, and tribal natural resource managers. Traditional knowledge is sacred knowledge (Berkes et al., 1995), some of which may be appropriately known only within the tribal community (Lake et al., 2017). Also, holders of traditional knowledge are unlikely to engage with scientists and managers unless they perceive an opportunity to advance their goals (Charnley et al., 2007) and the

research framework accommodates both traditional and western knowledge (Lake et al., 2017). This said, many tribal elders, young adults, and managers are eager to participate in traditional knowledge documentation activities (e.g., PGIS workshops, interviews). Our team found that the following research design elements promoted successful collaboration: (i) dialogue to elicit tribal community goals and potential concerns about proposed forest science research; (ii) a protocol for protecting culturally-sensitive data (e.g., a non-disclosure agreement); (iii) an oral history approach to knowledge sharing, particularly featuring visual aids (e.g., archival photographs, maps); (iv) opportunities to engage tribal youth in the transmission and documentation of traditional knowledge (e.g., PGIS trainings). Such protocols can promote the revitalization of traditional knowledge, engagement of knowledge holders, and restoration of forests and culturally-important resources in and beyond the eastside Cascades of the Pacific Northwest.

6. Conclusion

This study was motivated by calls for research that integrates traditional knowledge into the understanding of forest ecology and restoration (Turner et al., 2000; Hessburg and Agee, 2003; Charnley et al., 2007; Lake et al., 2017). Eastside Cascades forests, which have been altered by utilitarian forestry practices and the interruption of historical fire regimes (Stine et al., 2014; Hessburg et al., 2015), have been our focus. We endeavored to generate insights by examining traditional knowledge of fire use from a perspective that integrated anthropology and landscape ecology. This approach revealed a pronounced CFR in the MMC zone, but not in the drier DMC and SG zones. This approach also highlighted the interrelated influences of culture, tribal ecological principles, the seasonal round, and fire use practices on the CFR. Our results suggest that the CTWS used fire in the zone that was appropriate to this combination of factors, but not in the drier zones due to comparatively less vegetative competition with cultural foods, and generally more frequent fire recurrence intervals. Another conclusion generated by our integrative approach is that the role of the CFR in the MMC zone was to maintain openings initially created by large conflagrations and that this regime operated at the landscape-level, spanning multiple mountains and buttes of the eastside Cascades. An application of this finding is that the MMC zone may be a priority area for traditional knowledge-based restoration, owing to the disruption of the CFR, in combination with wildfire suppression policies of the past century.

Acknowledgements

We thank the Confederated Tribes of Warm Springs Natural Resources Branch, the Culture and Heritage Committee, the Culture and Heritage Program, and CTWS tribal elders for enabling data collection (oral history interviews, PGIS workshop, huckleberry enhancement field observations) and for feedback to the research design and preliminary findings. We thank Paul Hessburg, Keala Hagmann, Bob Gray, Brion Salter, and James Dickenson for suggestions regarding the landscape ecological component of the research design and for contributing to development of the instruments about reference forest conditions. We appreciate the insightful comments of an anonymous reviewer, which strengthened this manuscript. Finally, we appreciate the Special Collections of the libraries of the University of Washington and Reed College for access to the ethnobotanical documents of this study.

Funding

This work was supported by the USDA Forest Service, Pacific Northwest Research Station, USA. Key Forest Service sources included a grant from the Civil Rights Action Group (CRAG) Research with Underserved Communities fund and the National Fire Plan.

Appendix A. CTWS traditional knowledge (TK) regarding thin-leaf huckleberry resource

TK major category	TK specific category	Data
Traditional fire use	Spatial extent of cultural fire regime (CFR) in moist mixed conifer zone	~220,000 hectares (estimated)
		CFR area spanned 2 Cascade Range mountains (Mt. Hood, Mt. Jefferson) and several buttes
		24 (at least) huckleberry resource sites
	Historical forest structure, as influenced by CFR	Forest matrix included sizable openings
		Openings characterized by minimal canopy cover, minimal competing understory vegetation, and scattered, small-diameter conifers
	Burn timing and frequency	Early fall (generally)
		Several-year recurrence interval: ignitions rotated around resource area
	Burn severity	Low severity
	Burn patch	Small, controllable patch size (a "section" of resource area), < 1 hectare (estimated)
	Fire control techniques	Burning timed to occur with precipitation events
		Clearance of flammable litter, collected in part to dry huckleberries, thereby controlling fuel load
		Fire guards encircled burn area
		Sparks extinguished by wet materials (e.g., gunnysacks)
		Belief in seers' ability to forecast precipitation onset
		Belief that the Creator would control fire spread
	TK practices other than fire use	Tree girdling
		Rotational harvest of huckleberry sites across resource area
		Respect for appropriate harvest start time: wait until berries are mature
		Exercise attention in traversing resource area to avoid damaging plants
	Demographic characteristics of designated fire specialists	"Scouts" or "seers" (older men) determined appropriate ignition conditions and timing
		Men primarily responsible for fire control; women assisted
	Recentness of fire use	Late 1920s to early 1940s
Tribal ecological principles	Target conditions	Relatively open sites with scattered, small-diameter conifers
		Traversable harvest areas: sparse downed woody debris, due to fuel gathering to dry huckleberries
		Minimal competing understory vegetation
		Field structure: Dense occurrence of huckleberry plants
	Reasons for burning	Control competing understory vegetation
		Maintain and/ or expand canopy openings
		Removal of debris to facilitate navigability for harvesters
		Stimulate sprouting of new huckleberry plant growth
		Replenish soil fertility; "cleanse soil"
		Control insect populations

Seasonal round	Socio-economic and cultural utility of huckleberries	Important dietary resource Tea ingredient (huckleberry leaves) Trade good Focus of ceremonial feast Interfamilial and intergenerational ceremonial gifting
	Harvest volume	2.5 - 8 gallons (estimated) / harvester/ day
	Preservation techniques	Air drying Fire /smoke augmented air drying, when cold or cloudy Canning (after 1940s)
	Encampment group size and demographics	Variable group size Multi-family groups, often spanning the three CTWS tribes Intergenerational group composition Mixed gender group composition (women and men)
	Mode of travel to encampment site	Horseback and horse-drawn wagons (until 1940s) Truck or car (post-World War II)
	Encampment duration	Variable encampment duration: some families stayed at a single base camp for the entire harvest season; others migrated among multiple sites Duration of entire harvest season: Several days to several weeks
	Encampment activities	Men handled pack horses and hunted game (deer, elk) Women and children harvested and processed berries Resources harvested other than huckleberries: other berry species, medicinal plants, basketry materials, game
	Land tenure	Harvest and encampment rights not exclusive to specific groups Cultural/language groups intermixed and circulated among gathering sites
Culture	Ceremonial huckleberry feast and associated multi-day festival	Event involved ritualistic blessings, songs, and festivities Ceremony honored the huckleberry plant and women gatherers Prior to the feast, designated women scouted the berry fields to assess ripeness; their return signaled the start of the feast Ceremony signaled the start of the harvest season
	Worldview and beliefs	Worldview of human-earth interdependence Harvest activities benefit the plants (e.g., resource productivity)
	Gender and generational aspects of TK	Older, designated men determined when and where to burn Women determined when to begin harvest Grandparents key to transmitting traditional knowledge to youth
	Intergenerational transmission of TK	Informal mode of transmission largely employed Children learned by watching and imitating their elders Elders sought and identified youth with a gift for TK, as basis for transmitting fire prayers and related knowledge Fasting rituals believed to be a mechanism for the Creator to reveal TK

References

Agee, J.K., 1993. Fire ecology of Pacific Northwest Forests. Island Press, Washington DC.

Aguilar, G.W., 2005. When the River Ran Wild! Indian Traditions on the Mid-Columbia and the Warm Springs Reservation. Oregon Historical Society Press in association with University of Washington Press, Portland, OR.

Anderson, M.K., Moratto, M.J., 1996. Native American land-use practices and ecological impacts. In: Sierra Nevada ecosystem project: final report to Congress Vol. 2. University of California Center for Water and Wildland Resources, Davis, CA, pp. 187–206.

Anderson, M.K., 1997. From tillage to table: The indigenous cultivation of geophytes for food in California. J. Ethnobiol. 17 (2), 149–169.

Anderson, M.K., Barbour, M.G., 2003. Simulated indigenous management: a new model for ecological restoration in national parks. Ecol. Restoration 21 (4), 269–277.

Anderson, M.K., Lake, F.K., 2016. Beauty, bounty, and biodiversity: the story of California Indian's relationship with edible native geophytes. Fremontia 44 (3), 44–51.

Anzinger, D.L., 2002. Big huckleberry (Vaccinium membranaceum) ecology and forest succession, Mt. Hood National Forest and Warm Springs Indian Reservation, Oregon, M.S. Thesis. Oregon State University, Corvallis.

Baker, W.L., Shinneman, D.J., 2004. Fire and restoration of pinon–juniper woodlands in the western United States: A review. For. Ecol. Manage. 189 (1–3), 1–21.

Barrett, S.W., Arno, S.F., 1982. Indian fires as an ecological influence in the northern Rockies. J. For. 80 (10), 647–651.

Berkes, F., Folke, C., Gadgil, M., 1995. Traditional ecological knowledge, biodiversity, resilience, and sustainability. In: Perrings, C.A. (Ed.), Biodiversity Conservation: Problems and Policies. Kluwer Academic Publishers, Dordrecht, pp. 281–287.

Besser, D.T., McLain, R., Cerveny, L.K., Biedenweg, K., Banis, D., 2014. Mapping landscape values: issues, challenges and lessons learned from fieldwork on the Olympic Peninsula, Washington. Environ. Pract. 16 (2), 138–150.

Bonnicksen, T.M., Anderson, M.K., Lewis, H.T., Kay, C.E., Knudson, R., 1999. Native American influences on the development of forest ecosystems. In: Sexton, W., Malk, A., Szaro, R., Johnson, N. Ecological stewardship: a common reference for ecosystem management, vol. II, pp. 439–470.

Boyd, R., 1999. Indians, Fire, and the Land in the Pacific Northwest. Oregon State University Press, Corvallis, OR.

Carroll, M.S., Cohn, P.J., Paveglio, T.B., Drader, D.R., Jakes, P.J., 2010. Fire burners to firefighters: the Nez Perce and fire. J. For. 108 (2), 71–76.

Charnley, S., Fischer, A.P., Jones, E.T., 2007. Integrating traditional ecological knowledge into forest biodiversity conservation in the Pacific Northwest. For. Ecol. Manage. 246 (1), 14–28.

Cissel, J.H., Swanson, F.J., Weisberg, P.J., 1999. Landscape management using historical fire regimes: Blue River. Oregon. Ecol. Appl. 9 (4), 1217–1231.

Confederated Tribes of Warm Springs Reservation of Oregon (CTWSRO), 1992. Integrated Resources Management Plan: Warm Springs Reservation, 1992-2001. Confederated Tribes of Warm Springs Reservation, Warm Springs, OR.

Confederated Tribes of Warm Springs Reservation of Oregon (CTWSRO), 2012. Integrated Resources Management Plan: Warm Springs Reservation. Confederated Tribes of Warm Springs Reservation, Warm Springs, OR.

Confederated Tribes of Warm Springs (CTWS), 2016. History, https://warmsprings-nsn.gov/history/ (accessed 12/28/18).

Couture, M.D., Ricks, M.F., Housley, L., 1986. Foraging behavior of a contemporary northern Great Basin population. J. California Great Basin Anthropol. 8 (2), 150–160.

Crawford, J.N., Mensing, S.A., Lake, F.K., Zimmerman, S.R., 2015. Late Holocene fire and vegetation reconstruction from the western Klamath Mountains, California, USA: A multi-disciplinary approach for examining potential human land-use impacts. Holocene 25 (8), 1341–1357.

Denevan, W.M., 1992. The pristine myth: The landscape of the Americas in 1492. Ann. Assoc. Am. Geograph. 82 (3), 369–385.

Durham, W.H., 1991. Coevolution: Genes, Culture, and Human Diversity. Stanford University Press, Stanford, CA.

Folwer, C.S., 2000. "We Live by Them" Native Knowledge of Biodiversity in the Great Basin of Western North America. In: Minnis, P.E., Elisens, W.J. (Eds.), Biodiversity and Native America. University of Oklahoma Press, Norman, OK, pp. 99–132.

French, D.H., 1957 (1999). Aboriginal control of huckleberry yield in the Northwest, in: Boyd, R. (Ed.), Indians, Fire, and the Land. Oregon State University Press, Corvallis, OR, pp. 31–35.

French, D.H., 1965. Ethnobotany of the Pacific Northwest Indian. Econ. Bot. 19 (4), 378–382.

Garibaldi, A., Turner, N., 2004. Cultural keystone species: implications for ecological conservation and restoration. Ecol. Soc. 9 (3). https://www.ecologyandsociety.org/vol9/iss3/art1/.

Goschke, L., 2016. Tribes, treaties, and the trust responsibility: a call for co-management of huckleberries in the Northwest. Colo. Nat. Resour. Energy Envtl. L. Rev. 27 (2), 315–360.

Gottesfeld, L.M.J., 1994. Aboriginal burning for vegetation management in northwest British Columbia. Hum. Ecol. 22 (2), 171–188.

Helliwell, R., 1987. Forest Plants of the Warm Springs Indian Reservation, Branch of Natural Resources, Confederated Tribes of Warm Springs, OR. Bureau of Indian

Affairs, Warm Springs Agency, Warm Springs, OR.
Hessburg, P.F., Salter, R.B., Richmond, M.B., Smith, B.G., 2000. Ecological subregions of the Interior Columbia Basin, USA. Appl. Vegetation Sci. 3 (2), 163–180.
Hessburg, P.F., Agee, J.K., 2003. An environmental narrative of Inland Northwest US forests, 1800–2000. For. Ecol. Manage. 178 (1–2), 23–59.
Hessburg, P.F., Agee, J.K., Franklin, J.F., 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. For. Ecol. Manage. 211 (1–2), 117–139.
Hessburg, P.F., Salter, R.B., James, K.M., 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landscape Ecol. 22 (1), 5–24.
Hessburg, P.F., Churchill, D.J., Larson, A.J., Haugo, R.D., Miller, C., Spies, T.A., North, M.P., Povak, N.A., Belote, R.T., Singleton, P.H., Gaines, W.L., 2015. Restoring fire-prone Inland Pacific landscapes: seven core principles. Landscape Ecol. 30 (10), 1805–1835.
Huffman, M.R., 2013. The many elements of traditional fire knowledge: synthesis, classification, and aids to cross-cultural problem solving in fire-dependent systems around the world. Ecol. Soc. 18 (4). https://www.ecologyandsociety.org/vol18/iss4/art3/.
Hummel, S., Lake, F.K., 2014. Forest site classification for cultural plant harvest by tribal weavers can inform management. J. For. 113 (1), 30–39.
Hunn, E.S., French, D.H., 1981. Lomatium: a key resource for Columbia Plateau native subsistence. Northwest Sci. 55 (2), 87–94.
Hunn, E.S., 1990. Nch'i-Wana, "The Big River:" Mid-Columbia Indians and Their Land. University of Washington Press, Seattle, WA.
Jimenez, M., 2002. Management Considerations Focusing on Big-Leaf Huckleberry, Vaccinium membranaceum, Confederated Tribes of Warm Springs, Warm Springs, OR.
Knudson, R., 1980. Fish, roots, game, and trade in the Columbia Plateau. J. For. 78 (9), 542–556.
Kuchler, A.W., 1964. Potential natural vegetation of the conterminous United States. Manual to accompany the map (No. 36). American Geographical Society.
Kimmerer, R.W., Lake, F.K., 2001. The role of indigenous burning in land management. J. For. 99 (11), 36–41.
Lake, F.K., 2007. Traditional ecological knowledge to develop and maintain fire regimes in northwestern California, Klamath-Siskiyou bioregion: Management and restoration of culturally significant habitats, Doctoral dissertation. Oregon State University.
Lake, F.K., 2013. Historical and cultural fires, tribal management and research issues in Northern California: trails, fires and tribulations. Occ.: Interdiscipl. Stud. Human. 5, 1–22. http://occasion.stanford.edu/node/121.
Lake, F.K., Long, J.W., 2014. Fire and tribal cultural resources. In: Long, J.W., Quinn-Davidson, L., Skinner, C.N., (Eds.), Science Synthesis to Support Socioecological Resilience in the Sierra Nevada and Southern Cascade Range. Gen. Tech. Rep. PSW-GTR-247. U.S. Department of Agriculture Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 173–186.
Lake, F.K., Wright, V., Morgan, P., McFadzen, M., McWethy, D., Stevens-Rumann, C., 2017. Returning fire to the land: celebrating traditional knowledge and fire. J. For. 115 (5), 343–353.
Langille, H.D., Plummer, F.G., Dodwell, A., Rixon, T.F., Leiberg, J.B., 1903. Historical conditions of the Cascade Range Forest Reserve, Oregon. U.S. Geological Survey, Professional Paper No. 9, Government Printing Office, Washington DC.
LeCompte, J.K., 2018. Restoration, Risk, and the (Non) Reintroduction of Coast Salish Fire Ecologies in Washington State. In: Fowler, C.T., Welch, J.R. (Eds.), Fire Otherwise: Ethnobiology of Burning for a Changing World. University of Utah Press, Salt Lake City, UT, pp. 128–150.
Lewis, H.T., Anderson, K., 2002. Omer Stewart's legacy of fire: anthropological and ecological contexts, in: Stewart, O.C., with Lewis H.T., Anderson, K. (Eds.), Forgotten Fires: Native American Burning of Prairies, Shrublands and Forests. University of Oklahoma Press, Norman, OK. pp. 3–16.
Logan, R., 1982. Historical Perspectives: The Warm Springs Forest through 1980. Warm Springs Reservation, Warm Springs, OR.
Long, J.W., Quinn-Davidson, L., Goode, R.W., Lake, F.K., Skinner, C.N., 2015. Restoring California black oak to support tribal values and wildlife, in: Standiford, R.B., Purcell, K.L. (Eds.), Proceedings of the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World. Gen. Tech. Rep. PSW-GTR-251. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Berkeley, CA, pp. 113–122.
Marsh, F., Helliwell, R., Rodgers, J., 1987. Plant Association Guide for the Commercial Forest of the Warm Springs Indian Reservation. Bureau of Indian Affairs, Warm Springs Agency, OR.
McBride, B.B., Sanchez-Trigueros, F., Carver, S.J., Watson, A.E., Stumpff, L.M., Matt, R., Borrie, W.T., 2016. Participatory geographic information systems as an organizational platform for the integration of traditional and scientific knowledge in contemporary fire and fuels management. J. For. 115 (1), 43–50.
Miller, R., Bates, J., Svejcar, A., Pierson, F., Eddleman, L., 2005. Biology, ecology, and management of western juniper (Juniperus occidentalis). Oregon State University Agricultural Experiment Station, Technical Bulletin 152, Corvallis, OR.
Minore, D., Smart, A.W., Dubrasich, M.B., 1979. Huckleberry and Ecology Management Research in the Pacific Northwest. Gen. Tech. Rep. PNW-GTR-093. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 60 pp.
Minore, D., 1984. *Vaccinium membranaceum* berry production seven years after treatment to reduce overstory tree canopies. Northwest Sci. 58 (3), 208–212.
Morgan, P., Bunting, S.C., Black, A.E., Merrill, T., Barrett, S., 1996. Fire regimes in the Interior Columbia River Basin: past and present. USDA Forest Service, Rocky Mountain Research Station Final Report for RJVA-INT-94913. Fire Sciences Laboratory, Missoula, MT.
Murdock, G.P., 1980. The Tenino Indians. Ethnology 19 (2), 129–149.
Norgaard, K.M., 2014. The politics of fire and the social impacts of fire exclusion on the klamath. Humboldt J. Soc. Relations 36 (1), 73–97.
Patton, M.Q., 2002. Qualitative Evaluation and Research Methods. SAGE Publications, Thousand Oaks, CA.
Perry, D.A., Hessburg, P.F., Skinner, C.N., Spies, T.A., Stephens, S.L., Taylor, A.H., Franklin, J.F., McComb, B., Riegel, G., 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. For. Ecol. Manage. 262 (5), 703–717.
Pitt, P.E., 2015. Addressing food sovereignty through access to Wi'wnu (Huckleberries): A case study of the Warm Springs Indian Reservation, M.S. thesis. The Evergreen State College.
Richards, R.T., Alexander, S.J., 2006. A Social History of Wild Huckleberry Harvesting in the Pacific Northwest. Gen. Tech. Rep. PNW-GTR-657. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 113 pp.
Senos, R., Lake, F.K., Turner, N., Martinez, D., 2006. Traditional ecological knowledge and restoration practice. In: Apostol, D., Sinclair, M. (Eds.), Restoring the Pacific Northwest: The Art and Science of Ecological Restoration in Cascadia. Island Press, Washington, DC, pp. 393–426.
Shinn, D.A., 1980. Historical perspectives on range burning in the Inland Pacific Northwest. J. Range Manage. 33 (6), 41–423.
Steen-Adams, M., Charnley, S., Adams, M., 2017. Historical perspective on the influence of wildfire policy, law, and informal institutions on management and forest resilience in a multiownership, frequent-fire, coupled human and natural system in Oregon, USA. Ecol. Soc. 22 (3). https://www.ecologyandsociety.org/vol22/iss3/art23/.
Stewart, O.C., 2009. Forgotten Fires: Native Americans and the Transient Wilderness. University of Oklahoma Press, Norman, OK.
Stine, P., Hessburg, P., Spies, T., Kramer, M., Fettig, C.J., Hansen, A., Lehmkuhl, J., O'Hara, K., Polivka, K., Singleton, P., Charnley, S., Merschel, A., White, R., 2014. The Ecology and Management of Moist Mixed Conifer Forests in Eastside Oregon and Washington: A Synthesis of the Relevant Biophysical Science and Implications for Future Land Management. Gen. Tech. Rep. GTR-PNW-897. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.
Turner, N.J., 1999. "Time to Burn:" Traditional use of fire to enhance resource production by aboriginal peoples in British Columbia. In: Boyd, R. (Ed.), Indians, Fire, and the Land in the Pacific Northwest. Oregon State University Press, Corvallis, OR, pp. 185–218.
Turner, N.J., Ignace, M.B., Ignace, R., 2000. Traditional ecological knowledge and wisdom of aboriginal peoples in British Columbia. Ecol. Appl. 10 (5), 1275–1287.
Turner, N.J., Peacock, S., 2005. Solving the perennial paradox: ethnobotanical evidence for plant resource management on the Northwest Coast. In: Deur, D., Turner, N.J. (Eds.) Keeping It living: Traditions of plant use and cultivation on the Northwest Coast of North America, pp. 101–50.
Turner, N.J., Deur, D., Mellott, C.R., 2011. "Up On the Mountain": Ethnobotanical Importance of Montane Sites In Pacific Coastal North America. J. Ethnobiol. (1), 4–44.
University of Washington Libraries, Special Collections (UWLSC), 2008. David H. and Katherine S. French papers, 1916-2006, http://archiveswest.orbiscascade.org/ark:/80444/xv30429/op=fstyle.aspx?t=k&q=DH+French (accessed 12/18/18).
USDA Forest Service, 2010. Preliminary Assessment: Huckleberry Enhancement. Mt. Hood National Forest, Estacada, OR.
USDA Forest Service, n.d.. Program Areas, Landscape Simulations. https://www.fs.fed.us/t-d/programs/forest_mgmt/projects/landscapesim/software.shtml (accessed 12/19/18).
USDA Forest Service ECOMAP Team, 2017. Kuchler Sections. https://data.fs.usda.gov/geodata/edw/edw_resources/meta/S_USA.PNV_KuchlerSections.xml (accessed 12/18/18).
Vale, T., 2002. Fire, Native Peoples, and the Natural Landscape. Island Press, Washington DC.
Voegelin, E.W., 1955. The Northern Paiute of Central Oregon: A Chapter in Treaty-Making Part 1. Ethnohistory 2 (2), 95–132.
Warm Springs Geo Visions' Cultural Resources Division (WSGVCRD), n.d. https://wsgeov.com/ceded-lands-map/ (accessed 12/18/18).
Wildland Fire Decision Support System (WFDSS), 2018, https://wfdss.usgs.gov/wfdss/WFDSS_Home.shtml (accessed 5/13/19).
Williams, G.W., 2000. Early fire use in Oregon. Fire Manage. Today 60 (3), 13–20.
Williams, G.W., 2009. The US Forest Service in the Pacific Northwest: A History. Oregon State University Press.
Zucker, J., Hummel, K., Høgfoss, B., Penniman, J.F., 1983. Oregon Indians: Culture, History and Current Affairs: An Atlas and Introduction. Oregon Historical Society Press, Portland, OR.
Zybach, B., 2003. The great fires: Indian burning and catastrophic forest fire patterns of the Oregon Coast Range, 1491–1951, Doctoral dissertation. Oregon State University.

CSIRO PUBLISHING

International Journal of Wildland Fire
http://dx.doi.org/10.1071/WF13158

The role of defensible space for residential structure protection during wildfires

Alexandra D. Syphard[A,D], *Teresa J. Brennan*[B] *and Jon E. Keeley*[B,C]

[A]Conservation Biology Institute, 10423 Sierra Vista Avenue, La Mesa, CA 91941, USA.
[B]US Geological Survey Western Ecological Research Center, Three Rivers, CA 93271, USA.
[C]Department of Ecology & Evolutionary Biology, University of California, 612 Charles E. Young Drive, South Los Angeles, CA 90095-7246, USA.
[D]Corresponding author. Email: asyphard@consbio.org

Abstract. With the potential for worsening fire conditions, discussion is escalating over how to best reduce effects on urban communities. A widely supported strategy is the creation of defensible space immediately surrounding homes and other structures. Although state and local governments publish specific guidelines and requirements, there is little empirical evidence to suggest how much vegetation modification is needed to provide significant benefits. We analysed the role of defensible space by mapping and measuring a suite of variables on modern pre-fire aerial photography for 1000 destroyed and 1000 surviving structures for all fires where homes burned from 2001 to 2010 in San Diego County, CA, USA. Structures were more likely to survive a fire with defensible space immediately adjacent to them. The most effective treatment distance varied between 5 and 20 m (16–58 ft) from the structure, but distances larger than 30 m (100 ft) did not provide additional protection, even for structures located on steep slopes. The most effective actions were reducing woody cover up to 40% immediately adjacent to structures and ensuring that vegetation does not overhang or touch the structure. Multiple-regression models showed landscape-scale factors, including low housing density and distances to major roads, were more important in explaining structure destruction. The best long-term solution will involve a suite of prevention measures that include defensible space as well as building design approach, community education and proactive land use planning that limits exposure to fire.

Received 16 September 2013, accepted 30 May 2014, published online 14 October 2014

Introduction

Across the globe and over recent decades, homes have been destroyed in wildfires at an unprecedented rate. In the last decade, large wildfires across Australia, southern Europe, Russia, the US and Canada have resulted in tens of thousands of properties destroyed, in addition to lost lives and enormous social, economic and ecological effects (Filmon 2004; Boschetti *et al.* 2008; Keeley *et al.* 2009; Blanchi *et al.* 2010; Vasquez 2011). The potential for climate change to worsen fire conditions (Hessl 2011), and the projection of continued housing growth in fire-prone wildlands (Gude *et al.* 2008) suggest that many more communities will face the threat of catastrophic wildfire in the future.

Concern over increasing fire threat has escalated discussion over how to best prepare for wildfires and reduce their effects. Although ideas such as greater focus on fire hazard in land use planning, using fire-resistant building materials and reducing human-caused ignitions (e.g. Cary *et al.* 2009; Quarles *et al.* 2010; Syphard *et al.* 2012) are gaining traction, the traditional strategy of fuels management continues to receive the most attention. Fuels management in the form of prescribed fires or mechanical treatments has historically occurred in remote, wildland locations (Schoennagel *et al.* 2009), but recent studies suggest that treatments located closer to homes and communities may provide greater protection (Witter and Taylor 2005; Stockmann *et al.* 2010; Gibbons *et al.* 2012). In fact, one of the most commonly recommended strategies in terms of fuels and fire protection is to create defensible space immediately around structures (Cohen 2000; Winter *et al.* 2009). Defensible space is an area around a structure where vegetation has been modified, or 'cleared,' to increase the chance of the structure surviving a wildfire. The idea is to mitigate home loss by minimising direct contact with fire, reducing radiative heating, lowering the probability of ignitions from embers and providing a safer place for fire fighters to defend a structure against fire (Gill and Stephens 2009; Cheney *et al.* 2001). Many jurisdictions provide specific guidelines and practices for creating defensible space, including minimum distances that are required among trees and shrubs as well as minimum total distances from the structure. These distances may be enforced through local ordinances or state-wide laws. In California, for example, a state law in 2005 increased the required total distance from 9 m (30 ft) to 30 m (100 ft).

Despite these specific guidelines on how to create defensible space, there is little scientific evidence to support the amount and location of vegetation modification that is actually effective

Journal compilation © IAWF 2014

at providing significant benefits. Most spacing guidelines and laws are based on 'expert opinion' or recommendations from older publications that lack scientific reference or rationale (e.g. Maire 1979; Smith and Adams 1991; Gilmer 1994). However, one study has provided scientific support for, and forms the basis of, most guidelines, policy and laws requiring a minimum of 30 m (100 ft) of defensible space (Cohen 1999, 2000). The modelling and experimental research in that study showed that flames from forest fires located 10–40 m (33–131 ft) away would not scorch or ignite a wooden home; and case studies showed 90% of homes with non-flammable roofs and vegetation clearance of 10–20 m (33–66 ft) could survive wildfires (Cohen 2000). However, the models and experimental research in that study focussed on crown fires in spruce or jack pine forests, and the primary material of home construction was wood. Therefore, it is unknown how well this guideline applies to regions dominated by other forest types, grasslands, or nonforested woody shrublands and in regions where wooden houses are not the norm.

Some older case studies showed that most homes with non-flammable roofs and 10–18 m (33–ft) of defensible space survived the 1961 Bel Air fire in California (Howard *et al.* 1973); most homes with non-flammable roofs and more than 10 m (33 ft) of defensible space also survived the 1990 Painted Cave fire (Foote and Gilless 1996). Also, several fire-behaviour modelling studies have been conducted in chaparral shrublands. One study showed that reducing vegetative cover to 50% at 9–30 m (30–ft) from structures effectively reduced fireline intensity and flame lengths, and that removal of 80% cover would result in unintended consequences such as exotic grass invasion, loss of habitat and increase in highly flammable flashy fuels (A. Fege and D. Pumphrey, unpubl. data). Another showed that separation distances adequate to protect firefighters varied according to fuel model and that wind speeds greater than 23 km h^{-1} negated the effect of slope, and wind speed above 48 km h^{-1} negated any protective effect of defensible space (F. Bilz, E. McCormick and R. Unkovich, unpubl. data, 2009). Results obtained through modelling equations of thermal radiation also found safety distances to vary as a function of fuel type, type of fire, home construction material and protective garments worn by firefighters (Zárate *et al.* 2008).

Although there is no empirical evidence to support the need for more than 30 m (100 ft) of defensible space, there has been a concerted effort in some areas to increase this distance, particularly on steep slopes. In California, a senate bill was introduced in 2008 (SB 1618) to encourage property owners to clear 91 m (300 ft) through the reduction of environmental regulations and permitting needed at that distance. Although this bill was defeated in committee, many local ordinances do require homeowners to clear 91 m (300 ft) or more, and there are reports that some people are unable to get fire insurance without 91 m (300 ft) of defensible space (F. Sproul, pers. comm.). In contrast, homeowner acceptance of and compliance with defensible space policies can be challenging (Winter *et al.* 2009; Absher and Vaske 2011), and in many cases homeowners do not create any defensible space.

It is critically important to develop empirical research that quantifies the amount, location and distance of defensible space that provides significant fire protection benefits so that guidelines and policies are developed with scientific support. Data that are directly applicable to southern California are especially important, as this region experiences the highest annual rate of wildfire-destroyed homes in the US. Not having sufficient defensible space is obviously undesirable because of the hazard to homeowners. However, there are clear trade-offs involved when vegetation reduction is excessive, as it results in the loss of native habitats, potential for increased erosion and invasive species establishment, and it potentially even increases fire risk because of the high flammability of weedy grasslands (Spittler 1995; Keeley *et al.* 2005; Syphard *et al.* 2006).

It is also important to understand the role of defensible space in residential structure protection relative to other factors that explain why some homes are destroyed in fires and some are not. Recent research shows that landscape-scale factors, such as housing arrangement and location, as well as biophysical variables characterising properties and neighbourhoods such as slope and fuel type, were important in explaining which homes burned in two southern California study areas (Syphard *et al.* 2012; 2013). Understanding the relative importance of different variables at different scales may help to identify which combinations of factors are most critical to consider for fire safety.

Our objective was to provide an empirical analysis of the role of defensible space in protecting structures during wildfires in southern California shrublands. Using recent pre-fire aerial photography, we mapped and measured a suite of variables describing defensible space for burned and unburned structures within the perimeters of major fires from 2001 to 2010 in San Diego County to ask the following questions:

1. How much defensible space is needed to provide significant protection to homes during wildfires, and is it beneficial to have more than the legally required 30 m (100 ft)?
2. Does the amount of defensible space needed for protection depend on slope inclination?
3. What is the role of defensible space relative to other factors that influence structure loss, such as terrain, fuel type and housing density?

Methods

Study area

The properties and structures analysed were located in San Diego County, California, USA (Fig. 1) – a topographically diverse region with a Mediterranean climate characterised by cool, wet winters and long summer droughts. Fire typically is a direct threat to structures adjacent to wildland areas. Native shrublands in southern California are extremely flammable during the late summer and fall (autumn) and when ignited, burn in high-intensity, stand-replacing crown fires. Although 500 homes on average have been lost annually since the mid-1900s (Calfire 2000), that rate has doubled since 2000. Most of these homes have burned during extreme fire weather conditions that accompany the autumn Santa Ana winds. The wildland–urban interface here includes more than 5 million homes, covering more than 28 000 km^2 (Hammer *et al.* 2007).

Property data

The data for properties to analyse came from a complete spatial database of existing residential structures and their

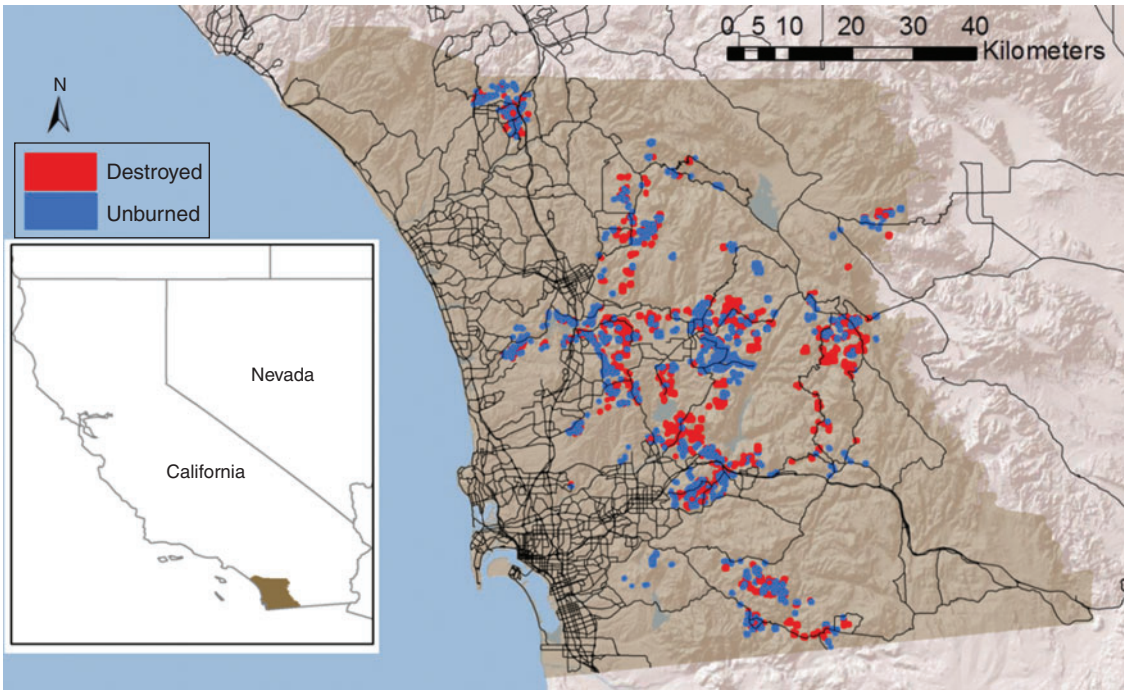


Fig. 1. Location of destroyed and unburned structures within the South Coast ecoregion of San Diego County, California, USA.

corresponding property boundaries developed for San Diego County (Syphard *et al.* 2012). This dataset included 687 869 structures, of which 4315 were completely destroyed by one of 40 major fires that occurred from 2001 to 2010. Our goal was to compare homes that were exposed to wildfire and survived with those that were exposed and destroyed. To determine exposure to fire, we only considered structures located both within a GIS layer of fire perimeters and within areas mapped as having burned at a minimum of low severity through thematic Monitoring Trends in Burn Severity produced by the USA Geological Survey and USDA Forest Service. From these data, we used a random sample algorithm in GIS software to select 1000 destroyed and 1000 unburned homes that were not adjacent to each other, to minimise any potential for spatial autocorrelation. Our final property dataset included structures that burned across eight different fires. More than 97% of these structures burned in Santa Ana wind-driven fire events (Fig. 1).

Calculating defensible space and additional explanatory variables

To estimate defensible space, we developed and explored a suite of variables relative to the distance and amount of defensible space surrounding structures, as well as the proximity of woody vegetation to the structure (Table 1). We measured these variables based on interpretation of Google Earth aerial imagery. We based our measurements on the most recent imagery before the date of the fire. In almost all cases, imagery was available for less than 1 year before the fire.

Our definition of defensible space followed the guidelines published by the California Department of Forestry and Fire Protection (Calfire 2006). 'Clearance' included all areas that were not covered by woody vegetation, including paved areas or grass. Although Google Earth prevents the identification of understorey vegetation, woody trees and shrubs were easily distinguished from grass, and our objective was to measure horizontal distances as required by Calfire rather than assess the relative flammability of different vegetation types. Trees or shrubs were allowed to be within the defensible space zone as long as they were separated by the minimum horizontal required distance, which was 3 m (10 ft) from the edge of one tree canopy to the edge of the next (Fig. 2). Although greater distances between trees or shrubs are recommended on steeper slopes, we followed the same guidelines for all properties. For all structures, we started the distance measurements by drawing lines from the centre of the four orthogonal sides of the structure that ended when they intersected anything that no longer met the requirements in the guidelines. A fair number of structures are not four sided; thus, the start of the centre point was placed at a location that approximated the farthest extent of the structure along each of four orthogonal sides.

We developed two sets of measurements of the distance of defensible space based on what is feasible for homeowners within their properties *v.* the total effective distance of defensible space. We made these two measurements because homeowners are only required to create defensible space within their own property, and this would reflect the effect of individual homeowner compliance. Therefore, even if cleared vegetation extended beyond the property line, the first set of distance measurements ended at the property boundary. The second set of measurements ignored the property boundaries and accounted for the total potential effect of treatment. For all measurements, we recorded the cover types (e.g. structure >3 m (10 ft) long, property boundary, or vegetation type) at which the distance measurements stopped (Table 1). Because property

Table 1. Defensible space variables measured for every structure

Urban veg, landscaping vegetation that was not in compliance with regulations within urban matrix; wildland veg, wildland vegetation that was not in compliance with regulations; orchard, shrub to tree-sized vegetation in rows; urban to wildland, landscaping vegetation that leads into wildland vegetation; structure, any building longer than 3 m (10 ft)

Variable	Definition
Distance defensible space within property	Measure of clearance from side of structure to property boundary calculated for four orthogonal directions from structure and averaged
Total distance defensible space	Measure of clearance from side of structure to end of clearance calculated for four orthogonal directions from structure and averaged
Cover type at end of defensible space	Type of cover encountered at end of measurement (urban veg, wildland veg, orchard, urban to wildland, structure)
Percentage clearance	Percentage of clearance calculated across the entire property
Neighbours' vegetation	Binary indicator of whether neighbours' uncleared vegetation was located within 30 m (100 ft) of the main structure
Vegetation touching structure	Number of sides on which woody vegetation touches main structure (1–4) Structure with more than 4 sides were viewed as a box and given a number between 1 and 4
Vegetation overhanging roof	Was vegetation overhanging the roof? (yes or no)

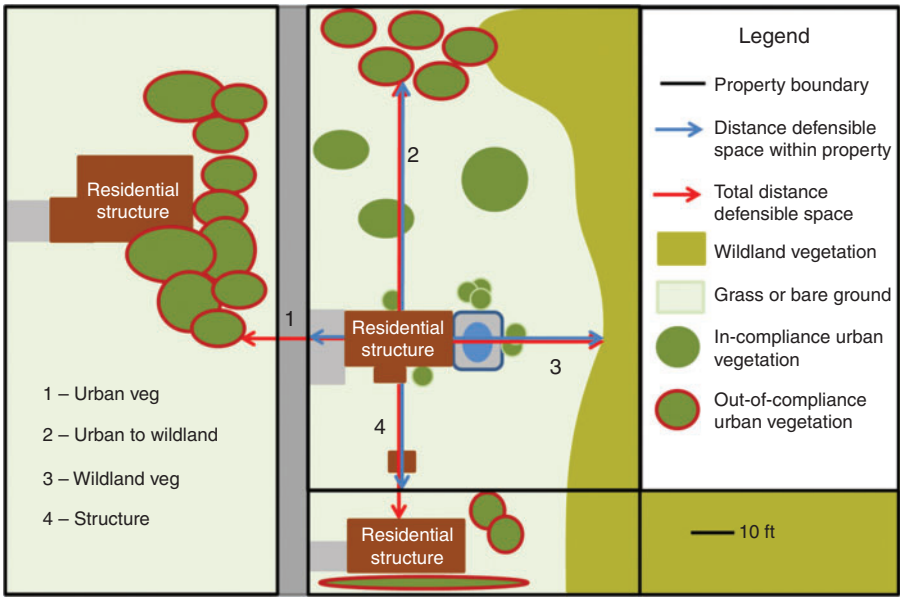


Fig. 2. Illustration of defensible space measurements. See Table 1 for full definition of terms.

owners usually can only clear vegetation on their own land, it is possible that the effectiveness of defensible space partly depends upon the actions of neighbouring homeowners. Therefore, we also recorded whether or not any neighbours' un-cleared vegetation was located within 30 m (100 ft) of the structure.

To assess the total amount of woody vegetation that can safely remain on a property and still receive significant benefits of defensible space, we calculated the total percentage of cleared land, woody vegetation and structure area across every property. This was accomplished by overlaying a grid on each property and determining the proportion of squares falling into each class. Preliminary results showed these three measurements to be highly correlated, so we only retained percentage clearance for further analysis. To evaluate the relative effect of woody vegetation directly adjacent to structures, we also calculated the number of sides of the structure with vegetation touching and recorded whether any trees were overhanging structures' roofs.

In addition to defensible space measurements, we evaluated other factors known to influence the likelihood of housing loss to fire in the region (Syphard *et al.* 2012, 2013). Using the same data as in Syphard *et al.* (2012, 2013), we extracted spatial information from continuous grids of explanatory variables for the locations of all structures in our analysis. Variables included interpolated housing density based on a 1-km search radius; percentage slope derived from a 30-m digital elevation model (DEM); Euclidean distance to nearest major and minor road and fuel type, which was based on a simple classification of US Forest Service data (Syphard *et al.* 2012), including urban, grass, shrubland and forest & woodland.

Analysis

We performed several analyses to determine whether relative differences in home protection are provided by different distances and amounts of defensible space, particularly beyond the legally required 30 m (100 ft), and to identify the effective treatment distance for homes on low and steep slopes.

Categorical analysis

For the first analysis, we divided our data into several groups to identify potential differences among specific categories of defensible space distance around structures located on shallow and steep slopes. We first sorted the full dataset of 2000 structures by slope and then split the data in the middle to create groups of homes with shallow slope and steep slope. We divided the data in half to keep the number of structures even within both groups and to avoid specifying an arbitrary number to define what constitutes shallow or steep slope. The two equal-sized subsets of data ranged from 0 to 9%, with a mean of 8% for shallow slope, and from 9 to 40%, with a mean of 27% for steep slope. Within these data subsets, we next created groups reflecting different mean distances of defensible space around structures. We also performed separate analyses based on whether defensible space measurements were calculated within the property boundary or whether measurements accounted for the total distance of defensible space.

Within all groups, we calculated the proportion of homes that were destroyed by wildfire. We performed Pearson's Chi-square tests of independence to determine whether or not the proportion of destroyed structures within groups was significantly different (Agresti 2007). We based one test on four equal-interval groups within the legally required distance of 30 m (100 ft): 0–7 m (0–25 ft), 8–15 m (26–50 ft), 16–23 m (51–75 ft) and 24–30 m (76–100 ft). A second test was based on three groups (24–30 m (75–100 ft), 31–90 m (101–300 ft) and >90 m (>300 ft) or >60 m (>200 ft)) to evaluate whether groups with mean defensible space distances >30 m (>100 ft) were significantly different from groups with <30 m (<100 ft). When defensible space distances were only measured to the property boundary, few structures had mean defensible space >90 m (>300 ft). Therefore, we used a cut-off of 60 m (200 ft) to increase the sample size in the Chi-square analysis. In addition to the Chi-square analysis, we calculated the relative risk among every successive pair of categories (Sheskin 2004). The relative risk was calculated as the ratio of proportions of burned homes within two groups of homes that had different defensible space distances.

Effective treatment analysis

In addition to comparing the relative effect of defensible space among different groups of mean distances, as described above, we also considered that the protective effect of defensible space for structures exposed to wildfire is conceptually similar to the effect of medication in producing a therapeutic response in people who are sick. In addition to pharmacological applications, treatment–response relationships have been used for radiation, herbicide, drought tolerance and ecotoxicological studies (e.g. Streibig *et al.* 1993; Cedergreen *et al.* 2005; Knezevic *et al.* 2007; Kursar *et al.* 2009). The effect produced by a drug or treatment typically varies according to the concentration or amount, often up to a point at which further increase provides no additional response. The effective treatment (ET50), therefore, is a specific concentration or exposure that produces a therapeutic response or desired effect. Here we considered the treatment to be the distance or amount of defensible space.

Using the software package DRC in R (Knezevic *et al.* 2007; Ritz and Streibig 2013), we evaluated the treatment–response relationship of defensible space in survival of structures during wildfire. To calculate the effective treatment, we fit a log-logistic model with logistic regression because we had a binary dependent variable (burned or unburned). We specified a 2-parameter model where the lower limit was fixed at 0 and the upper limit was fixed at 1. We again performed separate analyses for data subsets reflecting shallow and steep slope, as well as from measurements of defensible space taken within, or regardless of, property boundaries. We also performed analyses to find the effective treatment of percentage clearance of trees and shrubs within the property.

Multiple regression analysis

To evaluate the role of defensible space relative to other variables, we developed multiple generalised linear regression models (GLMs) (Venables and Ripley 1994). We again had a binary dependent variable (burned versus unburned), so we specified a logit link and binomial response. Although the proportion of 0s and 1s in the response may be important to consider for true prediction (King and Zeng 2001; Syphard *et al.* 2008), our objective here was solely to evaluate variable importance. We developed multiple regression models for all possible combinations of the predictor variables and used the corrected Akaike's Information Criterion (AICc) to rank models and select the best ones for each region using package MuMIn in R (R Development Core Team 2012; Burnham and Anderson 2002). We recorded all top-ranked models that had an AICc value within 2 of that of the model with lowest AICc to identify all models with empirical support. To assess variable importance, we calculated the sum of Akaike weights for all models that contained each variable. On a scale of 0–1, this metric represents the weight of evidence that models containing the variable in question are the best model (Burnham and Anderson 2002). The distance of defensible space measured within property boundaries was highly correlated with the distance of defensible space measured beyond property boundaries ($r = 0.82$), so we developed two separate analyses – one using variables measured only within the property boundary and the other using variables that accounted for defensible space outside of the property boundary as well as the potential effect of neighbours having uncleared vegetation within 30 m (100 ft) of the structure. A test to avoid multicollinearity showed all other variables within each multiple regression analysis to be uncorrelated ($r < 0.5$).

Surrounding matrix

To assess whether the proportion of destroyed structures varied according to their surrounding matrix, we summarised the most common cover type at the end of defensible space measurements (descriptions in Table 1) for all structures. These summaries

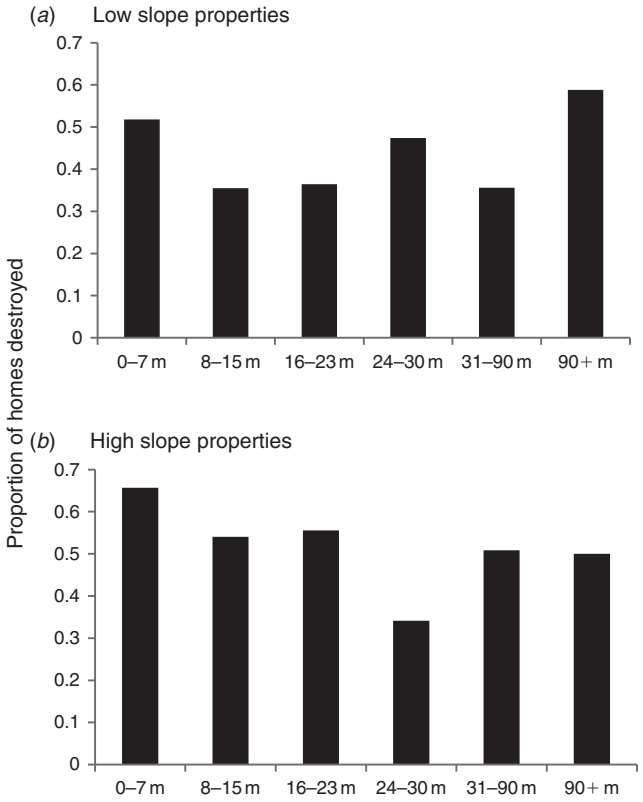


Fig. 3. Proportion of destroyed homes grouped by distances of defensible space based upon total distance of clearance within property boundary, for structures on (*a*) shallow slopes (mean 8%) and (*b*) steep slopes (mean 27%).

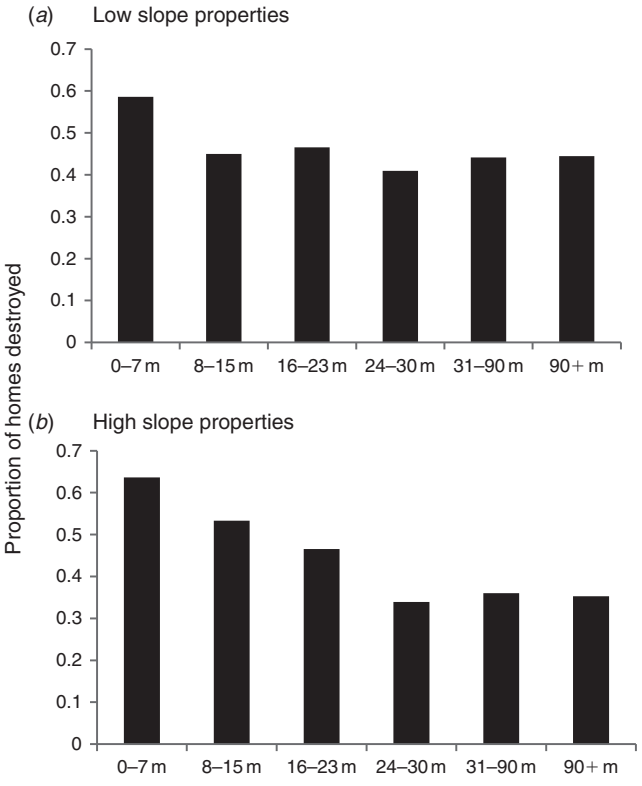


Fig. 4. Proportion of destroyed homes grouped by distances of defensible space based upon total distance of clearance regardless of property boundary, for structures on (*a*) shallow slopes (mean 8%) and (*b*) steep slopes (mean 27%).

were based on the majority surrounding cover type from the four orthogonal sides of the structure. We also noted cases in which there was a tie (e.g. two sides were urban vegetation and two sides were structures).

Results

Categorical analysis

When the distance of defensible space was measured both 'only within property boundaries' (Fig. 3) and 'regardless of property boundaries' (Fig. 4), the Chi-square test showed a significant difference ($P < 0.001$) in the proportion of destroyed structures among the four equal-interval groups of distance ranging from 0 to 30 m (0–100 ft). This relationship was consistent on both shallow-slope and steep-slope properties, although the relative risk analysis showed considerable variation among classes (Table 2) There was a steadily decreasing proportion of destroyed structures at greater distances of defensible space up to 30 m (100 ft) on the steep-slope structures with defensible space measured regardless of property boundaries (Fig. 4*b*). Otherwise, the biggest difference in proportion of destroyed structures occurred between 0 and 7 m (0–25 ft) and 8–15 m (26–50 ft) (Figs 3*a–b*, 4*a*).

When the distance of defensible space was measured in intervals from 24 m (75 ft) and beyond, the Chi-square test showed no significant difference among groups ($P = 0.96$ for shallow-slope properties and $P = 0.74$ for steep-slope properties) (Figs 3, 4), although again, the relative risk analysis showed considerable variation (Table 2).There was a slight increase in the proportion of homes destroyed at longer distance intervals when the defensible space was measured only to the property boundaries (Fig. 3*a–b*). This slight increase is less apparent when distances were measured regardless of boundaries (Fig. 4*a–b*).

The relative risk calculations showed that the ratio of proportions was generally more variable among successive pairs when the distances were measured within property boundaries (Table 2). For these calculations, the risk of a structure being destroyed was significantly lower when the defensible space distance was 8–15 m (25–50 ft) compared to 0–7 m (0–25 ft) on both shallow- and steep-slope properties. On the steep-slope properties, there was an additional reduction of risk when comparing 24–30 m (75–100 ft) to 16–23 m (50–75 ft). However, the risk of a home being destroyed was slightly significantly higher when there was 31–90 m (101–225 ft) compared to 16–23 m (50–75 ft). For distances that were measured regardless of property boundary (total clearance), the only significant differences in risk of burning were a reduction in risk for 8–15 m (25–50 ft) compared to 0–7 m (0–25 ft).

Table 2. Number of burned and unburned structures within defensible space distance categories (m), their relative risk and significance
A relative risk of 1 indicates no difference; <1 means the chance of a structure burning is less than the other group; >1 means the chance is higher than the other group. The relative risk is calculated for pairs that include the existing row and the row above. Confidence intervals are in parentheses

	Distance within property				Total distance			
	Burned	Unburned	Relative risk	*P*	Burned	Unburned	Relative risk	*P*
Shallow slope								
0–7	200	186			162	114		
8–15	109	198	0.69 (0.12)	<0.001	108	132	0.77	0.002
16–23	51	89	1.03 (0.30)	0.850	78	90	1.03	0.770
24–30	36	40	1.30 (0.39)	0.110	50	70	0.90	0.430
31–90	28	47	0.79 (0.24)	0.220	79	99	1.06	0.640
60 or 90+	10	6	1.67 (0.63)	0.040	8	9	1.01	0.830
Steep slope								
0–7	245	128			224	128		
8–15	174	148	0.82 (0.10)	0.001	158	139	0.84	0.008
16–23	85	68	1.03 (0.16)	0.750	73	83	0.87	0.210
24–30	29	56	0.61 (0.17)	0.004	26	50	0.73	0.080
31–	29	28	1.49 (0.48)	0.050	39	68	1.06	0.760
60 or 90+	5	5	0.98 (0.47)	0.950	4	8	0.91	0.830

Table 3. Effective treatment results reflecting the distance (in metres, with feet in parentheses) and percentage clearance within properties that provided significant improvement in structure survival during wildfires
The property mean is the average distance of defensible space or percentage clearance that was calculated on the properties before the wildfires and provides a means to compare the effective treatment result to the actual amount on the properties

	All parcels effective treatment ($n = 2000$)	Parcel mean	Shallow slope (mean 8%) effective treatment ($n = 1000$)	Parcel mean	Steep slope (mean 27%) effective treatment ($n = 1000$)	Parcel mean
Defensible space within parcel	10 (33)	13 (44)	4 (13)	14 (45)	25 (82)	11 (35)
Total distance defensible space	10 (32)	19 (63)	5 (16)	20 (67)	20 (65)	18 (58)
Mean percentage clearance on property	36	48	31	51	37	35

Effective treatment analysis

Analysis of the treatment–response relationships among defensible space and structures that survived wildfire showed that, when all structures are considered together, the mean actual defensible space that existed around structures before the fires was longer than the calculated effective treatment (Table 3). Regardless of whether the defensible space was measured within or beyond property boundaries, the estimated effective treatment of defensible space was nearly the same at 10 m (32–33 ft).

The effective treatment distance was much shorter for structures on shallow slopes (4–5 m (13–16 ft)) than for structures on steep slopes (20–25 m (65–82 ft)), but in all cases was <30 m (<100 ft). Although longer distances of defensible space were calculated as effective on steeper slopes, these structures actually had shorter mean distances of defensible space around their properties than structures on low slopes (Table 3).

The calculated effective treatment of the mean percentage clearance on properties was 36% for all properties, 31% for structures on shallow slopes and 37% for structures on steep slopes (Table 3). In total, the properties all had higher actual percentage clearance on their property than was calculated to be effective. However, this mainly reflects the shallow-slope properties, as those structures on steep slopes had less clearance than the effective treatment.

Multiple regression analysis

When defensible space was measured only to the property boundaries, it was not included in the best model, according to the all-subsets multiple regression analysis (Table 4). However, it was included in the best model when factoring in the distance of defensible space measured beyond property boundaries (Table 5). In both multiple regression analyses, low housing density and shorter distances to major roads were ranked as the most important variables according to their Akaike weights. Slope and surrounding fuel type were also in both of the best models as well as other measures of defensible space, including the percentage clearance on property and whether vegetation was overhanging the structure's roof. The number of sides in which vegetation was touching the structure was included in the best model when defensible space was only measured to the property boundary. The total explained deviance for the multiple regression models was low (12–13%) for both analyses.

Table 4. Results of multiple regression models of destroyed homes using all possible variable combinations and corrected Akaike's Information Criterion (AICc)

Includes variables measured within property boundary only. Top-ranked models include all those ($n = 12$) with AICc within 2 of the model with the lowest AICc. Relative variable importance is the sum of 'Akaike weights' over all models including the explanatory variable

Variable in order of importance	Relative variable importance	Model-averaged coefficient	Number inclusions in top-ranked models
Housing density	1	−0.003	12
Distance to major road	1	−0.0005	12
Percentage clearance	1	−0.02	12
Slope	1	0.03	12
Vegetation overhang roof	1	0.5	12
Fuel type	0.67	Factor	9
Vegetation touch structure	0.49	0.07	6
Distance defensible space within property	0.45	−0.0002	5
South-westness	0.36	−0.0007	3
Distance to minor road	0.28	−0.0002	1
D^2 of top-ranked model			0.123

Table 5. Results of multiple regression models of destroyed homes using all possible variable combinations and corrected Akaike's Information Criterion (AICc)

Includes variables measured beyond property boundary. Top-ranked models include all those ($n = 6$) with AICc within 2 of the model with the lowest AICc. Relative variable importance is the sum of 'Akaike weights' over all models including the explanatory variable

Variable in order of importance	Relative variable importance	Model-averaged coefficient	Number inclusions in top-ranked models
Housing density	1	−0.003	6
Distance to major road	1	−0.0005	6
Total distance defensible space	1	−0.004	6
Percentage clearance	1	−0.01	6
Vegetation overhang roof	0.99	0.4	6
Slope	0.99	0.03	6
Fuel type	0.86	Factor	4
South-westness	0.42	−0.0009	2
Distance to minor road	0.36	−0.0009	2
Neighbours' vegetation	0.27	0.08	1
Vegetation touch structure	0.27	0.18	1
D^2 of top-ranked model			0.125

Surrounding matrix

The cover type that most frequently surrounded the structures at the end of the defensible space measurements was urban vegetation, followed by urban vegetation leading into wildland vegetation, and wildland vegetation (Fig. 5). Many structures were equally surrounded by different cover types. There were no significant differences in the proportion of structures destroyed depending on the surrounding cover type. However, a disproportionately large proportion of structures burned (28 *v.* 9% unburned) when they were surrounded by urban vegetation that extended straight into wildland vegetation.

Discussion

For homes that burned in southern Californian urban areas adjacent to non-forested ecosystems, most burned in high-intensity Santa Ana wind-driven wildfires and defensible space increased the likelihood of structure survival during wildfire. The most effective treatment distance varied between 5 and 20 m (16–58 ft), depending on slope and how the defensible space was measured, but distances longer than 30 m (100 ft) provided no significant additional benefit. Structures on steeper slopes benefited from more defensible space than structures on shallow slopes, but the effective treatment was still less than 30 m (100 ft). The steepest overall decline in destroyed structures occurred when mean defensible space increased from 0–7 m (0–25 ft) to 8–15 m (26–50 ft). That, along with the multiple regression results showing the significance of vegetation touching or overhanging the structure, suggests it is most critical to modify vegetation immediately adjacent to the house, and to move outward from there. Similarly, vegetation overhanging the structure was also strongly correlated with structure loss in Australia (Leonard *et al.* 2009).

In terms of fuel modification, the multiple regression models also showed that the percentage of clearance was just as, or more important than, the linear distance of defensible space.

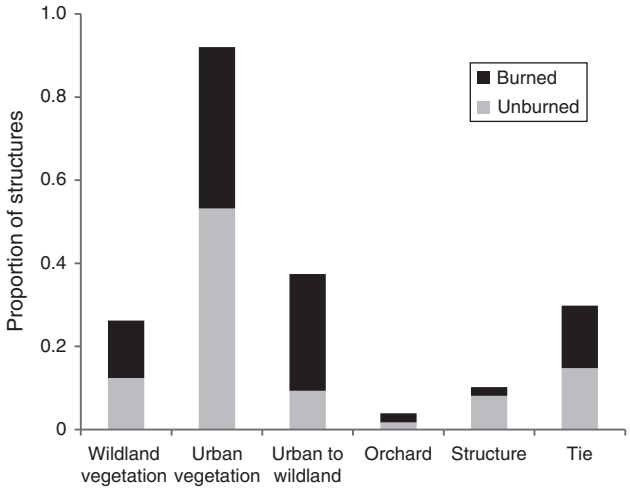


Fig. 5. Proportion of destroyed and unburned structures based on the primary surrounding cover type at the end of defensible space measurements. There were no significant differences in the proportion of burned and unburned structures within cover types ($P = 0.14$). Cover types are defined in Table 1.

However, as with defensible space, percentage clearance did not need to be draconian to be effective. Even on steep slopes, the effective percentage clearance needed on the property was <40%, with no significant advantage beyond that. Although these steep-slope structures benefited more from clearance, they tended to have less clearance than the effective amount, which may be why slope was such an important variable in the multiple regression models. Shallow-slope structures, in contrast, had more clearance on average than was calculated to be effective, suggesting these property owners do not need to modify their behaviours as much relative to people living on steep slopes.

Although the term 'clearance' is often used interchangeably with defensible space, this term is incorrect when misinterpreted to mean clearing all vegetation, and our results underline this difference. The idea behind defensible space is to reduce the continuity of fuels through maintenance of certain distances among trees and shrubs. Although we could not identify the vertical profile of fuels through Google Earth imagery, the fact that at least 60% of the horizontal woody vegetative cover can remain on the property with significant protective effects demonstrates the importance of distinguishing defensible space from complete vegetation removal. Thus, we suggest the term 'clearance' be replaced with 'fuel treatment' as a better way of communicating fire hazard reduction needs to home owners.

The percentage cover of woody shrubs and trees was not evenly distributed across properties, and we did not collect data describing how the cover was distributed. Considering the importance of defensible space and vegetation modification immediately adjacent to the structure, it should follow that actions to reduce cover should also be focussed in close proximity to the structure. The hazard of vegetation near the structure has apparently been recognised for some time (Foote *et al.* 1991; Ramsey and McArthur 1994), but it is not stressed enough, and rarely falls within the scope of defensible space guidelines or ordinances.

In addition to the importance of vegetation overhanging or touching the structure, it is important to understand that ornamental vegetation may be just as, if not more, dangerous than native vegetation in southern California. Although the results showed no significant differences in the cover types in the surrounding matrix, there was a disproportionately large number of structures destroyed (28% burned *v.* 9% unburned) when ornamental vegetation on the property led directly into the wildland. Ornamental vegetation may produce highly flammable litter (Ganteaume *et al.* 2013) or may be particularly dangerous after a drought when it is dry, or has not been maintained, and species of conifer, juniper, cypress, eucalypt, *Acacia* and palm have been present in the properties of many structures that have been destroyed (Franklin 1996). Nevertheless, ornamental vegetation is allowed to be included as defensible space in many codes and ordinances (Haines *et al.* 2008).

One reason that longer defensible space distances did not significantly increase structure protection may be that most homes are not destroyed by the direct ignition of the fire front but rather due to ember-ignited spot fires, sometimes from fire brands carried as far as several km away. Although embers decay with distance, the difference between 30 and 90 m (100 and 300 ft) may be small relative to the distance embers travel under the severe wind conditions that were present at the time of the fires. The ignitability of whatever the embers land on, particularly adjacent to the house, is therefore most critical for propagating the fire within the property or igniting the home (Cohen 1999; Maranghides and Mell 2009).

Aside from roofing or home construction materials and vegetation immediately adjacent to structures (Quarles *et al.* 2010; Keeley *et al.* 2013), the flammability of the vegetation in the property may also play a role. Large, cleared swaths of land are likely occupied at least in part by exotic annual grasses that are highly ignitable for much of the year. Conversion of woody shrubs with higher moisture content into low-fuel-volume grasslands could potentially increase fire risk in some situations by increasing the ignitability of the fuel; and if the vegetation between a structure and a fire is not readily combustible, it could protect the structure by absorbing heat flux and filtering fire brands (Wilson and Ferguson 1986).

The slight increase in proportion of structures destroyed with longer distances of defensible space within parcel boundaries was surprising. However, that increase was not significant in the Chi-square analysis, although there were some significant differences in the pairwise relative risk analysis. Nevertheless, the largest significant effect of defensible space was between the categories of 0–7 m (0–25 ft) to 8–15 m (26–50 ft), and it may be that differences in categories beyond these distances are not highly meaningful or reflect an artefact of the definition of distance categories. These relationships at longer distances are likely also weak compared to the effect of other variables operating at a landscape scale. Although the categorical analysis allowed us to answer questions relative to legal requirements and specific distances, the effective treatment analysis was important for identifying thresholds in the continuous variable.

The multiple regression models showed that landscape factors such as low housing density and longer distances to major roads were more important than distance of defensible space for explaining structure destruction, and the importance of

these variables is consistent with previous studies (Syphard *et al.* 2012, 2013), despite the smaller spatial extent studied here. Whereas this study used an unburned control group exposed to the same fires as the destroyed structures, previous studies accounted for structures across entire landscapes. The likelihood of a fire destroying a home is actually a result of two major components: the first is the likelihood that there will be a fire, and the second is the likelihood that a structure will burn in that fire. In this study, we only focussed on structure loss given the presence of a fire, and the total explained variation for the multiple regression models was quite low at ~12%. However, when the entire landscape was accounted for in the total likelihood of structure destruction, the explained variation of housing density alone was >30% (Syphard *et al.* 2012). One reason for the relationship between low housing density and structure destruction is that structures are embedded within a matrix of wildland fuel that leads to greater overall exposure, which is consistent with Australian research that showed a linear decrease of structure loss with increased distance to forest (Chen and McAneney 2004). That research, however, only focussed on distance to wildland boundaries and did not quantify variability in defensible space or ornamental vegetation immediately surrounding structures. Thus, fire safety is important to consider at multiple scales and for multiple variables, which will ultimately require the cooperation of multiple stakeholders.

Conclusions

Structure loss to wildfire is clearly a complicated function of many biophysical, human and spatial factors (Keeley *et al.* 2009; Syphard *et al.* 2012). For such a large sample size, we were unable to account for home construction materials, but this is also well understood to be a major factor, with older homes and wooden roofs being most vulnerable (Franklin 1996; Cohen 1999, 2000). In terms of actionable measures to reduce fire risk, this study shows a clear role for defensible space up to 30 m (100 ft). Although the effective distances were on average much shorter than 30 m (100 ft), we recognise that additional distance may be necessary to provide sufficient protection to firefighters, which we did not address in this study (Cheney *et al.* 2001). In contrast, the data in this study do not support defensible space beyond 30 m (100 ft), even for structures on steep slopes. In addition to the fact that longer distances did not contribute significant additional benefit, excessive vegetation clearance presents a clear detriment to natural habitat and ecological resources. Results here suggest the best actions a homeowner can take are to reduce percentage cover up to 40% immediately adjacent to the structure and to ensure that vegetation does not overhang or touch the structure.

In addition to defensible space, this study also underlines the potential importance of land use planning to develop communities that are fire safe in the long term, in particular through their reduction to exposure to wildfire in the first place. Localised subdivision decisions emphasising infill-type development patterns may significantly reduce fire risk in the future, in addition to minimising habitat loss and fragmentation (Syphard *et al.* 2013). This study was conducted in southern California, which has some of the worst fire weather in the world and many properties surrounded by large, flammable exotic trees. Therefore, recommendations here should apply to other non-forested ecosystems as well as many forested regions.

Acknowledgements

We acknowledge funding from the US Geological Survey Fire Risk Scenario Project and note that use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

References

Absher JD, Vaske JJ (2011) The role of trust in residents' fire wise actions. *International Journal of Wildland Fire* **20**, 318–325. doi:10.1071/WF09049

Agresti A (2007) 'An Introduction to Categorical Data Analysis', 2nd edn. (Wiley: New York)

Blanchi R, Lucas C, Leonard J, Finkele K (2010) Meteorological conditions and wildfire-related house loss in Australia. *International Journal of Wildland Fire* **19**, 914–926. doi:10.1071/WF08175

Boschetti L, Roy D, Barbosa P, Justice C (2008) A MODIS assessment of the summer 2007 extent burned in Greece. *International Journal of Remote Sensing* **29**, 2433–2436. doi:10.1080/01431160701874561

Burnham KP, Anderson DR (2002) 'Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach', 2nd edn. (Springer-Verlag: New York)

Calfire (2000) 'Wildland Fire Hazard Assessment Final Report on FEMA.' (California Department of Forestry and Fire Protection: Sacramento, CA)

Calfire (2006) 'General Guidelines for Creating Defensible Space.' (California Department of Forestry and Fire Protection: Sacramento, CA)

Cary GJ, Flannigan MD, Keane RE, Bradstock RA, Davies ID, Lenihan JM, Li C, Logan KA, Parsons RA (2009) Relative importance of fuel management, ignition management and weather for area burned: evidence from five landscape–fire–succession models. *International Journal of Wildland Fire* **18**, 147–156. doi:10.1071/WF07085

Cedergreen N, Ritz C, Streibig JC (2005) Improved empirical models for describing hormesis *Environmental Toxicology and Chemistry* **24**, 3166–3177. doi:10.1897/05-014R.1

Chen K, McAneney J (2004) Quantifying bushfire penetration into urban areas in Australia. *Geophysical Research Letters* **31**, L12212. doi:10.1029/2004GL020244

Cheney P, Gould J, McCaw L (2001) The dead-man zone – a neglected area of firefighter safety. *Australian Forestry* **64**, 45–50. doi:10.1080/00049158.2001.10676160

Cohen JD (1999) Reducing the wildland fire threat to homes: where and how much? In 'Proceedings of the Symposium on Fire Economics, Planning, and Policy: Bottom Lines', 5–9 April 1999, San Diego, CA. (Eds A Gonzales-Caban, PN Omi) USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-173, pp. 189–195. (Albany, CA)

Cohen JD (2000) Home ignitability in the wildland–urban interface. *Journal of Forestry* **98**, 15–21.

Filmon G (2004) Firestorm 2003, provincial review. Report to the Provincial Government of British Columbia (Vancouver, BC) Available at http://bcwildfire.ca/History/ReportsandReviews/2003/FirestormReport.pdf [Verified 9 August 2014]

Foote EID, Gilless JK (1996) Structural survival. In 'California's I-Zone.' (Ed R Slaughter) pp. 112–121. (CFESTES: Sacramento, CA)

Foote EID, Martin RE, Gilless JK (1991) The defensible space factor study: a survey instrument for post-fire structure loss analysis. In 'Proceedings of the 11th Conference on Fire and Forest Meteorology', 16 April 1991, Bethesda, MD. (Eds PL Andrews, DF Potts) pp. 66–73. (Society of American Foresters: Bethesda, MD)

Franklin SE (1996) California's catastrophic intermix fires causes, culprits and cures. *American Fire Journal* **48**, 20–23.

Ganteaume A, Jappiot M, Corrine L (2013) Assessing the flammability of surface fuels beneath ornamental vegetation in wildland–urban interfaces in Provence (south-eastern France). *International Journal of Wildland Fire* **22**, 333–342. doi:10.1071/WF12006

Gibbons P, van Bommel L, Gill MA, Cary GJ, Driscoll DA, Bradstock RA, Knight E, Moritz MA, Stephens SL, Lindenmayer DB (2012) Land management practices associated with house loss in wildfires. *PLoS ONE* **7**, e29212. doi:10.1371/JOURNAL.PONE.0029212

Gill AM, Stephens SL (2009) Scientific and social challenges for the management of fire-prone wildland–urban interfaces. *Environmental Research Letters* **4**, 034014. doi:10.1088/1748-9326/4/3/034014

Gilmer M (1994) 'California Wildfire Landscaping.' (Taylor Publishing Company: Dallas, TX)

Gude PH, Rasker R, van den Noort J (2008) Potential for future development on fire-prone lands. *Journal of Forestry* **106**, 198–205.

Haines TK, Renner CR, Reams MA (2008) A review of state and local regulation for wildfire mitigation. In 'The Economics of Forest Disturbances: Wildfires, Storms, and Invasive Species'. (Eds TP Holmes, JP Prestemon, KL Abt) pp. 273–293. (US Forest Service: Washington, DC) Available at http://www.treesearch.fs.fed.us/pubs/32690 [Verified 9 August 2014]

Hammer RB, Radeloff VC, Fried JS, Stewart SI (2007) Wildland–urban interface housing growth during the 1990s in California, Oregon, and Washington. *International Journal of Wildland Fire* **16**, 255–265. doi:10.1071/WF05077

Hessl AE (2011) Pathways for climate change effects on fire: models, data, and uncertainties *Progress in Physical Geography* **35**, 393–407. doi:10.1177/0309133311407654

Howard RA, North DW, Offensend FL, Smart CN (1973) 'Decision Analysis of Fire Protection Strategy for the Santa Monica Mountains: an Initial Assessment.' (Stanford Research Institute: Menlo Park, CA)

Keeley JE, Baer-Keeley M, Fotheringham CJ (2005) Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecological Applications* **15**, 2109–2125. doi:10.1890/04-1222

Keeley JE, Safford HD, Fotheringham CJ, Franklin J, Moritz MA (2009) The 2007 southern California wildfires: lessons in complexity. *Journal of Forestry* **107**, 287–296.

Keeley JE, Syphard AD, Fotheringham CJ (2013) The 2003 and 2007 wildfires in southern California. In 'Natural Disasters and Adaptation to Climate Change'. (Eds S Boulter, J Palutikof, DJ Karoly, D Guitart) pp. 42–52. (Cambridge University Press: Oxford, UK)

King G, Zeng L (2001) Logistic regression in rare events data. *Political Analysis* **9**, 137–163. doi:10.1093/OXFORDJOURNALS.PAN.A004868

Knezevic SZ, Streibig JC, Ritz C (2007) Utilizing R software package for dose-response studies: the concept and data analysis. *Weed Technology* **21**, 840–848. doi:10.1614/WT-06-161.1

Kursar TA, Engelbrecht BMJ, Burke A, Tyree MT, El Omari B, Giraldo JP (2009) Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology* **23**, 93–102. doi:10.1111/J.1365-2435.2008.01483.X

Leonard J, Blanchi R, Lipkin F, Newnham G, Siggins A, Opie K, Culvenor D, Cechet B, Corby N, Thomas C, Habili N, Jakab M, Coghlan R, Lorenzin G, Campbell D, Barwick M (2009) Building and land-use planning research after the 7th February Victorian bushfires: preliminary findings. CSIRO and Bushfire CRC. (Melbourne)

Maire RG (1979) 'Landscape for Fire Protection.' (University of California Agriculture Extension Service: Los Angeles, CA)

Maranghides A, Mell WE (2009) A case study of a community affected by the Witch and Guejito fires. NIST Technical Note 1635. (Washington, DC)

Quarles SL, Valachovic Y, Nakamura GM, Nader GA, DeLasaux J (2010) Home survival in wildfire-prone areas: building materials and design considerations. University of California, Agriculture and Natural Resources, ANR Publication 8393. (Richmond, CA) Available at http://anrcatalog.ucdavis.edu/pdf/8393.pdf [Verified 9 August 2014]

R Development Core Team (2012) R: a language and environment for statistical computing. (R Foundation for Statistical Computing, Vienna, Austria) Available at http://www.R-project.org/ [Verified 23 August 2013]

Ramsey GC, McArthur NA (1994) Planning in fire-prone areas: building survival. In 'Bushfire! Looking to the Future: Papers from the Nature Conservation Council of NSW Seminar', June 1994. (Eds C Brown, L Tohver) pp. 142–150. (Envirobook: Sydney)

Ritz C, Streibig JC (2013) Package 'drc' analysis of dose-response curves. Available at http://cran.r-project.org/web/packages/drc/index.html [Verified 9 August 2014]

Schoennagel T, Nelson CR, Theobald DM, Carnwath GC, Chapman TB (2009) Implementation of National Fire Plan treatments near the wildland–urban interface in the western United States. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 10 706–10 711. doi:10.1073/PNAS.0900991106

Sheskin DJ (2004) 'Handbook of Parametric and Nonparametric Statistical Procedures', 3rd edn. (Chapman & Hall and CRC: Boca Raton, FL).

Smith E, Adams G (1991) 'Incline Village/Crystal Bay Defensible Space Handbook.' (University of Nevada: Reno, NV)

Spittler TE (1995) Fire and the debris flow potential of winter storms. In 'Brushfires in California Wildlands: Ecology and Resource Management.' (Eds JE Keeley, T Scott) pp. 113–120. (International Association of Wildland Fire: Fairfield, WA)

Stockmann K, Burchfield J, Calkin D, Venn T (2010) Guiding preventative wildland fire mitigation policy and decisions with an economic modeling system. *Forest Policy and Economics* **12**, 147–154. doi:10.1016/J.FORPOL.2009.09.009

Streibig JC, Rudemo M, Jensen JE (1993) Dose-response curves and statistical models. In 'Herbicide Bioassays.' (Eds JC Streibig, P Kudsk) pp. 29–55. (CRC: Boca Raton, FL)

Syphard AD, Franklin J, Keeley JE (2006) Simulating the effects of frequent fire on southern California coastal shrublands. *Ecological Applications* **16**, 1744–1756. doi:10.1890/1051-0761(2006)016[1744:STEOFF]2.0.CO;2

Syphard AD, Radeloff VC, Keuler NS, Taylor RS, Hawbaker TJ, Stewart SI, Clayton MK (2008) Predicting spatial patterns of fire on a southern California landscape. *International Journal of Wildland Fire* **17**, 602–613. doi:10.1071/WF07087

Syphard AD, Keeley JE, Massada AB, Brennan TJ, Radeloff VC (2012) Housing arrangement and location determine the likelihood of housing loss due to wildfire. *PLoS ONE* **7**, e33954. doi:10.1371/JOURNAL.PONE.0033954

Syphard AD, Bar Massada A, Butsic V, Keeley JE (2013) Land use planning and wildfire: development policies influence future probability of housing loss. *PLoS ONE* **8**, e71708. doi:10.1371/JOURNAL.PONE.0071708

Vasquez T (2011) The Russian inferno of 2010. *Weatherwise* **64**, 20–25. doi:10.1080/00431672.2011.551592

Venables WM, Ripley BD (1994) 'Modern Applied Statistics with S-Plus.' (Springer-Verlag: New York)

Wilson AAG, Ferguson IS (1986) Predicting the probability of house survival during bushfires. *Journal of Environmental Management* **3**, 259–270.

Winter G, McCaffrey S, Vogt CA (2009) The role of community policies in defensible space compliance. *Forest Policy and Economics* **11**, 570–578. doi:10.1016/J.FORPOL.2009.07.004

Witter M, Taylor RS (2005) Preserving the future: a case study in fire management and conservation from the Santa Monica Mountains. In 'Fire, Chaparral, and Survival in Southern California'. (Ed. RW Halsey) pp. 109–115. (Sunbelt Publications: San Diego, CA)

Zárate L, Arnaldos J, Casal J (2008) Establishing safety distances for wildland fires. *Fire Safety Journal* **43**, 565–575. doi:10.1016/J.FIRESAF.2008.01.001

View publication stats

Research Article

Does Prescribed Fire Promote Resistance to Drought in Low Elevation Forests of the Sierra Nevada, California, USA?

Phillip J. van Mantgem[1*], Anthony C. Caprio[2], Nathan L. Stephenson[3], and Adrian J. Das[3]

[1] US Geological Survey, Western Ecological Research Center,
1655 Heindon Road, Arcata, California 95521, USA

[2] National Park Service, Sequoia and Kings Canyon National Parks,
47050 Generals Highway, Three Rivers, California 93271, USA

[3] US Geological Survey, Western Ecological Research Center,
47050 Generals Highway, Three Rivers, California 93271, USA

[*]Corresponding author: Tel.: +1-707-825-5189; e-mail: pvanmantgem@usgs.gov

ABSTRACT

Prescribed fire is a primary tool used to restore western forests following more than a century of fire exclusion, reducing fire hazard by removing dead and live fuels (small trees and shrubs). It is commonly assumed that the reduced forest density following prescribed fire also reduces competition for resources among the remaining trees, so that the remaining trees are more resistant (more likely to survive) in the face of additional stressors, such as drought. Yet this proposition remains largely untested, so that managers do not have the basic information to evaluate whether prescribed fire may help forests adapt to a future of more frequent and severe drought.

During the third year of drought, in 2014, we surveyed 9950 trees in 38 burned and 18 unburned mixed conifer forest plots at low elevation (<2100 m a.s.l.) in Kings Canyon, Sequoia, and Yosemite national parks in California, USA. Fire had occurred in the burned plots from 6 yr to 28 yr be-

RESUMEN

El fuego prescripto es una herramienta primordial utilizada para restaurar los bosques del oeste de los EEUU luego de más de una centuria de exclusión del fuego, reduciendo el peligro de incendios mediante la remoción de combustibles vivos y muertos (pequeños árboles y arbustos). Se asume comúnmente que la reducción en la densidad del bosque luego de un fuego prescripto también reduce la competencia por los recursos entre los árboles remanentes, de manera tal que éstos son más resistentes (tienen más probabilidad de sobrevivir) frente a un estrés adicional como la sequía. Sin embargo esta suposición permanece aún sin verificar, por lo cual los gestores no tienen información básica para evaluar si el fuego prescripto puede ayudar a los bosques a adaptarse a un futuro con sequías más frecuentes y severas.

Durante el tercer año de sequía, en 2014, relevamos datos de 9950 árboles en 38 parcelas quemadas y 18 parcelas sin quemar en bosques mixtos de coníferas de elevaciones bajas (<2100 msnm) en los parques nacionales de Kings Canyon, Sequoia, y Yosemite en California, EEUU. El fuego había ocurrido en las parcelas quemadas entre 6 años y 28 años antes de

fore our survey. After accounting for differences in individual tree diameter, common conifer species found in the burned plots had significantly reduced probability of mortality compared to unburned plots during the drought. Stand density (stems ha^{-1}) was significantly lower in burned versus unburned sites, supporting the idea that reduced competition may be responsible for the differential drought mortality response. At the time of writing, we are not sure if burned stands will maintain lower tree mortality probabilities in the face of the continued, severe drought of 2015. Future work should aim to better identify drought response mechanisms and how these may vary across other forest types and regions, particularly in other areas experiencing severe drought in the Sierra Nevada and on the Colorado Plateau.

nuestro relevamiento. Después de considerar las diferencias en el diámetro individual de los árboles y durante la sequía, las especies de coníferas encontradas en las parcelas quemadas redujeron significativamente la probabilidad de muerte comparadas con las parcelas no quemadas. La densidad del rodal (fustes ha^{-1}) fue significativamente menor en sitios quemados versus los no quemados, apoyando la idea que una reducción en la competencia puede ser la responsable de la mortalidad diferencial en respuesta a la sequía. En el momento de escribir este artículo, no estamos seguros si los rodales quemados mantendrán una mortalidad baja en vistas a la sequía continua y severa de 2015. El trabajo a futuro debería apuntar a identificar mejor los mecanismos de respuesta a la sequía y como éstos pueden variar en otros tipos de bosques y regiones, particularmente en otras áreas que están experimentando sequías severas en Sierra Nevada y en la meseta de Colorado.

Keywords: drought, fire effects, forest management, prescribed fire, Sierra Nevada, tree mortality

Citation: van Mantgem, P.J., A.C. Caprio, N.L. Stephenson, and A.J. Das. 2016. Does prescribed fire promote resistance to drought in low elevation forests of the Sierra Nevada, California, USA? Fire Ecology 12(1): 13–25. doi: 10.4996/fireecology.1201013

INTRODUCTION

Drought is a major disturbance agent in forest ecosystems, causing tree mortality directly (Adams *et al.* 2009) or by making trees more vulnerable to insects (bark beetles) or pathogens (Weed *et al.* 2013). While reduced precipitation often defines drought, higher temperatures lead to increased evapotranspiration that also causes drought stress. Indeed, chronic drought caused by long-term warming trends is believed to be an underlying cause of increased "background" (non-catastrophic) tree mortality across western North America (van Mantgem *et al.* 2009, Peng *et al.* 2011). Recent observations from the American Southwest have shown that the co-occurrence of reduced precipitation and high temperatures—"hotter drought" (Allen *et al.* 2015)—can lead to massive forest die-back, in which entire stands are lost (Breshears *et al.* 2005, Allen *et al.* 2010).

Fire exclusion has also led to unforeseen changes in many western forests, particularly in those forests that historically experienced high frequency and low severity fire (Allen *et al.* 2002, Brown *et al.* 2004, Agee and Skinner 2005, Noss *et al.* 2006). Fire exclusion in these forests has typically resulted in high fuel accumulations, high densities of trees, and increasing dominance of fire-intolerant species. In response, many public land agencies support large prescribed fire programs aimed at reducing understory fuels and forest density.

Prescribed fire has been generally successful at reducing severe fire hazard (van Wagtendonk 1996, Hurteau and North 2009, Fulé *et al.* 2012) by removing surface fuels, along with shrubs and small trees (ladder fuels). It is commonly assumed that following fire there is less competition among remaining trees so that they have increased resistance (more likely to survive) to additional stressors, such as drought.

Published findings on mechanical thinning and drought response provide mixed results. Thomas and Waring (2014) suggested that mechanical thinning treatments conferred improved forest resistance (remaining unchanged when subjected to disturbance) and resilience (capacity to return to original conditions) to drought. Other work suggests that the influence of mechanical thinning may be conditional on timing of treatments, the size structure of residual trees, and potential threshold responses (D'Amato *et al.* 2013). Moreover, the response of individual trees to drought is likely complex, partially dependent on local competitive environments and cumulative impacts of past drought events (Macalady and Bugmann 2014).

Can prescribed fire create conditions that enhance forest drought resistance? The answer to this question has profound implications for forest management over the coming decades. Drought-induced forest decline was identified as a key emerging threat to US forests in the recent National Climate Assessment (Joyce *et al.* 2014). Indeed, drought is expected to be more frequent and severe in coming decades across the southwestern United States (Garfin *et al.* 2014, Cook *et al.* 2015), underscoring the importance for land management agencies to develop cost-effective adaptation strategies to drought (Millar *et al.* 2007). Prescribed fire may serve as an adaptation tool, helping forests withstand expected warmer and drier future conditions, but this effect remains largely untested. California is currently experiencing its most severe drought in at least the last 120 years, and perhaps as much as a millennium, driven by low precipitation and record high temperatures (Griffin and Anchukaitis 2014). Aerial observations across California suggest that by 2014 forests at lower elevations experienced significant drought stress (Asner *et al.* 2016). We used this drought as a natural experiment, assessing whether or not past prescribed fires were associated with increased drought resistance (reduced tree mortality) in low elevation forests (<2100 m a.s.l.) at three national parks in the southern Sierra Nevada of California, USA.

METHODS

Study Area

We sampled burned and unburned mixed conifer forests in Kings Canyon, Sequoia, and Yosemite national parks (Table 1, Figure 1). Lower elevation forests at these parks were observed to be responding to drought with elevated mortality by 2014 (Figure 2), while forests at higher elevations did not visibly display elevated mortality by 2014. Prior to the initiation of a prescribed burn program or the management of lightning ignited fires by the parks in the late 1960s, these forests generally had not burned since the 1860s or 1870s (Schwilk *et al.* 2006, Swetnam *et al.* 2009). The climate of this area is mediterranean, with wet, snowy winters and long, dry summers. The weather station at Grant Grove (2011 m elevation a.s.l.), near the majority of our plots, reported annual average minimum and maximum air temperatures of 1.9 °C and 13.6 °C, and mean annual precipitation of 109 cm (30 yr average, 1951 to 1980). Compared to these long-term averages, 2013 and 2014 were unusually hot and dry. Average annual minimum and maximum air temperatures for these years were 3.1 °C and 15.8 °C, with mean annual precipitation of 59 cm. The Yosemite Valley weather station (1210 m elevation a.s.l.) reported similar trends.

Table 1. Summary statistics of burned and unburned forest monitoring plots. Average values (±1 standard deviation) are presented for plot elevation, stand density, stand basal area, and quadratic mean stem diameter (QMD). Note that slope measurements were missing for one burned plot and for five unburned plots. Live and dead tree summary statistics in 2014, with species composition presented in terms of proportional basal area.

Plot type	Plot count (*n*)	Elevation (m)	Slope (%)	Aspect (°)	Density (trees ha^{-1})	Basal area (m^2 ha^{-1})	QMD (cm)
Burned	38	1901 ± 152	21 ± 15	187 ± 114	414 ± 358	72.6 ± 94.9	52.9 ± 30.7

	Tree status	Tree count	QMD (cm)	Species comprising ≥1 % of basal area*
Burned	Live	2100	53.1 ± 30.7	ABCO 35 %, CADE 19 %, PIPO 9 %, PILA 8 %, QUCH 8 %, SEGI 8 %, QUKE 6 %, PIXX 2 %, CONU 1 %, PIJE 1 %, TOCA 1 %
	Dead	57	33.7 ± 40.7	ABCO 54 %, CADE 21 %, PILA 16 %, PIJE 4 %, PIPO 4 %, PIXX 2 %

Plot type	Plot count (*n*)	Elevation (m)	Slope (%)	Aspect (°)	Density (trees ha^{-1})	Basal area (m^2 ha^{-1})	QMD (cm)
Unburned	18	1804 ± 219	17 ± 13	167 ± 89	894 ± 540	70.1 ± 31.9	35.4 ± 13.0

	Tree status	Tree count	QMD (cm)	Species comprising ≥1 % of basal area*
Unburned	Live	7435	35.7 ± 13.1	ABCO 41 %, CADE 35 %, QUKE 9 %, PILA 8 %, PIPO 3 %, QUCH 2 %, ABMA 1 %, CONU 1 %
	Dead	358	14.5 ± 8.6	CADE 39 %, ABCO 26 %, PILA 14 %, PIPO 10 %, QUKE 10 %

*Percentages may not add to 100 due to rounding. ABCO = *Abies concolor,* ABMA = *A. magnifica* Andr. Murray, CADE = *Calocedrus decurrens,* CONU = *Cornus nuttallii* Audubon, PIJE = *Pinus jeffreyi* Grev. & Balf., PILA = *P. lambertiana, PIPO = P. ponderosa,* PIXX = unknown *Pinus,* QUCH = *Quercus chrysolepis* Liebm., QUKE = *Q. kelloggii* Newb., SEGI = *Sequoiadendron giganteum* (Lindley) Buchholz, TOCA = *Torreya californica* Torrey.

Data Sources

We used two primary data sources for this project: the US Geological Survey-led Sierra Nevada Forest Dynamics Plot Network (van Mantgem and Stephenson 2007) and the National Park Service fire effects monitoring (FMH) plots for Sequoia and Kings Canyon national parks (NPS 2003). The Sierra Nevada Forest Dynamics Plot Network is a globally unique and ongoing plot-based forest monitoring project that has annually tracked the birth, death, and growth of nearly 30 000 individual trees across all major forest types on the western slope of the Sierra Nevada since the early 1980s. This network includes several plots in low elevation forests with and without a recent history of prescribed fire. The FMH fire effects monitoring data records forest conditions before and after prescribed fire. Sequoia and Kings Canyon national parks were early adopters of these fire-effects monitoring protocols and have maintained an active program since the 1980s. Stand conditions at these sites differ according to pre-fire conditions and variability in fire effects. This plot-based program also tracks individual tree birth, death and growth, but at staggered intervals (typically pre-fire, and post fire at 0-, 1-, 2-, 5-, 10-year intervals, and every 10 yr thereafter).

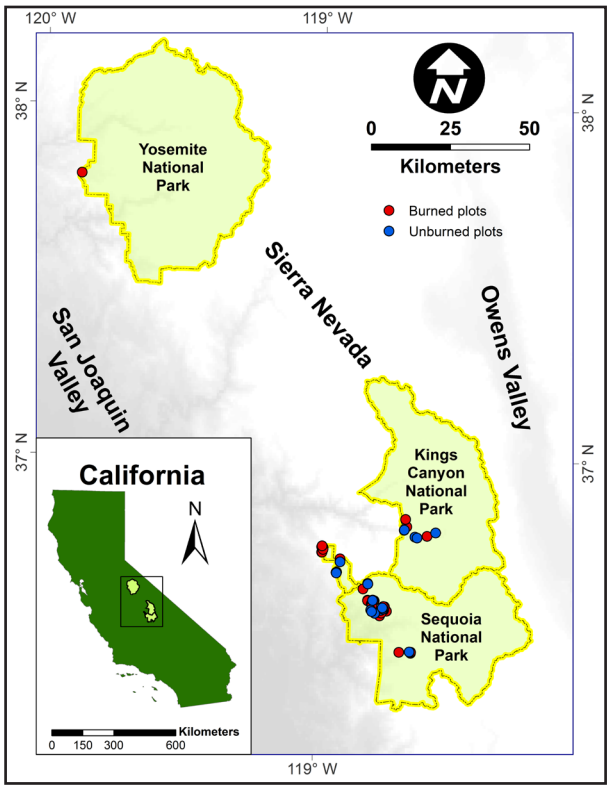


Figure 1. Locations of burned an unburned plots used for analysis at Kings Canyon, Sequoia, and Yosemite national parks, California, USA.



Figure 2. Drought-related tree mortality at a low elevation forest in Sequoia National Park. Photo credit: Nate Stephenson, US Geological Survey.

There are a number of unburned FMH plots, established as unburned reference sites or prior to a prescribed fire that then did not occur. A major difference between these monitoring programs is plot size, with the Sierra Nevada Forest Dynamics plots generally at 1.0 ha, and the FMH plots at 0.1 ha. However, model testing did not provide evidence for systematic differences between individual tree response in the Sierra Nevada Forest Dynamics and FMH plot networks. Similarly, the single large plot at Yosemite National Park was composed of the same vegetation type as the other plots, met our criteria for analysis, and testing did not reveal significant differences in the mortality response in this plot compared to the plots found in Kings Canyon and Sequoia national parks.

In 2014, we conducted mortality assessments of trees that had died in 2013 or 2014 for individually marked trees in mixed conifer forests at all Sierra Nevada Forest Dynamics plots, and all FMH plots at Sequoia and Kings Canyon national parks. We considered only low elevation forests, here defined as <2100 m a.s.l., which is the upper elevation boundary of ponderosa pine forests in the southern Sierra Nevada (Fites-Kaufman *et al.* 2007). We wanted to avoid measuring fire-caused tree mortality, and so excluded plots that had been burned ≤5 yr prior (van Mantgem *et al.* 2011). We focused on tree survivorship as an immediate drought response, noting if individual trees were alive or dead (no green needles). For the Sierra Nevada Forest Dynamics plots, annual assessments of tree mortality allowed observations of the exact year in which tree mortality occurred. Assessing trees that had died in 2013 or 2014 in the FMH plots was less straightforward; we excluded trees that were listed as dead in previous years and counted trees as newly dead within the past two years if they were retaining dead reddish needles and did not have a past history of severe crown scorch (>90% crown volume scorch). Dead trees meeting these criteria in the FMH plots were scarce, so to increase our sample size of dead trees we expanded each side of the FMH plot by 10 m, covering an additional 0.18 ha to search for dead trees only. Our final sample was 9353 live trees and 415 dead trees in 38

burned and 18 unburned plots at Kings Canyon, Sequoia, and Yosemite national parks. Fire had occurred in the burned plots from 6 yr to 28 yr before our survey. For a subset of our plots, prescribed fire had been applied once (14 plots) or twice (4 plots) prior to the most recent prescribed fire. A history of repeated prescribed fire did not appear to influence our results.

Analyses

We compared burned and unburned plots in terms of stem density (trees ha^{-1}), stand basal area (m^2 ha^{-1}), and quadratic mean diameter using randomization tests, creating 1000 samples with replacement (Manly 1997). We compared the proportion of stem density composed of dead versus live trees in burned and unburned stands with logistic regression, using a quasi-binomial response distribution to account for overdispersion. While this analysis shows differences in the observations of tree mortalities between burned and unburned plots, these differences may arise from the unburned plots having greater numbers of small trees that may be at higher risk of mortality. To account for differences across stem sizes, we estimated individual tree mortality probabilities for our most common conifer species, which included white fir (ABCO, *Abies concolor* [Gordon & Glend.] Lindley, n = 3759 live trees and 123 dead trees), incense cedar (CADE, *Calocedrus decurrens* [Torrey] Florin, n = 3021 live trees and 152 dead trees), sugar pine (PILA, *Pinus lambertiana* Douglas, n = 777 live trees and 59 dead trees), and ponderosa pine (PIPO, *P. ponderosa* Laws, n = 428 live trees and 39 dead trees). Other conifers were sparse (generally fewer than 100 individuals) or lacked observations of mortality. We used generalized linear mixed models (GLMM, Gelman and Hill 2007) to estimate individual tree mortality probabilities, which allows us to analyze tree status (0 = live, 1 = dead), considering both individual-level variables (characteristics of individual trees) and plot-level variation. Our base model estimated two-year (2013 and 2014) mortality probability m_{ij} of tree i in plot j as:

$$logit(m_{ij}) = \beta_0 + a_j + (\beta_{logDBH} \times logDBH_{ij}) + (\beta_{CADE} \times Spp_{CADEij}) + (\beta_{PILA} \times Spp_{PILAij}) + (\beta_{PIPO} \times Spp_{PIPOij}), \quad (1)$$

$$a_j \sim N(0,\sigma^2),$$

where *logDBH* is the log-transformed (base 10) DBH (stem diameter at breast height, 1.37 m), and *Spp* is an indicator variable for species identity, with white fir (ABCO) used as the reference species. The variable a_j represents plot-level variations in the regression intercept. We considered varying-intercepts with varying-slope models, but these formulations did not improve model performance. We evaluated improvements to this base model with additional variables, including a term for a history of prescribed burning.

Selection for the GLMMs was done using the Akaike Information Criterion adjusted for sample size (AICc) (Burnham and Anderson 2002), with differences in AICc (ΔAICc) >2 used as evidence of substantial model dissimilarity. We used the area under the receiver operating characteristic curve (AUC, Saveland and Neuenschwander 1990) to characterize candidate model accuracy (predicted proportions of Type I and Type II errors), with values of AUC >0.70 suggesting acceptable model accuracy (Hosmer and Lemeshow 2000). Model fit was checked by binning the data and plotting average predicted mortality probability against the observed proportion of dead trees. The proportion of variation explained using the individual-level variables only (marginal R^2) and the combined individual- and plot-level variables (conditional R^2) of the fitted models were calculated following Nakagawa and Schielzeth (2013). We calculated bootstrapped (1000 realizations) confidence intervals for parameter estimates from the models with the best support according to AICc. Analyses were conducted using the R

statistical language (R Development Core Team 2015) with the lme4 (Bates *et al.* 2015) and MuMIn (Barton 2015) packages.

RESULTS

The burned and unburned plots were different in some dimensions of stand condition in 2014 (Table 1). The average length of time since prescribed fire in the burned plots was 15 yr, while the unburned plots likely had not experienced fire for >100 yr (Schwilk *et al.* 2006, Swetnam *et al.* 2009). The burned plots had lower average stem density in the burned plots compared to the unburned plots (randomization test, $P = 0.001$). In contrast, burned plots had slightly higher average basal area compared to unburned plots, but this difference was non-significant (randomization test, $P = 0.417$). Quadratic mean diameter was greater in the burned plots compared to the unburned plots (randomization test, $P = 0.001$). Logistic regression indicated that the density of recently dead trees was negatively related to a history of prescribed fire ($\beta_{BurnStatus} \pm 1$ SE $= -1.62 \pm 0.44$, $P < 0.001$).

GLMM results showed that the two-year (2013 and 2014) probability of individual tree mortality varied by tree size (*logDBH*), species identity (*Spp*), and history of prescribed burning (*BurnStatus*) (Tables 2 and 3). Common conifer species appeared to respond somewhat individualistically to a history of prescribed burning (i.e., there was support for *Spp* × *BurnStatus* interaction terms), with *Pinus* species having the greatest sensitivity to history of prescribed burning. Individual tree mortality probabilities also varied substantially with size among species. Residual plots did not suggest model misspecifications and AUC = 0.77. Adding an additional term for the years since prescribed burning was not supported (ΔAICc = 0.19). The individual-level effects of the model explained a relatively low amount of variation in tree mortality (marginal $R^2 = 0.11$), although the inclusion of the plot-level effect improved the model performance (conditional $R^2 = 0.37$). Excluding the *BurnStatus* term resulted in a relatively large proportional reduction in the marginal R^2 (marginal $R^2 = 0.05$). Prediction plots show that trees in plots that experienced prescribed fire had lower mortality probabilities (with some overlap in confidence intervals, particularly for white fir), and that these differences were most pronounced in small trees (Figure 3).

DISCUSSION

Our results suggest that a common forest restoration tool, prescribed fire, may increase resistance to drought. After accounting for

Table 2. Model selection for GLMMs of two-year tree mortality probabilities for common conifers, including terms for tree size (*logDBH,* log-transformed stem diameter), species identity (*Spp*), and history of prescribed fire (*BurnStatus,* unburned or past prescribed fire) using AICc. Evidence for substantial model dissimilarity was ΔAICc > 2.

Model class	Model predictors	df	log likelihood	AICc	ΔAICc
Base model	*logDBH* + *Spp*	6	–1381	2773	14.6
	logDBH × *Spp*	9	–1375	2769	10.0
BurnStatus	*logDBH* × *Spp* + *BurnStatus*	10	–1371	2762	3.3
	logDBH × *Spp* + *BurnStatus* × *logDBH*	11	–1371	2764	5.1
	logDBH × *Spp* + *BurnStatus* × *Spp*	13	–1366	2759	0.0
	logDBH × *Spp* × *BurnStatus*	17	–1366	2766	7.3

Table 3. GLMM parameter estimates for individual-level effects of two-year tree mortality probabilities for common conifers. Species differences are shown relative to white fir (ABCO). Species codes follow Table 1 and model terms follow Table 2. Parameter 95% confidence intervals were derived from 1000 bootstrapped samples.

Individual-level effect	Estimate	Standard error	95% CI
logDBH	–0.85	0.16	–1.11 to –0.55
Spp_{CADE}	–0.41	0.20	–0.84 to –0.01
Spp_{PILA}	0.44	0.24	–0.02 to 0.88
Spp_{PIPO}	0.66	0.32	–0.07 to 1.30
$logDBH \times Spp_{CADE}$	0.47	0.21	0.09 to 0.84
$logDBH \times Spp_{PILA}$	0.63	0.25	0.18 to 1.04
$logDBH \times Spp_{PIPO}$	–0.07	0.33	–0.96 to 0.61
BurnStatus	–0.84	0.48	–1.88 to 0.08
$BurnStatus \times Spp_{CADE}$	–0.56	0.42	–2.19 to 0.47
$BurnStatus \times Spp_{PILA}$	–0.83	0.49	–2.47 to 0.26
$BurnStatus \times Spp_{PIPO}$	–2.00	0.84	–9.98 to –0.38

differences in individual tree diameter, common conifer species found in plots with a history of prescribed fire had significantly reduced mortality probabilities compared to trees in unburned plots. Small trees had high mortality probabilities, but the effect of past prescribed fire did not appear to be dependent on tree size (i.e., there was not strong support for an interaction between *logDBH* and *BurnStatus*). The support for the interaction term between species identity and history of prescribed burning suggests that *Pinus* species may be particularly sensitive to changes in stand conditions. Stand density (stems ha^{-1}) was significantly lower in burned versus unburned sites, supporting the idea that reduced competition may be at least partly responsible for the differential drought mortality response. However, basal area (m^2 ha^{-1}) was not significantly lower in burned versus unburned sites, so the role of competition in determining the differential mortality response is not clear.

At the time of writing, we are not sure if burned stands will maintain lower tree mortality probabilities in the face of the continued, severe drought of 2015. Future work should aim to better identify drought response mechanisms. While the causal links among prescribed fire, reduced stand density, and reduced mortality under drought are intuitively appealing, our data were insufficient to test this directly. Plot sizes were generally too small (0.1 ha) to confidently measure individual-level competitive interactions (i.e., many trees will be at the plot margins, with unknown competitive environments outside of the plot boundary) (Das 2012). We also did not collect information on other potentially important mortality predictors, such as individual tree growth history (Das *et al.* 2007), insect and pathogen pressure, and plot-level environmental conditions (e.g., soil depth or water holding capacity). Future work should attempt to combine both direct and indirect influences of tree mortality across a broader geographic area, likely using a more sophisticated analytical framework such as structural equation models (Youngblood *et al.* 2009).

While reconstructing historical forest structure is problematic (Stephenson 1999), recent analyses of inventories of productive ponderosa pine forests conducted in 1911 for trees ≥15.2 cm DBH near our study sites identified average stand densities of 72.7 trees ha^{-1}

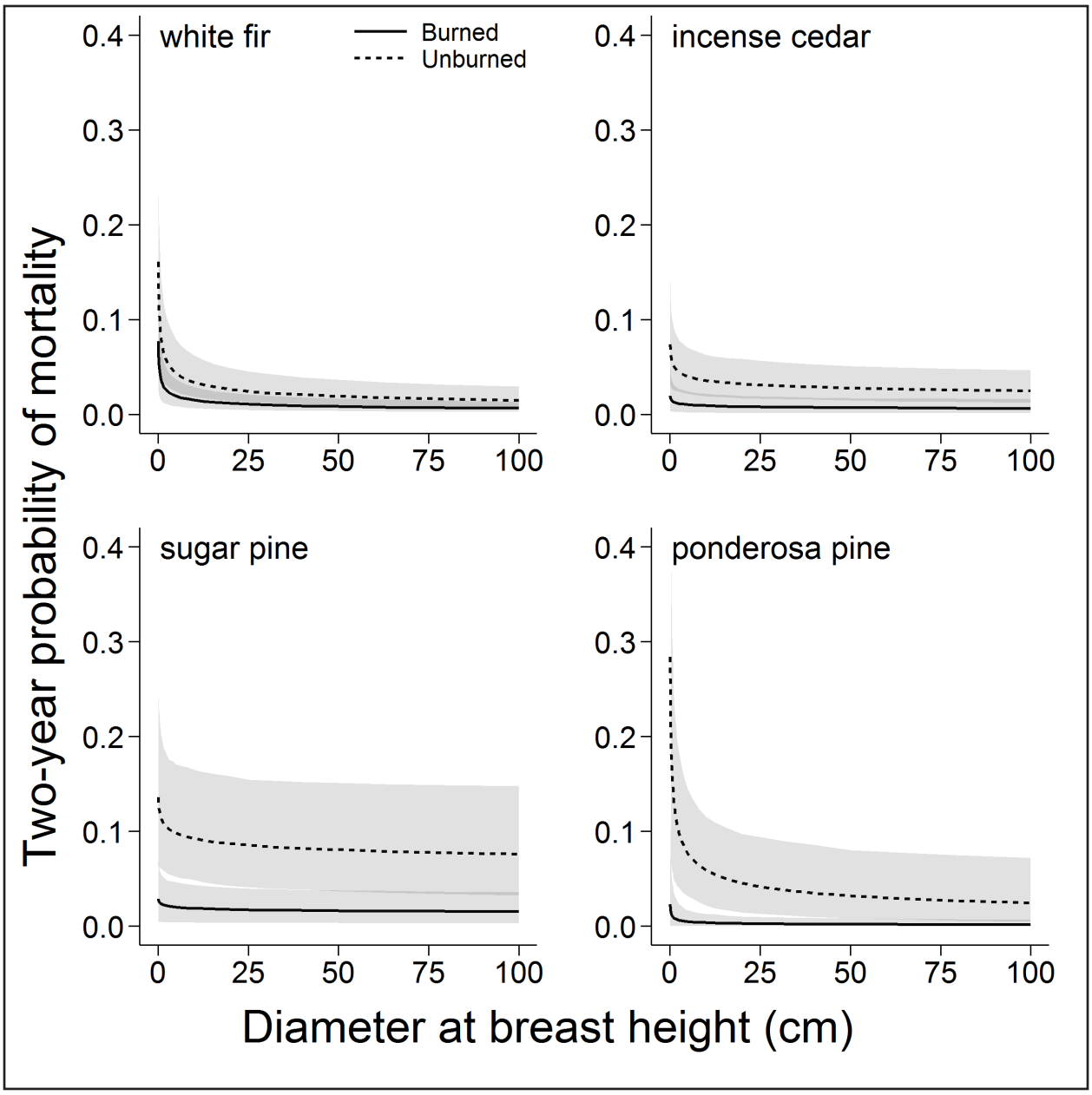


Figure 3. Predicted individual tree mortality probabilities for common conifer species in burned and unburned plots. The heavy lines represent modeled average trends and the shaded band represents 95% bootstrapped confidence intervals from uncertainty in the average mortality probability.

and basal area of 21.5 m^2 ha^{-1} (Collins *et al.* 2015). Using the same stem diameter range, our burned plots had an average stand density of 159 trees ha^{-1} and average basal area of 74.0 m^2 ha^{-1}. These statistics suggest that, even after prescribed burning, our forests contain many more trees relative to estimates of historical averages. It could be that forests with structures more closely approximating these presumed historical conditions may be more resistant and resilient (*sensu* Walker *et al.* 2004) to drought.

It may be possible to eventually manage for drought resistant and resilient forest structures. Such knowledge would provide a target when designing prescriptions using fire (per-

haps in combination with mechanical thinning) under expected future climatic conditions. We currently do not know if prescribed fire prescriptions will need to be more aggressive to promote resistance and resilient to drought. If prescribed prescriptions do need to be more aggressive, how much and under what conditions? These are critical management concerns, as many regions in the western United States are expected to see increased frequency and intensity of both drought and wildfire (Littell *et al.* 2009, Williams *et al.* 2012, Cook *et al.* 2015). It may be possible that prescribed fire can serve as an adaptation tool for both of these threats, using existing resources and human capital. Yet many barriers exist to maintaining, let alone expanding, the deployment of prescribed fire, particularly logistical constraints and air quality concerns (Ryan *et al.* 2013). Our study also underscores the need to maintain plot-based forest monitoring networks, in both treated and untreated stands, to gauge the success of prescribed fire. Overcoming obstacles to the use of prescribed fire may prove crucial to the future integrity of western forests.

ACKNOWLEDGEMENTS

We thank the many field crews who collected and organized the forest plot data. P. Moore, J. Yee, and three anonymous reviewers provided helpful comments on the manuscript. This project was partially supported by the National Park Service and the US Geological Survey Southwest Climate Science Center. Any use of trade names is for descriptive purposes only and does not imply endorsement by the US government.

LITERATURE CITED

Adams, H.D., M. Guardiola-Claramonte, G.A. Barron-Gafford, J.C. Villegas, D.D. Breshears, C.B. Zou, P.A. Troch, and T.E. Huxman. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proceedings of the National Academy of Sciences 106: 7063–7066. doi: 10.1073/pnas.0901438106

Agee, J.K., and C.N. Skinner. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211: 83–96. doi: 10.1016/j.foreco.2005.01.034

Allen, C.D., D.D. Breshears, and N.G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6(8): art129. doi: 10.1890/ES15-00203.1

Allen, C.D., A.K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D.D. Breshears, E.H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J.-H. Lim, G. Allard, S.W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259: 660–684. doi: 10.1016/j.foreco.2009.09.001

Allen, C.D., M. Savage, D.A. Falk, K.F. Suckling, T.W. Swetnam, T. Schulke, P.B. Stacey, P. Morgan, M. Hoffman, and J.T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications 12: 1418–1433. doi: 10.1890/1051-0761(2002)012[1418:EROSPP]2.0.CO;2

Asner, G.P., P.G. Brodrick, C.B. Anderson, N. Vaughn, D.E. Knapp, and R.E. Martin. 2016. Progressive forest canopy water loss during the 2012–2015 California drought. Proceedings of the National Academy of Sciences 113: E249–E255. doi: 10.1073/pnas.1523397113

Barton, K. 2015. MuMIn: Multi-Model Inference. R package version 1.15.1. <http://CRAN.R-project.org/package=MuMIn>. Accessed 14 April 2013.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48. doi: 10.18637/jss.v067.i01

Breshears, D.D., N.S. Cobb, P.M. Rich, K.P. Price, C.D. Allen, R.G. Balice, W.H. Romme, J.H. Kastens, M.L. Floyd, J. Belnap, J.J. Anderson, O.B. Myers, and C.W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Science of the United States of America 102: 15144–15148. doi: 10.1073/pnas.0505734102

Brown, R.T., J.K. Agee, and J.F. Franklin. 2004. Forest restoration and fire: principles in the context of place. Conservation Biology 18: 903–912. doi: 10.1111/j.1523-1739.2004.521_1.x

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer-Verlag, New York, New York, USA.

Collins, B.M., J.M. Lydersen, R.G. Everett, D.L. Fry, and S.L. Stephens. 2015. Novel characterization of landscape-level variability in historical vegetation structure. Ecological Applications 25: 1167–1174. doi: 10.1890/14-1797.1

Cook, B.I., T.R. Ault, and J.E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1(1): e1400082. doi: 10.1126/sciadv.1400082

D'Amato, A.W., J.B. Bradford, S. Fraver, and B.J. Palik. 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. Ecological Applications 23: 1735–1742. doi: 10.1890/13-0677.1

Das, A. 2012. The effect of size and competition on tree growth rate in old-growth coniferous forests. Canadian Journal of Forest Research 42: 1983–1995. doi: 10.1139/x2012-142

Das, A., J. Battles, N.L. Stephenson, and P.J. van Mantgem. 2007. The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada. Canadian Journal of Forest Research 37: 580–597. doi: 10.1139/X06-262

Fites-Kaufman, J., P. Rundel, N. Stephenson, and D.A. Weixelman. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. Pages 456–501 in M. Barbour, T. Keeler-Wolf, and A.A. Schoenherr, editors. Terrestrial vegetation of California, third edition. University of California Press, Berkeley, USA. doi: 10.1525/california/9780520249554.003.0017

Fulé, P.Z., J.E. Crouse, J.P. Roccaforte, and E.L. Kalies. 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? Forest Ecology and Management 269: 68–81. doi: 10.1016/j.foreco.2011.12.025

Garfin, G., G. Franco, H. Blanco, A. Comrie, P. Gonzalez, T. Piechota, R. Smyth, and R. Waskom. 2014. National climate assessment: Southwest region. Pages 462–486 in J.M. Melillo, T.C. Richmond, and G.W. Yohe, editors. Climate change impacts in the United States: the third national climate assessment. US Global Change Research Program, Washington, D.C., USA.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York, New York, USA.

Griffin, D., and K.J. Anchukaitis. 2014. How unusual is the 2012–2014 California drought? Geophysical Research Letters 41: 9017–9023. doi: 10.1002/2014GL062433

Hosmer, D.W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley & Sons, New York, New York, USA. doi: 10.1002/0471722146

Hurteau, M., and M. North. 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. Frontiers in Ecology and the Environment 7: 409–414. doi: 10.1890/080049

Joyce, L.A., S.W. Running, D.D. Breshears, V.H. Dale, R.W. Malmsheimer, R.N. Sampson, B. Sohngen, and C.W. Woodall. 2014. Forests. Pages 175–194 in J.M. Melillo, T.C. Richmond, and G.W. Yohe, editors. Climate change impacts in the United States: the third national climate assessment. US Global Change Research Program, Washington, D.C., USA.

Littell, J.S., D. McKenzie, D.L. Peterson, and A.L. Westerling. 2009. Climate and wildfire area burned in western US ecoprovinces, 1916–2003. Ecological Applications 19: 1003–1021. doi: 10.1890/07-1183.1

Macalady, A.K., and H. Bugmann. 2014. Growth-mortality relationships in piñon pine (*Pinus edulis*) during severe droughts of the past century: shifting processes in space and time. PloS ONE 9(5): e92770. doi: 10.1371/journal.pone.0092770

Manly, B.F.J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Second edition. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Millar, C.I., N.L. Stephenson, and S.L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17: 2145–2151. doi: 10.1890/06-1715.1

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4: 133–142. doi: 10.1111/j.2041-210x.2012.00261.x

Noss, R.F., J.F. Franklin, W.L. Baker, T. Schoennagel, and P.B. Moyle. 2006. Managing fire prone forests in the western United States. Frontiers in Ecology and the Environment 8: 481–487. doi: 10.1890/1540-9295(2006)4[481:MFFITW]2.0.CO;2

NPS [National Park Service]. 2003. Fire monitoring handbook. Fire Management Program Center, National Interagency Fire Center, Boise, Idaho, USA.

Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nature Climate Change 1: 467–471. doi: 10.1038/nclimate1293

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ryan, K.C., E.E. Knapp, and J.M. Varner. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Frontiers in Ecology and the Environment 11: e15–e24. doi: 10.1890/120329

Saveland, J.M., and L.F. Neuenschwander. 1990. A signal detection framework to evaluate models of tree mortality following fire damage. Forest Science 36: 66–76.

Schwilk, D.W., E.E. Knapp, S.M. Ferrenberg, J.E. Keeley, and A.C. Caprio. 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. Forest Ecology and Management 232: 36–45. doi: 10.1016/j.foreco.2006.05.036

Stephenson, N.L. 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecological Applications 9: 1253–1265. doi: 10.1890/1051-0761(1999)009[1253:RCFGSF]2.0.CO;2

Swetnam, T.W., C.H. Baisan, A.C. Caprio, P.M. Brown, R. Touchan, R.S. Anderson, and D.J. Hallett. 2009. Multi-millennial fire history of the Giant Forest, Sequoia National Park, California, USA. Fire Ecology 5(3): 120–150. doi: 10.4996/fireecology.0503120

Thomas, Z., and K.M. Waring. 2014. Enhancing resiliency and restoring ecological attributes in second-growth ponderosa pine stands in northern New Mexico, USA. Forest Science 61: 93–104.

van Mantgem, P.J., and N.L. Stephenson. 2007. Apparent climatically-induced increase of mortality rates in a temperate forest. Ecology Letters 10: 909–916. doi: 10.1111/j.1461-0248.2007.01080.x

van Mantgem, P.J., N.L. Stephenson, J.J. Battles, E.K. Knapp, and J.E. Keeley. 2011. Long-term effects of prescribed fire on mixed conifer forest structure in the Sierra Nevada, California. Forest Ecology and Management 261: 989–994. doi: 10.1016/j.foreco.2010.12.013

van Mantgem, P.J., N.L. Stephenson, J.C. Byrne, L.D. Daniels, J.F. Franklin, P.Z. Fulé, M.E. Harmon, A.J. Larson, J.M. Smith, A.H. Taylor, and T.T. Veblen. 2009. Widespread increase of tree mortality rates in the western United States. Science 323: 521–524. doi: 10.1126/science.1165000

van Wagtendonk, J.W. 1996. Use of a deterministic fire model to test fuel treatments. Pages 1155–1167 in: D.C. Erman, editor. Sierra Nevada Ecosystem Project, final report to Congress, volume II. Wildlands Resources Center Report No. 37, Centers for Water and Wildlands Resources, University of California, Davis, USA.

Walker, B., C.S. Holling, S.R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability and transformability in social-ecological systems. Ecology and Society 9(2): 5.

Weed, A.S., M.P. Ayres, and J.A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs 83: 441–470. doi: 10.1890/13-0160.1

Williams, A.P., C.D. Allen, A.K. Macalady, D. Griffin, C.A. Woodhouse, D.M. Meko, T.W. Swetnam, S.A. Rauscher, R. Seager, H.D. Grissino-Mayer, J.S. Dean, E.R. Cook, C. Gangodagamage, M. Cai, and N.G. McDowell. 2012. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3: 292–297. doi: 10.1038/nclimate1693

Youngblood, A., J. Grace, and J. McIver. 2009. Delayed conifer mortality after fuel reduction treatments: interactive effects of fuel, fire intensity, and bark beetles. Ecological Applications 19: 321–337. doi: 10.1890/07-1751.1

Northwest Forest Plan Just Futures Collaborative

Recommendations for Tribal Sovereignty and Environmental Justice in the Northwest Forest Plan Amendment Draft Environmental Impact Statement

What: This white paper provides recommendations around Tribal sovereignty and environmental justice that we hope will be useful to organizations and individuals as they comment on the Draft Environmental Impact Statement for the Northwest Forest Plan (NWFP) amendment. We hope that these suggestions reach a diversity of organizations and individuals with divergent visions of federal land management. We encourage organizations and individuals to consider where their values align with Tribal sovereignty and environmental justice.

Who: The Northwest Forest Plan Just Futures Collaborative is a campus-community collaboration out of the University of Oregon. FUSEE has joined University of Oregon and Portland State University faculty, graduate students, and undergraduate students with expertise in Indigenous studies and/or environmental justice in this work. Our purpose is to amplify Tribal sovereignty and environmental justice issues in the lands managed by the US Forest Service (USFS) through the Northwest Forest Plan (NWFP). Ultimately, we envision contributing to paradigm shifts in land management and beyond that prioritize environmental justice, holistic worldviews, reciprocity, and Tribal sovereignty.

Review Process: We consulted with several Tribal, NGO, and academic experts to review this document. We recognize that the Northwest Forest Plan encompasses the territories of 80+ Tribal nations, and our review process does not reflect the diversity of perspectives that exist across these many nations. The consulted Tribal experts reviewed this document as individuals and do not represent Tribal governments or organizations.

Acronyms

CE: Categorical Exclusion
DEIS: Draft Environmental Impact Statement
EA: Environmental Assessment
EIS: Environmental Impact Statement
EJ: Environmental Justice
NGO: Non-Governmental Organization
NWFP: Northwest Forest Plan

Contents

Tribal Inclusion Measures 2
Beneficial Fire Use 3
Guide to Avoiding Colonial Environmentalism in Public Comments 5
Additional Environmental Justice (EJ) Concerns 8
Contact Information 11

Tribal Inclusion Measures

The DEIS includes many important measures to expand Tribal inclusion across the NWFP area, through expanded measures for cultural harvesting and access, co-stewardship agreements, fire stewardship, workforce development, and youth education. Alternative B's approach to Tribal inclusion is strongest because it includes concrete requirements that national forests must meet within specified timeframes. When Tribal consultation, collaboration, and co-stewardship is optional, many national forests fail to meaningfully engage Tribes (see NWFP Tribal monitoring reports).

We suggest the following:

- Retain all Tribal inclusion plan components (Goals, Desired Conditions, Objectives, Standards, Guidelines, and potential Management Approaches) in Alternative B. Strengthen Tribal inclusions plan components in Alternatives C and D by including (most or all) approaches from Alternative B.
- Include the FAC's full Tribal Inclusion recommendation preamble (pg. 8-9) into the Record of Decision and any other relevant areas, with special emphasis on the section:

  > *Over a century of fire suppression, coupled with regulatory restrictions, removal of Indigenous practitioners and practices (including cultural fire), as well as assimilationist policies from the boarding school era, have led to today's increased risks from catastrophic wildfire and has also created structural barriers and mechanisms preventing Indigenous peoples from enacting sustainable stewardship. The NWFP amendment must signal a shift in Tribal relations across NWFP forests and include an apology for the exclusion of Tribal communities from the original formulation of the NWFP and call for healing and reparations for over a century of settler colonialism, land dispossession, criminalization and marginalization of Indigenous cultural stewardship practices, and mismanagement of Tribal lands.*

- Add Tribal inclusion measures to Alternative B and C that are included in Alternative D but not in B, which include Tribal involvement in protecting rare and listed plants, post-disturbance management, and first foods management. These plan components are:
  - TRIBAL-FORSTW-ALL-GOAL-08–D
  - TRIBAL-FORSTW-ALL-GOAL-09-D
  - TRIBAL-FORSTW-ALL-PMA-D

- For restoring dry, serpentine, and wet meadow-associated culturally significant species, use TRIBAL-FORSTW-ALL-OBJ-03-D from Alternative D rather than TRIBAL-FORSTW-ALL-OBJ-03 from Alternative B across Alternatives B and C.
  - TRIBAL-FORSTW-ALL-OBJ-03-D uses "10 projects" as the metric rather than 2000 acres, which can better allow for different scales of stewardship as defined by Tribes.
- Change TRIBAL-FORSTW-ALL-DC-05 and TRIBAL-FORSTW-ALL-DC-09 to incorporate stronger language from Federal Advisory Committee Desired Condition 1-16, which reads:

    - "Cultural burning is recognized as an inherent Tribal right and responsibility that has existed for millennia and is rooted in Tribal laws and Indigenous knowledge, practices, and belief systems. The Forest accommodates cultural burning and coordinates, consults, and collaborates with Tribes in order to create conditions conducive for this Tribal sovereign practice."

- National forests should accommodate both cultural fire and Tribally-led prescribed fire, allowing Tribes to define for themselves the management techniques needed to achieve their objectives.
- Change TRIBAL-FORSTW-ALL-STD-06 to remove this sentence: "A closure shall affect the smallest practicable area for the minimum period necessary for activities of the applicable Tribe." This sentence could be used to justify restricting the scope of closure orders desired by Tribes.
- Move Potential Management Approaches to Standards or Guidelines so they are enforceable, especially:
    - TRIBAL-FORSTW-ALL-PMA-A through TRIBAL-FORSTW-ALL-PMA-H

Beneficial Fire Use

Beneficial fire is one of the principal means that Indigenous peoples use to steward the land, protect built dwellings, nurture biological productivity, and sustain vital resources for traditional foods, fibers, medicines, and ceremonies. The Forest Service's fire suppression and fire exclusion policies have significantly altered landscapes and degraded ecosystems and habitats that are nurtured by Native peoples and in turn nourish Native cultures. From its criminalization of Indigenous cultural burning to its militarization of fire management through fire "fighting," the agency's fire exclusion policies represent an insidious form of environmental racism. Alternative B's approach to beneficial fire is strongest because of its support of Indigenous cultural burning and co-stewardship agreements.

Remedying cultural and ecological harms caused by fire exclusion requires fire *inclusion,* in addition to expanding Tribal partnerships as discussed above. Authorizing greater fire use while imposing limits on aggressive firefighting represents an essential step toward environmental justice for Indigenous peoples. In the Pacific Northwest native forests need Native fires, and Tribal inclusion requires fire inclusion. Likewise, fire inclusion requires Tribal inclusion, whether through cultural fire or Indigenous-led prescribed fire with cultural objectives.

The DEIS presents numerous supportive statements on beneficial fire use for cultural and ecological purposes. Indigenous cultural burning is rightfully supported across all action alternatives, and statements favoring prescribed burning and managing wildfires for resource benefits are present in alternatives B and C. These praiseworthy statements signify a necessary change in Forest Service fire policy that better recognizes Tribal sovereignty. The DEIS could go further in incorporating more of the FAC recommendations on Indigenous cultural burning and/or Indigenous-led prescribed fire with cultural objectives, as discussed in the prior section.

Additionally, the DEIS lacks analysis on how existing bureaucratic barriers to fire use will be overcome. And it lacks disclosure of where and how beneficial fire use will be allowed and applied. The fact that the Northwest Forest Plan amendment is tiered to the agency's Wildfire Crisis Strategy is a warning sign that fuels reduction for fire suppression may continue to dominate Forest Service fire management, turning fire use provisions in the Northwest Forest Plan amendment into broken promises.

We suggest the following:

- Expand the discussion of the numerous social, cultural, economic, and ecological benefits of cultural burning and prescribed fire, and contrast these effects with the costs and impacts of mechanical fuels reduction treatments alone and conventional wildfire suppression operations.

- Describe the numerous safety risks, economic costs, and direct environmental impacts of conventional wildfire suppression operations to make the case for alternative fire use practices.

- Tier the authorization of beneficial fire use from Indigenous cultural burning, prescribed fire, and managed wildfire to the Federal Wildland Fire Policy (1995/2001) and the growing literature on Indigenous fire use.

- Provide spatial fire management information on the locations of Potential Operational Delineations (PODs) and fire management zones where wildfires could be managed for resource benefits.

- Require that any/all fuels reduction or fire resilience projects include a fire use component (e.g. prescribed pile burning and/or broadcast understory burning) and specify that the primary objective of these fuels projects is to prepare sites for managing future fire for resource benefit rather than fire suppression.

- Indigenous peoples use fire lighting, not firefighting, and mature/old-growth trees are an outcome, not an objective, of Indigenous fire use. Frequent low intensity burning helps nurture soil, water, and fuel conditions that enabled some trees to grow big and old, with wide range of tree species' diversity, and survive occasional passage of wildfires.

- Follow the Good Fire II Report's Recommendation #3 to identify barriers to the exercise of reserved, retained, and other rights by Tribes and their members, including the right to engage in cultural burning and prescribed fire. Make clear to employees and representatives of that agency that the exercising of these rights is welcome and encouraged.

- Work to remove bureaucratic barriers to beneficial fire inclusion and managed wildfire. This includes following the Good Fire II Report's Recommendation #35 to create concrete policies that allow for managed ignitions under particular conditions.

- Implement recommendations #15, 16, and 92 from the Wildlife Fire Mitigation and Management Commission's "On Fire" report to empower Tribes to plan and implement more beneficial fire

through expansion of the Tribal wildland fire workforce and legal authority to promote cultural burning.

Guide to Avoiding Colonial Environmentalism in Public Comments

Federal land management and wilderness preservation movements have long perpetuated Indigenous erasure and environmental racism. Today, environmental groups still perpetuate harm to Indigenous communities and landscapes when they advocate for a "hands-off" approach that denies/erases the violence that settler land management has enacted to Indigenous ecologies. Here are some considerations for moving past colonial environmentalism in your public comments and forest advocacy:

What's your historical baseline?

- Pacific Northwest forests have been dramatically altered by 150+ years of genocide and the associated shift from Indigenous ecologies to settler colonial land management. Exclusion of Indigenous cultural fire regimes, wildfire suppression, timber management, invasive species introduction and spread, and climate change have led to shifted forest species composition (e.g. loss of oak woodland, expansion of Douglas-fir and other conifers), tree and canopy density, and other altered landscape conditions that are not sustainable now or in the future.
- **Avoid** using a *settler ecological baseline* when describing a "natural" forest and advocating for hands-off approaches that leave colonial forest conditions intact.
    - Understandings of "natural" often ignore long-term, ongoing Indigenous land relations that shape environmental conditions, as well as the changes in forests that have come with genocide as mentioned above.
    - Similarly, the concepts of *wild* and *wilderness* are colonialist and discriminatory as these terms have been used as part of the racial othering of Indigenous peoples to justify the oppression of Indigenous people and the erasure of their legacy and living connections with their homelands.
- **Avoid** rigid understandings of "mature" and "old growth" tree and forests that often represent overly dense forests and altered species compositions that have emerged through colonial management and the exclusion of Indigenous stewardship.
- **Instead, say this:** Draw from specific Tribal climate adaptation plans and Indigenous science syntheses (see resources below) for culturally-informed ecological baseline and stewardship orientations.
- **Instead, say this:** Across the NWFP area, the Forest Service should collaborate with Tribes to identify and manage for desired ecological conditions. Whenever possible, barriers should be removed for Tribes to engage in stewardship that meets their objectives.

- **Instead, say this:** Old growth forests across the Pacific Northwest are not wildernesses, and have always been stewarded and managed by Tribes for a variety of cultural objectives.
- **Resources**
    - Eisenberg et al 2024 "Braiding Indigenous and Western Knowledge for Climate-Adapted Forests"
    - PNW Tribal Climate Change Project – Tribal Climate Change Adaptation Plans database
    - Karuk Climate Adaptation Plan 2019
    - Whyte 2018 "Settler Colonialism, Ecology, and Environmental Injustice"
    - Worl 2022 "Restoring What? And For Whom?"
    - Eichler 2021 "Settler Colonialism and the US Conservation Movement: Contesting Histories, Indigenizing Futures."

Which species matter?

- **Avoid** perpetuating single-species approaches. The 1994 Northwest Forest Plan focused too much on single, charismatic species like the spotted owl and other threatened & endangered species. These species are important, but focusing on single species is a colonial approach to environmental management.
- **Instead, say this:** Across the NWFP area, the Forest Service should manage for a diversity of habitat and ecosystem types, collaborating with Tribes to identify management actions that foster biological diversity and benefit culturally important species to Tribes. This could include prioritizing for ESA or threatened species, but monolithic management for one desired species typically doesn't achieve the desired outcome.
- **Instead, say this:** The Forest Service should also support Tribal management for first foods species, as defined by Tribes.
- **Resources**
    - Eisenberg et al 2024
    - Karuk Climate Adaptation Plan 2019
    - Hoagland and Albert 2023 "Wildlife Stewardship on Tribal Lands"
    - Conservation Northwest 2019 "Connecting First Foods and conservation"
    - Amelia and Joaquin Marchand 2023 "Rights of Nature, Indigenous, and Advocacy Perspectives" livestream from Gonzaga Climate Center
    - Reed and Norgaard 2021 "Fire is Food"

Whose science are you citing?

- **Avoid** biasing your advocacy by only drawing from western science, which is rooted in European and colonial understandings of the world. Western science presents an incomplete understanding of forest, fire, and landscape ecology. Land management that emerges from only western science perpetuates settler colonial harm to land and people.

- **Avoid** referring to Indigenous knowledge solely in the past tense, which erases present-day Indigenous knowledges that are constantly adapting and evolving.
- **Instead, say this:** Cite Indigenous science in addition to western science in public comments, and call on the Forest Service to engage Indigenous science in updating and implementing the NWFP.
- **Resources**
    - Lake 2021 "Indigenous fire stewardship: Federal/Tribal partnerships"
        - See Dr. Frank Lake's full list of publications
    - Fisk et al 2024 "Evolving wildlife management cultures of governance through Indigenous Knowledges and perspectives"
    - Medin and Bang 2014 "Who's Asking?"

Are you tokenizing Indigenous knowledges?

- **Avoid** the common settler environmentalist practice of referencing Indigenous knowledge and stewardship only when it fits existing advocacy goals.
- **Avoid** referring to Indigenous knowledge and stewardship in the past-tense, as a static, historical body of knowledge to draw from and inject into settler colonial management frameworks.
- **Avoid** referencing or treating Tribes as stakeholders rather than sovereign nations.
- **Avoid** paternalistic and white savior assumptions that Tribes need help or that you know what they need.
- **Instead, say this:** The USFS should create decision-making structures and share power to honor Tribal sovereignty, including fulfilling governmental trust responsibilities and upholding Tribal Treaty Rights. This includes the expansion of co-stewardship and co-management agreements where Tribal nations (both federally recognized and not federally recognized) have decision-making power over their territories.
- **Instead, say this:** The USFS should include additional language that incorporates empowerment of Tribal decision making, self-defining terminology, and self-autonomy, thus substantiating Tribal sovereignty. For example, the USFS should revise existing plan components to place decision making in Tribal hands, where appropriate (i.e., use language such as "At Tribal request" or "As determined by Tribes" etc.)
- **Instead, say this:** The USFS should promote and incorporate a more holistic worldview consistent with Indigenous concepts of kinship and stewardship toward the ecological world and all species that share our planet. Move away from an anthropocentric approach to "resource" management and more toward ecosystem stewardship where the rights of nature are valued alongside those of humans.
- **Resources**
    - Gilio-Whitaker 2017 **"**The Problem with the Ecological Indian Stereotype"

- Adlam and Martinez 2021 "Decolonizing Prescribed Fire"
- Martinez et al 2024 "Indigenous Fire Futures"
- Anderson 2024 "What's Misunderstood about Indigenous Cultural Fire is Sovereignty"
- Karuk Knowledge Sovereignty Reports:
  - Part I: Karuk Traditional Ecological Knowledge and the Need for Knowledge Sovereignty 2014
  - Part II: Retaining Knowledge Sovereignty 2016

Additional Environmental Justice (EJ) Concerns

Environmental justice matters to assess and address the uneven burdens and benefits created by and/or exacerbated by federal lands management. Tribal inclusion is at the forefront of an environmental justice (EJ) approach to federal lands management because all federal lands are Indigenous lands and because environmental justice centers Tribal sovereignty. However, it is not the only environmental justice concern relevant to the Northwest Forest Plan (NWFP). This section addresses some of these additional environmental justice concerns.

The DEIS fails to offer appropriate landscape level analysis or plan components to address EJ concerns. The EJ appendix focuses on identifying which communities are to be considered as EJ communities in project-level analysis, using race, ethnicity, and income. Addressing predictable EJ concerns should happen on a landscape level across the NWFP management area, not only (but also) in site-specific project design and outreach. In other words, analysis and plan components (including Standards and Guidelines) should be found in the Environmental Impact Statement (EIS), rather than deferring such analysis only to the Environmental Assessment (EA) or Categorical Exclusion (CE) for each individual site-specific project (such as individual timber sales).

We suggest the following:

- Incorporate all management suggestions from Chapter 10-Environmental Justice of the "Synthesis of Science to Inform Land Management Within the Northwest Forest Plan Area" (pages 839-841).
- Consider how the NWFP amendment is consistent with the Presidential Memorandum "Promoting Diversity and Inclusion in Our National Parks, National Forests, and Other Public Lands and Waters" (2017), including the two sections "Enhancing Diversity and Inclusion in the Federal Workforce" and "Enhancing Opportunities for all Americans to Experience Public Lands and Waters."

Toxicities

- Assess the air and water quality impacts of pesticides, herbicides, fire retardants, and other chemicals used in the forest as part of NWPF management. These should be assessed in relation to worker exposure, in relation to nearby communities exposed through drift, and in relation to food, including first foods, and water, including drinking water, upon which many communities rely. Mandate assessing and addressing these concerns within project-specific analysis.

Recreational access and equity

- Provide analysis and discussion of inequities in access to recreational opportunities and different cultural uses of the NWFP area at the landscape scale, not only (but also) in site-specific project design. Include clear plan components in all alternatives that site-specific project analysis should:
    - Assess and protect sites with recreation use by diverse communities and that are disproportionately used by certain underrepresented or historically-excluded communities (by race, ethnicity, income, disability, etc.) following EO 14096's mandate to improve equitable access to public lands as environmental justice praxis.
    - Assess and protect sites in relationship to the economic impact that disruption of recreation will have on local communities, especially given that recreation is the primary economic contributor of NWFP lands to the regional economy.
    - Assess and protect sites for lesser-known recreation values by diverse communities.
    - Survey for and protect culturally or historically sensitive and/or meaningful sites for diverse communities.

Youth education and mentorship

- Maintain and build on ECON-SUST-DC-3 and ECON-SUST-GOAL-1 from the DEIS to promote meaningful youth education and mentorship opportunities on every national forest in the plan area, particularly in the realms of prescribed, cultural, and wildland fire mentorship and training.

Environmental workforce

The DEIS acknowledges that the environmental workforce is largely "composed of low-income Hispanic or Latino immigrants and undocumented workers" (3-145) who travel long distances for work. Similarly, other Communities of Interest, "Nontimber Forest Products Gathering" and "Recreation," also travel frequently to different sites across NWFP locations. Without landscape scale analysis, it is unlikely that these groups will be adequately considered in site-specific project analysis since they are unlikely to be present at the time of Environmental Assessment. Although the DEIS mentions that evaluating for EJ implications within EJ communities and Communities of Interest should include "opportunities for meaningful involvement in the decision-making process" made available (3-141), it does not offer any recommendations to do so.

- Create an additional ECON-SUST-GOAL that aims to remove financial barriers to public participation, invests in communication beyond translation, and uses regional liaisons or trusted channels of communication to form connections with Communities of Interest.

In DEIS Section 3.8.1.12 Environmental Justice, the subsection titled "Environmental Workforce" (3-145) acknowledges some of the inequitable labor practices that this workforce faces. However, this section fails to provide a more in-depth analysis of how the workforce is distributed and quantify the size and scale of this workforce. More discussion is needed on the equity implications of using temporary migrant workers to compensate for labor shortages. Without comprehensive immigration reform, this form of employment is predicated on inequitable power dynamics perpetuated by centuries

of neocolonial practices. Furthermore, the DEIS refers to certain types of labor performed by the environmental workforce as "unskilled" (3-121; 3-151) or "low-skilled" (3-122) labor. This type of language is demeaning to workers that have accumulated decades of experience by doing this type of work and erodes class solidarity by reinforcing a hierarchy of labor.

- Provide mechanisms to consistently inspect for and aggressively enforce federal, state, and local wage and safety regulations for contractors in the NWFP management area, including regarding wage theft, worker intimidation, and heat and catastrophic wildfire smoke exposure.
- Consult regularly with workers and worker-organizations to develop protocols for worker protections in the implementation of NWFP projects. More thoroughly address and assess the over-representation of Indigenous, Black, and other marginalized and racialized communities in certain forms of work and the specific vulnerabilities of that work.
- Create an additional ECON-SUST-DC that incentivizes safe, sustainable, and equitable working conditions for forest workers and fair compensation for this work.
- Use language that elevates the importance of the environmental workforce and does not demean worker labor or reinforce the segmentation and hierarchical arrangement of the workforce.
- Provide landscape level analysis of disproportionate harm to forest and fire workers caused by catastrophic wildfire caused smoke and heat (both of which are exacerbated by climate change).

  Resources
  - Davis et al 2023 "Multiple Stories, Multiple Marginalities: The Labor-Intensive Forest and Fire Stewardship Workforce in Oregon"
  - Costa 2021 "Temporary work visa programs and the need for reform"

Economic sustainability objective

The DEIS's ECON-SUST-OBJ-01 focuses exclusively on treatment of acres. This type of framing prioritizes efficiency and incentivizes the use of contracting tools which favor selection of contractors who, in addition to meeting the base selection criteria (which does not include local benefits) can get the most work done, the most quickly, for the lowest price. Efficiency does not always equate to effectiveness; by using acres treated as the sole metric of success, it incentivizes practices that contribute to worker inequity and ignore working conditions and local benefits. As noted by Rural Voices for Conservation Coalition, "Although low-price contracting might appear to save the government money, in reality it costs the American taxpayer more money when poor quality work has to be redone, and when poorly-paid workers have to apply for food stamps and other public assistance, or seek medical care without insurance." Additionally, low-bid contracting perpetuates inequities as Latine contractors tend to attain labor-intensive service contracts (LISCs) while white contractors tend to secure more technical work included in master stewardship agreements and stewardship contracts.

- Create an additional ECON-SUST-DC that incentivizes safe, sustainable, and equitable working conditions for forest workers and fair compensation for this work.
- Create an additional ECON-SUST-GOAL that incentivizes increased communication and collaboration between federal agencies, especially land management agencies, the Department of Labor, and OSHA to enforce wage and safety regulations.

- Add language to ECON-SUST-GOAL-03 to incentivize federal land management agencies to prioritize Best Value contracting practices, such as Stewardship contracting rather than BPAs.
- **Resources**
    - Rural Voices for Conservation Coalition 2006 "Workforce and Labor Issue Paper"
    - Deak et al 2021 "Documenting Twenty Years of the Contracted Labor-Intensive Forestry Workforce on National Forest System Lands in the United States"
    - Machado, M.A., Downey, J., Huber-Stearns, H., and Davis, E.J. (2025). "The Labor-Intensive Forestry and Fire Workforce in the US Northwest: Recommendations for Improving Equity and Growth" [Manuscript in preparation].

Contact Information

For more information, contact: sdwald(at)uoregon.edu; mfowlern(at)uoregon.edu; dehliaw(at)uoregon.edu

Version 1/6/2025

CENTRAL OREGON LANDWATCH

2843 NW Lolo Drive., Ste. 200 | Bend, OR 97703
Phone (541) 647-2930
www.colw.org

Attachment 2

Cited Literature Copies – USDA Reports

USDA Forest Service
U.S. DEPARTMENT OF AGRICULTURE

Pacific Northwest Research Station | General Technical Report PNW-GTR-1003 | July 2022

Northwest Forest Plan—The First 25 Years (1994–2018): Status and Trends of Northern Spotted Owl Habitats

Raymond J. Davis, Damon B. Lesmeister, Zhiqiang Yang, Bruce Hollen, Bridgette Tuerler, Jeremy Hobson, John Guetterman, and Andrew Stratton



NORTHWEST FOREST PLAN
THE FIRST 25 YEARS (1994–2018)

In accordance with Federal civil rights law and U.S. Department of Agriculture (USDA) civil rights regulations and policies, the USDA, its Agencies, offices, and employees, and institutions participating in or administering USDA programs are prohibited from discriminating based on race, color, national origin, religion, sex, gender identity (including gender expression), sexual orientation, disability, age, marital status, family/parental status, income derived from a public assistance program, political beliefs, or reprisal or retaliation for prior civil rights activity, in any program or activity conducted or funded by USDA (not all bases apply to all programs). Remedies and complaint filing deadlines vary by program or incident.

Persons with disabilities who require alternative means of communication for program information (e.g., Braille, large print, audiotape, American Sign Language, etc.) should contact the responsible Agency or USDA's TARGET Center at (202) 720-2600 (voice and TTY) or contact USDA through the Federal Relay Service at (800) 877-8339. Additionally, program information may be made available in languages other than English.

To file a program discrimination complaint, complete the USDA Program Discrimination Complaint Form, AD-3027, found online at https://www.usda.gov/oascr/complaint-resolution and at any USDA office or write a letter addressed to USDA and provide in the letter all of the information requested in the form. To request a copy of the complaint form, call (866) 632-9992. Submit your completed form or letter to USDA by: (1) mail: U.S. Department of Agriculture, Office of the Assistant Secretary for Civil Rights, 1400 Independence Avenue, SW, Washington, D.C. 20250-9410; (2) fax: (202) 690-7442; or (3) email: program.intake@usda.gov.

USDA is an equal opportunity provider, employer, and lender.

Contributing Authors

Raymond J. Davis is Northwest Forest Plan Interagency Monitoring Program monitoring lead for old forests and northern spotted owls, U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, 3200 SW Jefferson Way, Corvallis, OR 97331; **Damon B. Lesmeister** is a research wildlife biologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331; **Zhiqiang Yang** is a computer scientist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 507 25th Street, Ogden, UT 84401; **Bruce Hollen** is state wildlife biologist, U.S. Department of the Interior, Bureau of Land Management, Oregon State Office, 1220 SW 3rd Avenue Portland, OR 97204; **Bridgette Tuerler** is a spotted owl biologist (retired), U.S. Department of the Interior, Fish and Wildlife Service, Oregon Office, PO Box 2336, Battle Ground, WA 98604; **Jeremy Hobson** is a fire geographic information system specialist, U.S. Department of the Interior, National Park Service, Division of Fire and Aviation Management, National Interagency Fire Center, 3833 S Development Avenue, Boise, ID 83705; **John Guetterman** is a geographic information system specialist, U.S. Department of the Interior, Bureau of Land Management, Medford District, 3040 Biddle Road, Medford, OR 97504; **Andrew Stratton** is regional geodatabase manager, U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Data Resources Management, 3106 Pierce Parkway, Suite D, Springfield, OR 97477.

Cover: Art by Uta Briggs.

Abstract

Davis, Raymond J.; Lesmeister, Damon B.; Yang, Zhiqiang; Hollen, Bruce; Tuerler, Bridgette; Hobson, Jeremy; Guetterman, John; Stratton, Andrew. 2022. Northwest Forest Plan—the first 25 years (1994–2018): status and trends of northern spotted owl habitats. Gen. Tech. Rep. PNW-GTR-1003. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 38 p. https://doi.org/10.2737/PNW-GTR-1003.

This is the fourth in a series of periodic monitoring reports on status and trends of forests used by northern spotted owls (*Strix occidentalis caurina*; NSO) for nesting, roosting, and dispersal on federally administered lands within the Northwest Forest Plan (NWFP) area (NSO range in the United States) since its implementation in 1994. The objective of this monitoring is to determine if federal forest lands are providing sufficient conservation of forests that are important elements of NSO habitat, and thus populations. Here we present models on the amount, distribution, and spatial arrangement of nesting, roosting, and dispersal forest types across the NWFP area, and losses and gains resulting from disturbance and forest succession, respectively. Forests suitable for nesting and roosting are one of the most critical components of NSO habitat, defined as the area with the full range of environmental conditions necessary to support occupancy, survival, and reproduction. Given the importance of habitat to support population recovery, this is the first monitoring report to model habitat using distribution and amount of suitable nesting/roosting forest at multiple spatial scales, and in combination with abiotic environmental covariates. We used estimates of territory occupancy in conjunction with available habitat to estimate changes in population size and distribution of territorial NSOs on federal lands at the start and end of this monitoring cycle (1993 and 2017).

We found a 3 percent net increase (from 8,890,500 to 9,155,700 ac) of nesting/roosting forest on federal lands between 1993 and 2017. This net gain occurred despite gross losses from wildfire of 7.9 percent (703,700 ac), 2.9 percent from timber harvest (257,700 ac), and 0.9 percent from insects or other causes (83,700 ac), indicating that processes of forest succession more than compensated for the losses resulting from disturbance during the first 25 years of the NWFP. Dispersal forest on federal lands increased by 1 percent, but dispersal-capable landscapes decreased by 9 percent because of forest losses on surrounding nonfederal lands and large wildfires on federal lands. The forest landscape that allowed for owl movement between one reserved area to another became more confined and fragmented. Despite net increases in NSO forests on federal lands during the monitoring period, the population of territorial owls on federal lands decreased by an estimated 61.8 percent. A primary cause for population declines on federal lands was displacement from native habitat by the invasive barred owl (*S. varia*), which highlights the increasing threat to NSO persistence.

Keywords: Northwest Forest Plan, effectiveness monitoring, northern spotted owl, territory occupancy, habitat, barred owl.

Preface

Monitoring northern spotted owl (*Strix occidentalis caurina*) populations and the forests used by them within the Northwest Forest Plan (NWFP) area was approved by an Intergovernmental Advisory Committee. The program is consistent with the framework for effectiveness monitoring described in "The Strategy and Design of the Effectiveness Monitoring Program for the Northwest Forest Plan" and follows protocols and guidance in the "Northern Spotted Owl Effectiveness Monitoring Plan for the Northwest Forest Plan," both published in 1999. The interagency effectiveness monitoring framework was implemented to meet requirements for tracking the status and trends of older forests, populations and habitats of northern spotted owls and marbled murrelets (*Brachyramphus marmoratus*), watershed conditions, social and economic conditions, and tribal relationships. Monitoring is conducted in 1- to 5-year intervals and results are documented in a series of technical reports. This report, and the others in the current series, covers the first 25 years of the NWFP.

Contents

1 **Introduction**
1 **Habitat Monitoring Under the NWFP**
2 **Phase II Monitoring Under the NWFP**
2 **Data Sources**
2 Physiographic Province Map
3 Forest-Capable Area Map
3 Modeling Regions
4 Land Use Allocation Map
6 Forest Disturbance Maps
8 Forest Structure and Species Composition Maps
8 NSO Presence Data
8 **Methods**
8 Mapping Nesting/Roosting Forest
10 Forest Fragmentation Analysis
10 Dispersal-Capable Landscape Analysis
10 Habitat Modeling for Estimating Number of Occupied Territories
12 **Results**
12 Mapping Nesting/Roosting Forest
14 Habitat Fragmentation Analysis
16 Dispersal-Capable Landscape Analysis
18 Habitat Modeling for Estimating Number of Occupied Territories
19 **Discussion**
21 **Conclusion**
22 **Acknowledgments**
22 **Metric Equivalents**
23 **References**
29 **Appendix 1—Bookend Map Area Estimates of Nesting/Roosting Forests**
33 **Appendix 2—Bookend Map Area Estimates of Dispersal Forests**
37 **Appendix 3—Estimating Northern Spotted Owl Pair Territories**

Introduction

More than a quarter century has passed since the design and implementation of the Northwest Forest Plan (NWFP). The NWFP amended 19 U.S. Department of Agriculture (USDA) Forest Service and 7 U.S. Department of the Interior Bureau of Land Management (BLM) resource management plans across three western states and two Forest Service regions within the range of the northern spotted owl (*Strix occidentalis caurina*; NSO) in the United States. As part of the NWFP, an interagency effectiveness monitoring framework was created to track status and trends of late-successional and old-growth forests, NSO populations and habitat, marbled murrelet (*Brachyramphus marmoratus*) populations and habitat, watershed conditions, social and economic conditions, and tribal relationships (Mulder et al. 1999). In 2016, the BLM in western Oregon revised its resource management plans, which adopted the interagency monitoring framework in its entirety (USDI BLM 2016a, 2016b).

This report is the fourth in the series of NSO habitat monitoring reports outlined in Lint et al. (1999). It covers 1993–2018, which marks the year the NWFP was designed (FEMAT 1993) and the following 25 years of NWFP implementation. The goal of this monitoring is to evaluate the success of the NWFP in arresting the downward trends in NSO habitat and populations that preceded its implementation, and in maintaining and restoring forest types necessary to support future NSO populations on federally administered forest lands throughout its range. Specific monitoring objectives are as follows:

- Assess status and trends in NSO demographic rates or population size and distribution on federal lands.
- Assess status and trends in the amount and distribution of NSO forests and habitat on federal lands.

Addressing objective 1, Franklin et al. (2021) provided information on demographic rates from a population meta-analysis of demographic study areas (1993–2018). Here we focused on objective 2 and combined occupancy rates reported by Franklin et al. (2021) in our models to estimate NSO population size and distribution on federal lands.

There has been a long history of inconsistent use of the term "habitat" to describe forest stands (e.g., a stand of "nesting, roosting, foraging habitat"), including its use in previous NWFP monitoring reports. Forest stands of various types, amounts, and spatial configurations are only part of what constitutes habitat. NSO habitat is more accurately defined as the combination of the environmental biotic and abiotic conditions on the landscape necessary to support owl occupancy, survival, and reproduction (see Lesmeister et al. 2018: 250). Here, forest cover type refers to forest structure and tree species composition associated with use by NSOs (e.g., nesting, roosting, foraging, and dispersal), while habitat refers to the combination of forest cover type and the other relevant environmental conditions.

Each monitoring report has used new or revised data and sometimes new or improved analytical methods. For example, in future efforts, Google Earth Engine™ may become the primary platform for monitoring trends in NSO forests and habitat. Given the improvements in analytical tools, the results in every report supersede, and should not be compared to, prior reports. Here we summarized an assessment of NSO forest types and habitat for 22.1 million ac of federally administered forest lands affected by the NWFP. We also included information on the surrounding 23.8 million ac of nonfederal forest lands to provide a broader landscape context across the 57 million ac that comprise the NSO geographic range in the United States.

Habitat Monitoring Under the NWFP

The status and trends of forests used by NSOs have been estimated every 5 years because it was believed that changes in forest vegetation would not be reliably discernible at more frequent intervals using the Landsat remotely sensed vegetation data that this broadscale monitoring program relies upon (Lint et al. 1999). This has proven to be mostly true for changes that result in gains in suitable forest types and habitat as a result of forest succession; however, our ability to detect losses from forest disturbance has now become very reliable and near-real time, thus future monitoring may entail annual updates.

Effectiveness monitoring evaluates assumptions made during development of the NWFP, which included that "habitat" (e.g., suitable forest) likely would not decline faster than the estimated 5 percent per decade (from wildfire and timber harvest combined) in the NWFP's final environmental impact statement (USDA and USDI 1994).

Assumptions outlined in Lint et al. (1999) were evaluated to determine the following:

- Suitable forest conditions within late-successional reserves (LSRs) would improve over time at a rate controlled by successional processes in forest stands that were not suitable when the NWFP was developed. Given the slow process of old-forest development, these gains were not expected to produce any significant changes in suitable forest conditions for several decades.
- Forest conditions outside of reserved land use allocations (LUAs) were declining because of timber harvest and other habitat-altering disturbances, but many forest stands retained vegetation structure across the landscape to facilitate NSO movements.
- Catastrophic events would likely halt or reverse gains of suitable forest in some reserves, but the repetitive design of reserves would provide resiliency, and not result in isolation of population segments.

Based on these assumptions, we addressed the following questions:

- What proportion of the total forested landscape on federal lands is covered by forest types used for owl nesting, roosting, and dispersal?
- What are the trends in the amount of and changes in distribution of these NSO forest types, particularly in large reserves?
- What are the trends in the amount and distribution of dispersal forest that allow for movement of owls between large reserves?
- What are the primary factors leading to loss and fragmentation of suitable forest types and NSO habitat?
- What are the trends in the estimated number of occupied territories over the duration of the monitoring program?

We evaluated these questions at three broad geographic scales: (1) by physiographic province, (2) by state, and (3) for the geographic range of the NSO. Within these spatial extents, we assessed forest types and habitat conditions inside broad federal LUAs representing reserved and nonreserved landscapes.

Phase II Monitoring Under the NWFP

The NSO monitoring plan was designed to occur in two phases. During phase I, NSO populations have been monitored separately by continuing demographic studies using mark-recapture methods on territorial owls in federal study areas and habitat (e.g., forests used by NSO). Thus, appropriate monitoring indicators for phase I have been population demographic rates (e.g., survival, recruitment, population growth) and changes in amount and distribution of suitable forests. Phase II was envisioned as a monitoring program based on predictive models of regional population dynamics driven by landscape-scale amounts and patterns of habitat. Relevant population-level indicators for phase II would then be population size and distribution (Lint et al. 1999).

For the past two decades, the monitoring program has studied relationships between various measures of NSO occupancy and demographic performance with forest conditions (type, quantity, quality, and distribution) at the home range and at landscape scales (Anthony et al. 2006; Dugger et al. 2005, 2016; Forsman et al. 2011; Franklin et al. 2000; Yackulic et al. 2019). These studies have provided critical information on if and what forest conditions could be used to predict owl occupancy, distribution, and demographic performance at a variety of spatial scales. Combining findings from other efforts, Glenn et al. (2017) developed a method to estimate NSO territory density across broad landscapes based on habitat carrying capacity, territorial spacing, and occupancy rate estimates. Here we report on the first application of phase II monitoring to predict population size and distribution on federal lands.

Data Sources

Many, but not all, of the data sources used in this report were initially developed and used in previous monitoring reports (Davis et al. 2011, 2016; Lint 2005). During each 5-year monitoring cycle, previously used data sources are occasionally updated to incorporate new research findings and other information, or to correct errors. More details of these data sources can be found in previous monitoring reports but are briefly described here.

Physiographic Province Map

The NWFP boundary was based on the geographic range of the NSO in the United States. Because the range is large, it was divided into 12 physiographic provinces (fig. 1) to reduce the complexity and diversity of such an extensive

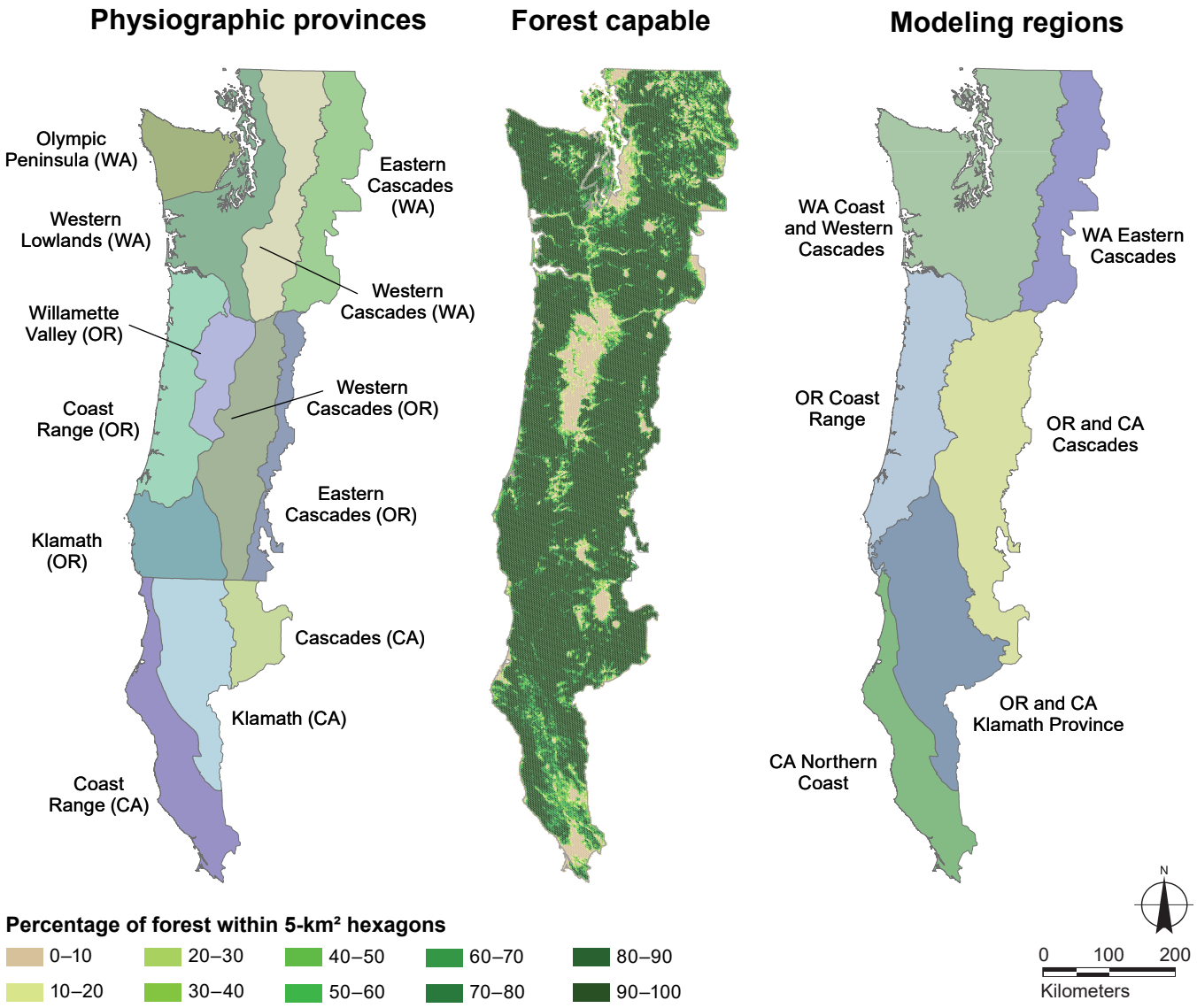


Figure 1—Physiographic provinces, percentage of forest-capable lands within 5-km² hexagons, and modeling regions within the range of the northern spotted owl in the United States.

geography, as well as for analytical purposes (FEMAT 1993; Thomas et al. 1990; USDA and USDI 1994). Physiographic provinces represent different forest zones, plant communities, and disturbance regimes that vary geographically with climate, topography, soils, and geology and were largely based on subdivisions by Franklin and Dyrness (1973).

Forest-Capable Area Map

This data source is a 30-m resolution (pixel size) raster map of areas capable of developing into forests (Davis et al. 2011). It is largely based on the U.S. Geological Survey Gap Analysis Program and the "impervious layer" from the National Land Cover Database (Herold et al. 2003, Vogelmann et al. 2001). It excludes urbanized areas, major roads, agricultural areas, water, lands above tree line, snow, rock, and other nonforested features. We used this map to exclude (mask) these areas for modeling, mapping and analytical purposes (fig. 1).

Modeling Regions

The NSO range was divided into six regions to model forest cover types used by the owl and for habitat modeling. They are a modified version of the physiographic provinces

described above. Boundary modifications were based on (1) ecological similarities between physiographic provinces and (2) balancing the occurrence and distribution of NSO location data used for model training and testing. We used geographic region information from population monitoring work (Anthony et al. 2006: app. A, Forsman et al. 2011) to combine some provinces and Environmental Protection Agency level III ecoregions (Omernik 1987) to guide final delineations of modeling regions (fig. 1).

Land Use Allocation Map

LUAs describe overarching forest management direction. The geographic information system (GIS) layer representing LUAs was originally delineated when the NWFP was developed (USDA and USDI 1994). It has been updated prior to each monitoring cycle to account for LUA changes that occurred in the prior 5 years as well as minor editing to correct mapping errors. Updates include federal surface ownership boundary adjustments, changes in federal land ownership (e.g., land exchanges, land acquisitions and disposals), and changes owing to forest resource management plan amendments or revisions. Since the last monitoring report, the BLM has revised its LUAs in western Oregon (USDI BLM 2016a, 2016b). However, the management objectives and direction for the new LUAs are similar to those in the NWFP (fig. 2). One noteworthy change in the BLM revision is the division of BLM forests into areas characterized as moist (northwestern and coastal Oregon) and dry (southwestern Oregon) to recognize ecological differences between the historical fire regimes of western Oregon, as well as different habitat treatments that are hypothesized to reduce the risk of loss of suitable habitat in the dry forest types.

Federal LUAs have specific management directions, so we classified these allocations into reserved and nonreserved lands. Reserved allocations are areas where the maintenance and restoration of older forests over time are expected under the current land use plans, including the following (GIS layer attribute codes in parentheses):

- Congressionally reserved areas (CR)—lands reserved by the U.S. Congress, such as wilderness areas, wild and scenic rivers, and national parks and monuments.
- Late-successional reserves (LSRs)—lands reserved for the protection and restoration of late-successional/old-growth (LSOG) forest ecosystems and habitat for associated species; this includes marbled murrelet reserves (LSR3) and NSO activity core reserves (LSR4).
- Managed late-successional areas (MLSAs)—areas for the restoration and maintenance of optimal levels of LSOG forest on a landscape scale where regular and frequent wildfires historically occurred. Silvicultural and fire hazard reduction treatments are allowed to help prevent older forest losses from large wildfires or disease and insect epidemics.
- Administratively withdrawn areas (AW)—areas identified in local forest and district plans, including recreation and visual retention areas, backcountry, and other areas where management emphasis does not include scheduled timber harvest.
- Adaptive management area in reserves (AMR)—areas identified to develop and test innovative management to integrate and achieve ecological, economic, and other social and community objectives. Emphasis on restoration of late-successional forests and managed as an LSR.

Nonreserved LUAs were designed for multiple land use objectives, including the following sustained-yield management for timber production:

- Matrix (other)—federal lands outside of reserved allocations where most timber harvest and silvicultural activities were expected to occur.
- Adaptive management area nonreserved (AMA)—identified to develop and test innovative management to integrate and achieve ecological, economic, and other social and community objectives. Commercial timber harvest was expected to occur in these areas, testing alternative approaches to meet NWFP objectives.

Standards and guidelines in the NWFP and revised BLM resource management plans allow for timber harvesting within LSRs that is designed to benefit the development of late-successional conditions. In the moist forests, stands (generally <80 years old) not currently providing nesting/roosting function for NSOs can be managed to speed the development of, or improve, NSO habitat quality in the long term. On BLM lands, these treatments are not to preclude or delay by 20 years or more the nesting/roosting function of a stand compared to development without treatment (USDI BLM 2016a: 64–67). Management direction for dry

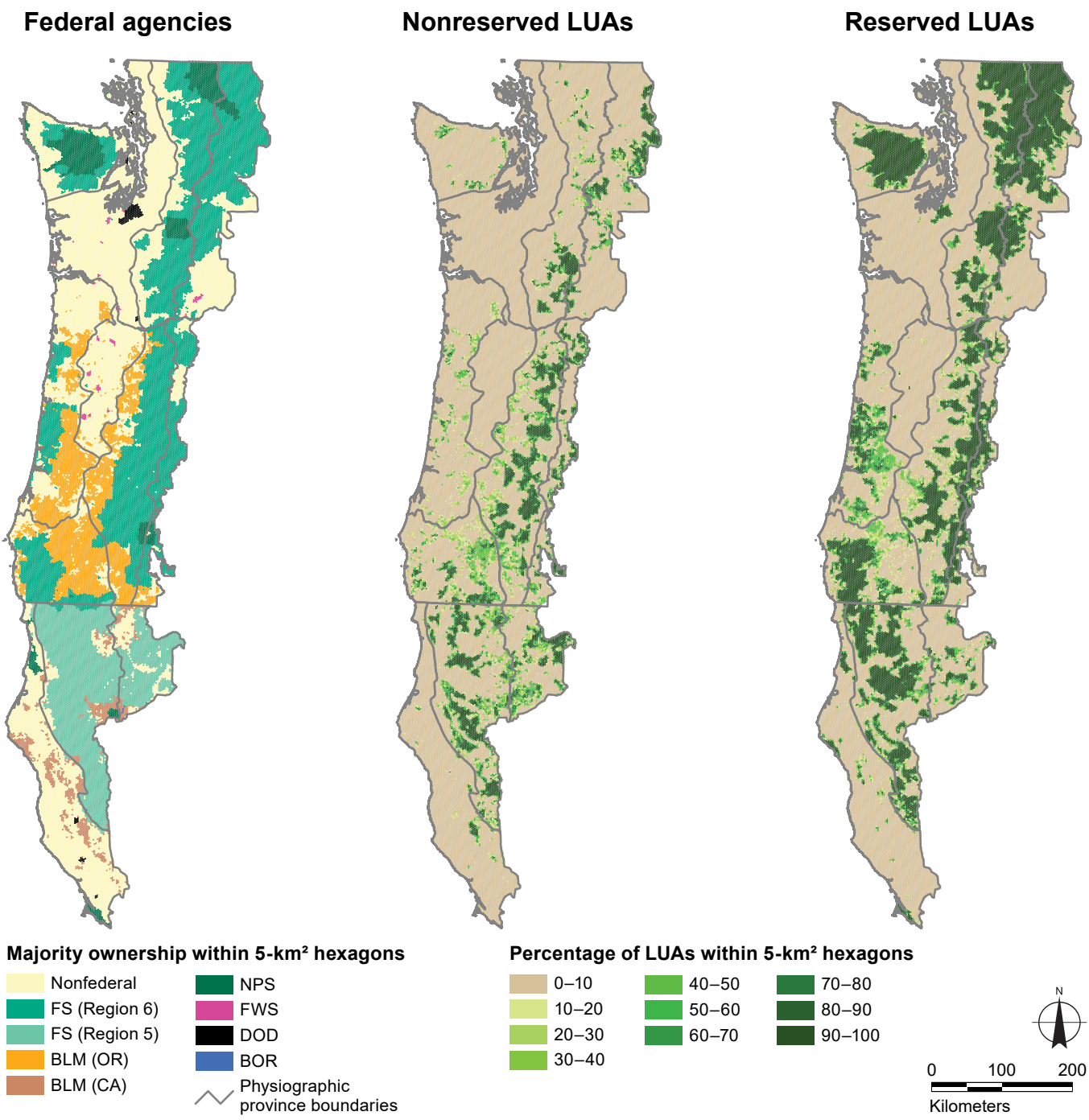


Figure 2—Maps of federal forest management agencies and land use allocations (LAUs) summarized as majority ownership and percentage of area in 5-km^2 hexagons within the range of northern spotted owls in the United States. FS = Forest Service, BLM = Bureau of Land Management, NPS = National Park Service, FWS = Fish and Wildlife Service, DOD = Department of Defense, BOR = Bureau of Reclamation.

forests is reflective of the more frequent, fire-driven stand and landscape dynamics. Focus is therefore on restoring resistance and resilience against fire, insects, and drought through vegetation treatments. Outside of BLM lands, timber harvesting in LSRs is allowed west of the Cascade crest in stands up to 80 years old (110 years in the Northern Coast Range Adaptive Management Area) regardless of stand origin (e.g., plantations or naturally regenerated) if it benefits the creation, hastens the transition to, or maintains late-successional forest conditions. East of the crest and in the Oregon and California Klamath Physiographic Provinces, silvicultural activities aimed at reducing the risk of large, high-severity wildfires are allowed. The focus of these treatments is to make the reserved forests in fire-prone environments less susceptible to losses from large-scale, high-severity fire. Such management activities are encouraged in LSRs even if a portion of the activities must take place in late-successional forests. Such activities in older stands may also be undertaken in LSRs in other provinces if fire risk is particularly high (USDA and USDI 1994: C-12).

We used the updated LUA layer, as of 2017, to frame the status and trend analyses in this report (fig. 2). Since NWFP implementation, there has been a slight overall increase in federal lands (1.8 percent) with an 8 percent increase in reserved LUAs, largely owing to new LSR designations by the BLM in western Oregon. As in previous monitoring reports, riparian reserves, another NWFP LUA, were not delineated because they were supposed to be delineated based on site-specific analyses.

Forest Disturbance Maps

Annual forest disturbance maps (30-m pixel resolution) were produced for forest-capable lands from 1986 to 2017 using an ensemble LandTrendr methodology (Cohen et al. 2018, Healey et al. 2018). These maps (fig. 3) are part of a larger national dataset produced by the USDA Forest Service Rocky Mountain Research Station's Landscape Change Monitoring System program (USDA FS 2021). Three types of annual maps of forest disturbance were produced:

- Year of detection—image taken the year change was detected. This year does not always represent the year of disturbance. Often, vegetation change caused by a disturbance was detected in the following year; but sometimes it was detected >1 year afterward, depending on Landsat image availability and other factors. Usually, disturbance was detected within 2 years of the disturbance event.
- Duration of disturbance—the duration of a disturbance was based on the number of years of consecutive disturbance segments. Short-duration (usually 1 year) disturbances are associated with events that quickly remove or alter forest vegetation cover (e.g., wildfires, timber harvesting, forest clearings, wind, floods, etc.). Disturbances lasting multiple years represent slow forest change and loss of cover caused by insects, disease, or other physiological stressors (Cohen et al. 2016).
- Severity of disturbance—the relativized difference in the normalized burn ratio (RdNBR) (Miller and Thode 2007) was used as our index of disturbance severity. We classified disturbance severity using class thresholds (low, moderate, high) identified by Reilly et al. (2017) that correlated RdNBR with tree mortality (percentage of live tree basal area change) from pre- and postfire forest inventory plots.

The last step in disturbance mapping was to assign a cause agent (wildfire, timber harvest, insect/disease, etc.) for each disturbance signal for each year. This procedure captured multiple disturbances that occurred in the same area (pixel) over time. Assignment of disturbance agent was based on expert rulesets incorporating the duration of the disturbance, its location in relationship to federal LUAs, relationship to aerial detection survey maps for insects and disease (Coleman et al. 2018, Johnson 2016), spatial relationship to mapped wildfire perimeters (e.g., National Interagency Fire Center, Monitoring Trends in Burn Severity), and when inside wildfire perimeters, the year of detection in relationship to the wildfire year. If a disturbance inside a wildfire perimeter predated the wildfire year by >2 years, it was attributed to some other cause (e.g., insects or timber harvest). We classified disturbance cause agents into four general classes using the rules below:

- Timber harvest—including thinning and regeneration. Classified as abrupt disturbances (duration <4 years) outside of CR lands (e.g., wilderness areas) where timber harvesting is not allowed in the reserved area's

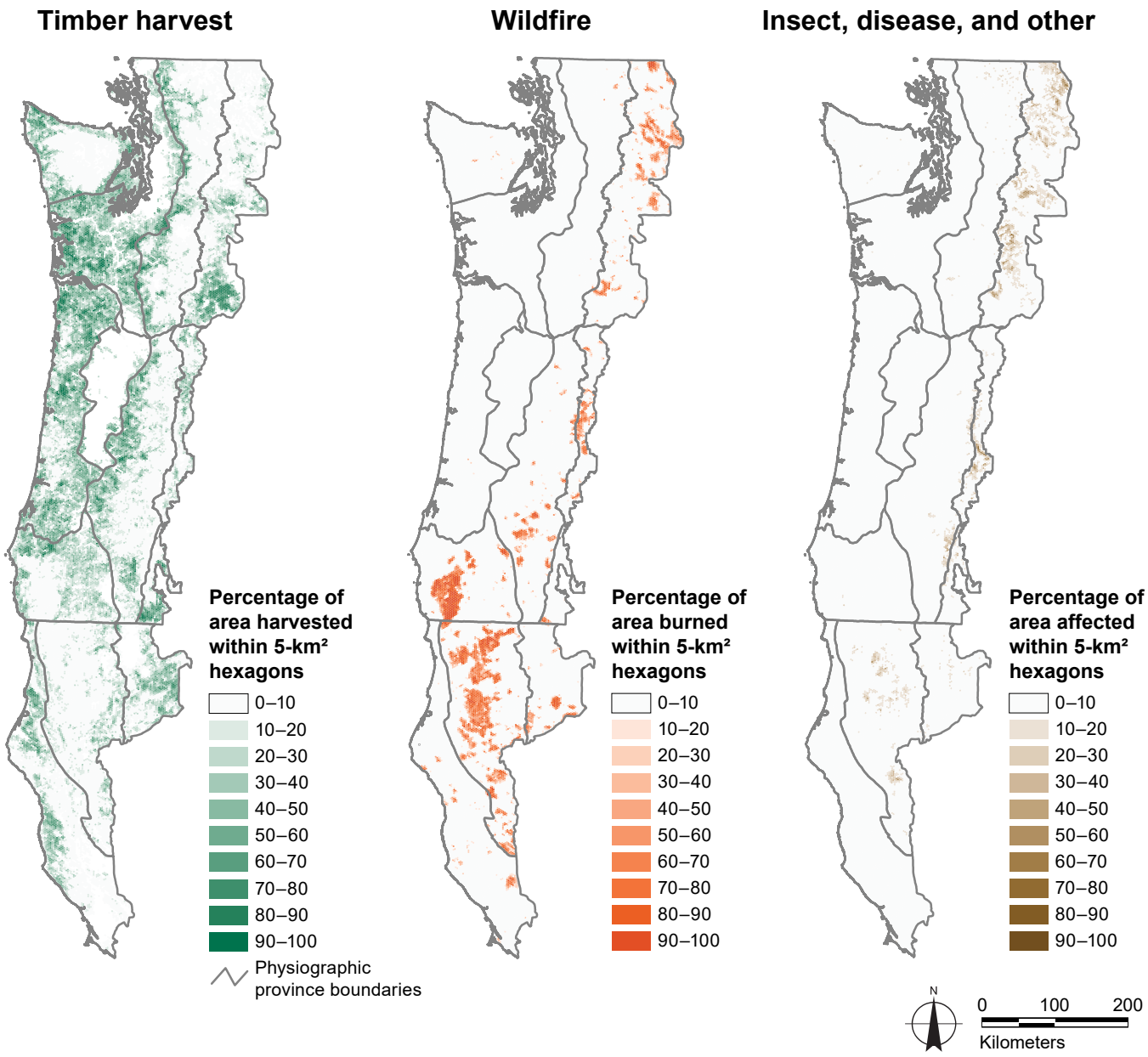


Figure 3—Cumulative forest disturbances over 25 years (1993–2017) summarized as percentage of disturbed area in 5-km² hexagons within the range of northern spotted owls in the United States.

management plan. During our monitoring period, new CRs have been designated; and for these, harvest attribution only applied to disturbances prior to the year of designation. Abrupt disturbances within wildfire perimeters were attributed to harvesting if they occurred prior to the fire year.

- Wildfire—a disturbance with duration of 1 year that occurred the same year, or the year following a fire and within a mapped wildfire perimeter.
- Insect and disease—disturbances with long durations (≥4 years, persistent), or more than four (chronic) disturbances detected. Also, this includes small disturbance patches shorter duration (patch size <9 pixels) when they occurred with a "potential insect/disease area" (PIDA). The PIDA was generated using a focal mean analysis on a binary map of pixels exhibiting persistent or chronic disturbance signals (duration ≥4 years or more than four disturbance events). A focal

mean using a 1-km radius (equivalent to a 776-ac area) was compared against aerial detection survey polygons for the region to identify a mapping threshold to represent PIDAs. We observed that when at least 10 percent of this area contained persistent/chronic disturbance signals, it matched well with aerial detection survey data.

- Other disturbance—All detected disturbances not assigned above.

Forest Structure and Species Composition Maps

Annual forest vegetation structure and composition maps (30-m pixel resolution) for forest-capable lands from 1986 to 2017 were generated using the gradient nearest neighbor (GNN) imputation modeling and mapping methodology developed by Oregon State University Department of Forest Ecosystems and Society's Landscape Ecology, Modeling, Mapping, and Analysis program (LEMMA 2020). GNN is a multivariate, nonparametric modeling and mapping framework that inputs forest inventory plot data to individual map pixels based on Landsat surface reflectance and environmental similarity in the gradient space (Ohmann and Gregory 2002). The version of GNN used in our analysis was based on the composite Landsat images produced to map the forest disturbances above, matching plot measurements to Landsat image years (Bell et al. 2021).

Methodological changes, described in detail in the late-successional and old-growth monitoring report (Davis et al., in press), improved the quality of GNN compared to previous monitoring reports. This included using a consistent type of forest inventory plot for imputations, the ensemble LandTrendr imagery described above, imagery stabilization, and bootstrapped approximations utilizing multiple neighbors ($k = 7$) with weighted means proportional to the probability that a bootstrap sample would result in that plot being the nearest neighbor for a pixel (Davis et al., in press).

NSO Presence Data

NSO pair locations from demographic study areas, supplemented with other location data, were used to train species distribution models used for monitoring. We used the most biologically important pair location based on the following hierarchical ranking: (1) active nest, (2) fledged young, (3) primary roost location, (4) diurnal location, and (5) nocturnal detection from 1993. To reduce sampling bias in relationship to the larger modeling region background (Fourcade et al. 2014, Phillips et al. 2009) we reduced the geographically clumped nature of these data by using only one location per NSO territory. We then filled in the modeling region spaces between demographic study areas with NSO pair presence data from the late 1980s through the 1990s compiled for the 10-year monitoring report (Lint 2005). We limited our data to those collected prior to extensive barred owl invasion that likely affected NSO forest selection. These supplemental locations were geographically thinned out and spaced using nearest neighbor distances to randomly select a subset of these points (as described in Davis et al. 2011: 30, app. B). We did not limit the number of random supplemental locations to match the sample size from the demographic study area. Instead, we used all available location data from the 10-year monitoring report (Lint 2005) that occurred between our study areas. This procedure resulted in a more complete spatial distribution of NSO locations (less clumped) throughout each modeling region. All locations were compiled and checked for spatial accuracy.

Methods

Mapping Nesting/Roosting Forest

Maps of forest types associated with owl nesting and roosting were produced following methods from previous monitoring reports (Davis et al. 2011, 2016), and that methodology is described briefly below. Open-source machine learning software Maxent (Phillips et al. 2006, 2017, 2021) was used to develop a forest cover type model for each modeling region using 10 bootstrapped random samples. We used 75 percent of NSO locations for model training and 25 percent for model testing. Training locations were analyzed against a random sampling of 10,000 background locations from forest-capable pixels within the modeling region.

Based on findings of previous reports and analyses of NSO forest selection (Davis et al. 2011, 2016), we used five GNN forest structure metrics as model predictor variables that co-date the NSO location demography data: density (trees/ha) of large trees >75 cm diameter at breast

height (d.b.h.), percentage of live conifer tree canopy cover, average stand height (meters) of live dominant and codominant trees, mean live conifer diameter (centimeter at d.b.h.), and diameter diversity of live trees as an index of structural diversity based on live conifer tree densities in different diameter classes. Forest species composition GNN variables included proportion of total stand basal area comprising high-elevation tree species, pine species, evergreen hardwood species, oak woodland species, and redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.) (depending on the modeling region). Stand age was also included as a predictor variable.

The relative proportion of training locations were fit to each model predictor variable using linear, product, and hinge response functions. Each model maximized the likelihood ratio of average presence to average background (called the gain function) to best contrast environmental conditions at owl sites from background locations. A regularization multiplier function was applied to penalize high variance in model response functions, where higher variance incurred larger penalties (Merow et al. 2013). Model calibration was accomplished by adjusting the regularization multiplier function setting from 0.25 to 5.0 incrementally by 0.25 and evaluating the difference between the training and testing gain. Maxent is prone to overfitting, resulting in predicted distributions that are clustered around location points. Model overfitting was indicated when training gain was significantly higher than testing gain based on nonoverlapping 95 percent confidence intervals.

We evaluated model predictive performance using the area under the curve (AUC) statistic (Fielding and Bell 1997) based on the held-out test locations and by examining the ratio of the proportion of correctly predicted test locations to the proportion of available area within a moving window of modeled suitability—the predicted-vs-expected (P/E) curve as described in Hirzel et al. (2006). The best model was indicated by having the highest AUC, a monotonically increasing P/E curve with a high Spearman rank statistic, and similar training and testing gain (e.g., overlapping 95 percent confidence intervals).

All replicate model algorithms (Maxent lambda files) from the best model were coded into Google Earth Engine (GEE), where annual model predictor variables were uploaded, to produce a time series of maps based on their mean.[1] This monitoring cycle marks the first use of GEE to demonstrate automated analysis and map production for NSO monitoring. GEE is a cloud platform for massively parallel spatial analyses and computation and has provided many benefits in model development in terms of rapid comparison, visualization, and attribute calculation (Gorelick et al. 2017). Our use of GEE resulted in a considerable savings in time and effort that would normally be required for data management and analyses of such a large quantity of spatial data. Although we produced 31 years of maps (1986–2017) using Landsat 5, 7, and 8 image collections freely available in GEE, the following analyses focused on the years from 1993 to 2017 between which the analyses were bookended.

We used the logistic model output as the relative index of forest suitability for nesting and roosting by NSO pairs. The forest suitability index ranged from 0 to 1.0, where values closer to zero represent forest structure and species composition unsimilar to that found at NSO locations and higher values are more similar. Following procedures from Hirzel et al. (2006), we used the P/E curve to reclassify the continuous suitability index into four biologically meaningful map classes as follows:

- Unsuitable—Maxent logistic output from zero to the mean value between 0 and the P/E = 1 threshold. This map class represents forest types that NSOs normally avoid using for nesting and roosting.
- Marginal—Maxent logistic output from the unsuitable threshold to the P/E = 1 threshold, resulting in a map class that represents forest types approaching what NSOs will nest and roost in.
- Suitable—Maxent logistic output from the P/E = 1 threshold to 0.5. This map class represents forest types where nesting and roosting occurred higher than expected by random chance and up to average conditions associated with nesting and roosting.
- Highly suitable—Maxent logistic output from 0.5 to the highest suitability index value. This map class represents forest types with above-average conditions found at nesting and roosting locations.

[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

To produce rangewide maps of NSO nesting/roosting forest, we applied these mapping thresholds to the Maxent logistic outputs in GEE, producing mosaics of the reclassified maps from each modeling region for each year. The "suitable" and "highly suitable" map classes were combined to analyze trends in nesting/roosting forest.

Pixels can be misclassified as nesting/roosting forest following a high-severity disturbance (e.g., stand-replacing event) because rapid green up of ground vegetation creates surface reflectance in Landsat imagery that is similar to old forest (Bright et al. 2019). These misclassifications can produce errors in the forest vegetation maps used as modeling variables that are transferred to the forest type models and thus cause artificial gains in nesting/roosting forest. To correct for errors in these trends, we used high-severity disturbance maps from the Landscape Change Monitoring System program to mask out unrealistic recruitment of nesting/roosting forest in our time series as it takes decades, not a few years, for a stand-replaced forest to redevelop back into a nesting/roosting forest. Specifically, once a pixel of nesting/roosting forest was lost because of a high-severity disturbance, it was maintained as nonnesting for the remainder of the time series.

Forest Fragmentation Analysis

We used modified methods described by Soille and Vogt (2009) that were coded into GEE to conduct morphological spatial pattern analyses of the time series of nesting/roosting forest maps. These maps were classified into two spatial pattern types (fig. 4):

- Interior—30-m pixels classified as nesting/roosting forest (combined suitable and highly suitable classes) and >1 map pixel from unsuitable or marginal forest. The smallest patch containing interior consisted of a 3-by-3 pixel configuration (2 ac) with the center pixel classified as interior.
- Edge—30-m pixels classified as nesting/roosting forest and directly adjacent to unsuitable or marginal pixels.

Microclimate of interior forest pixels is expected to be similar to intact old forest because patches as small as 2.4 ac have similar microclimates as large intact forest conditions (Heithecker and Halpern 2007). Fragmentation results in lower amounts of interior forest and higher amounts of edge and can occur through two different processes: (1) severe forest disturbances that remove interior forest, or (2) forest succession where a nonnesting forest begins to transition into nesting/roosting forest.

Dispersal-Capable Landscape Analysis

Forest cover types used by dispersing juvenile NSOs moving away from natal areas, or by subadults and adults moving between territories, was mapped following methods in Davis et al. (2011: 40) and is briefly described here. We developed rangewide maps of suitable dispersal forest that included the extent of nesting/roosting forest classes (suitable and highly suitable) and all pixels of GNN data representing mean conifers ≥11 inches d.b.h. and canopy cover ≥40 percent (Thomas et al. 1990). Many of the forests classified as "suitable" dispersal forest may not meet dispersal forest requirements because dispersing juveniles use similar forests as nesting/roosting forests (Sovern et al. 2015) but do serve as an effective measure of landscape forest cover.

NSOs are capable of dispersing long distances, and gene flow from one part of the range to another can occur in a few generations (Forsman et al. 2002, Jenkins et al. 2019). Ninety percent of natal NSO movements from the Forsman et al. (2002) dispersal study occurred within 15.5 mi of the natal site, when the surrounding landscape was covered with ≥40 percent dispersal forest (Davis et al. 2011). Thus, we used a 15.5-mi radius roving circular analysis window to quantify the percentage of dispersal forest for both bookend periods (1993 and 2017), including all forest landownerships. We quantified the percentage of a 15.5-mi radius roving circular window that contained dispersal forest for both bookend periods and considered any pixel with ≥40 percent dispersal forest within the window part of the "dispersal-capable landscape."

Habitat Modeling for Estimating Number of Occupied Territories

Here we followed methods for habitat modeling and estimating density of occupied territories that were developed by Glenn et al. (2017), who reported high predictability based on independent data. Using estimates of occupied territory density, we calculated the likely number of territories occupied (TEROCC) within each demographic study area.

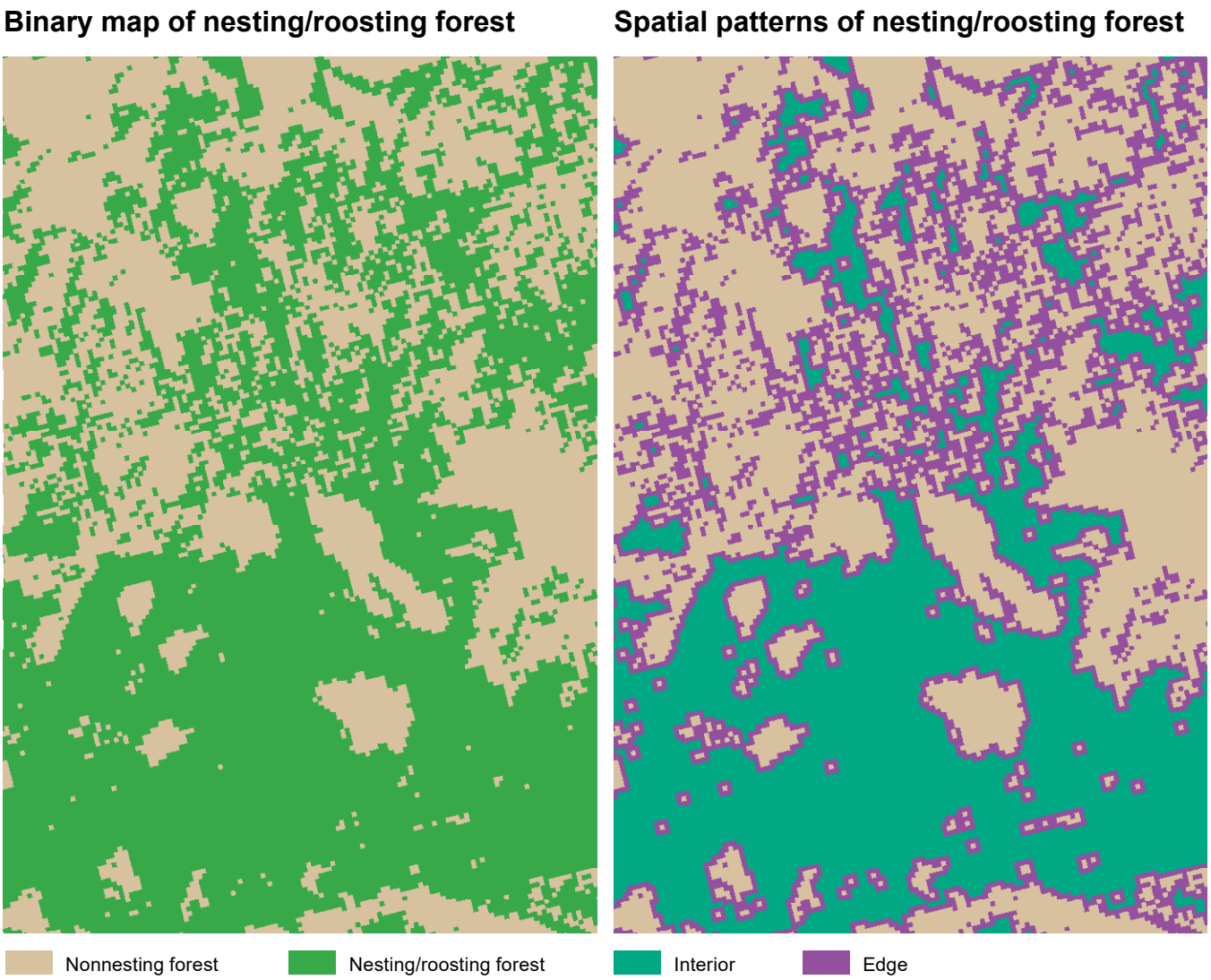


Figure 4—Nesting/roosting forest spatial pattern types produced by the morphological spatial pattern analysis.

We modeled the relationship between territorial owl pair locations and abiotic and biotic environmental conditions at multiple spatial scales (as opposed to the pixel scale used for forest type modeling) using Maxent. Nesting/roosting forest is an essential component of an owl pair's territory, so we used it as the basis for four model predictor variables spatially summarized in four ways: (1) percentage within a nest patch radius (200-m [0.2-mi] radius), (2) percentage within a territory radius (600- to 1900-m [0.4- to 1.2-mi] radii, depending on the modeling region), (3) percentage of edge nesting/roosting forest within a territory radius, and (4) distance (kilometers) from a patch of interior nesting/roosting forest. Abiotic predictor variables included elevation, topographic position index (the difference between a pixel's elevation and mean elevation within a 450-m [0.3-mi]radius), average annual precipitation, average monthly maximum temperature for August, and average monthly minimum temperature for December. All climate variables were based on the 1981–2010 climate normal (PRISM 2015).

Modeling, calibration, evaluation, and reclassification methods were identical to those described above (except that quadratic response functions were used instead of hinge). Model outputs represented a landscape-scale relative suitability index for use by territorial owl pairs and was reclassified into two map classes:

- Unsuitable—Maxent logistic output from 0 to the P/E = 1 threshold. This map class represents the biotic

and abiotic conditions normally avoided for nesting and roosting.

- Suitable—Maxent logistic output from the P/E = 1 threshold to the highest suitability index. This map class represents the biotic and abiotic conditions normally used for nesting and roosting.

We produced habitat maps for the start and end (bookend) years of the monitoring period (1993 and 2017) and estimated habitat carrying capacity and TEROCC by pairs for both years. This method relied on two forms of monitoring information: (1) habitat-based estimates of territory density using median nearest neighbor distance (NND) data, and (2) occupancy rate information provided by the population meta-analyses. We first produced estimates of habitat carrying capacity using 20 random replicates of territory centers within "suitable" habitat and spaced no nearer than the NND. We used a random point generator in open-source software QGIS (QGIS 2021) to fill the suitable habitat footprint for each modeling region until no more centers could be fit, thus an estimate of habitat carrying capacity. We calculated the mean and 95 percent confidence intervals for each point replicate to estimate habitat carrying capacity for each modeling region. To estimate TEROCC, we adjusted the habitat carrying capacity using occupancy rates reported in the latest population meta-analysis (Franklin et al. 2021) that included the effects of other environmental variables that affect occupancy, such as the presence of barred owls. To ensure that our TEROCC estimates were reasonable, we compared them to territory occupancy and realized population change estimates for all eight federal demographic study areas (Franklin et al. 2021).

We calculated change in TEROCC estimates between 1993 and 2017 TEROCC and compared those to realized population change estimates reported by Franklin et al. (2021). For our modeling time period, we calculated change in habitat carrying capacity and TEROCC on all federal lands and within reserved lands.

Results

Mapping Nesting/Roosting Forest

The nesting/roosting forest models had mean testing AUCs ranging from 0.78 to 0.92 and mean Spearman rank correlation coefficients from 0.87 to 0.98 ($P < 0.001$) (table 1).

Nesting/roosting forest was concentrated on federal lands at the beginning of the monitoring period (71.9 percent) and slightly more so at the end (72.5 percent). We estimated a rangewide gross loss of about 1,045,100 ac of nesting/roosting forest on federal lands since the NWFP was implemented (app. 1). This amounted to about 11.8 percent of what was present in 1993. Most of the losses (69.4 percent) occurred within the federally reserved LUAs, roughly in proportion to the amount of nesting/roosting

Table 1—Nesting/roosting forest modeling results for model calibration and testing statistics

Modeling region	Training sample	Testing sample	RM	Training gain	Testing gain	Testing AUC	Spearman rank
Washington coast and Cascades	250	83	0.50	1.15 (±0.03)	1.15 (±0.05)	0.88 (±0.01)	0.97 (±0.01)
Washington eastern Cascades	87	28	1.75	0.90 (± 0.05)	0.93 (±0.13)	0.85 (± 0.02)	0.87 (±0.07)
Oregon Coast Range	247	82	0.75	1.46 (±0.04)	1.48 (±0.07)	0.92 (±0.01)	0.93 (±0.04)
Oregon and California Cascades	596	198	2.75	0.70 (±0.01)	0.73 (±0.03)	0.80 (±0.01)	0.97 (±0.01)
Oregon and California Klamath	757	252	0.75	0.53 (±0.02)	0.52 (±0.03)	0.78 (±0.01)	0.98 (±0.01)
California coast	175	58	0.50	0.83 (±0.04)	0.69 (±0.12)	0.80 (±0.02)	0.90 (±0.06)

Means with 95 percent confidence intervals are shown in parenthesis.

RM = regularization multiplier setting, AUC = area under the curve.

forest that is reserved. Figure 5 shows the spatial pattern of net losses and gains of nesting/roosting forest within the owl's range on all forest lands.

On federal lands, wildfires accounted for 67.3 percent (703,700 ac) of nesting/roosting forest losses. Timber harvesting accounted for 24.7 percent (257,700 ac), while insects, disease, and other disturbances (e.g., blowdown, floods, etc.) accounted for 8 percent (83,700 ac). Considering both losses and gains from forest succession, we estimated a rangewide net increase in nesting/roosting

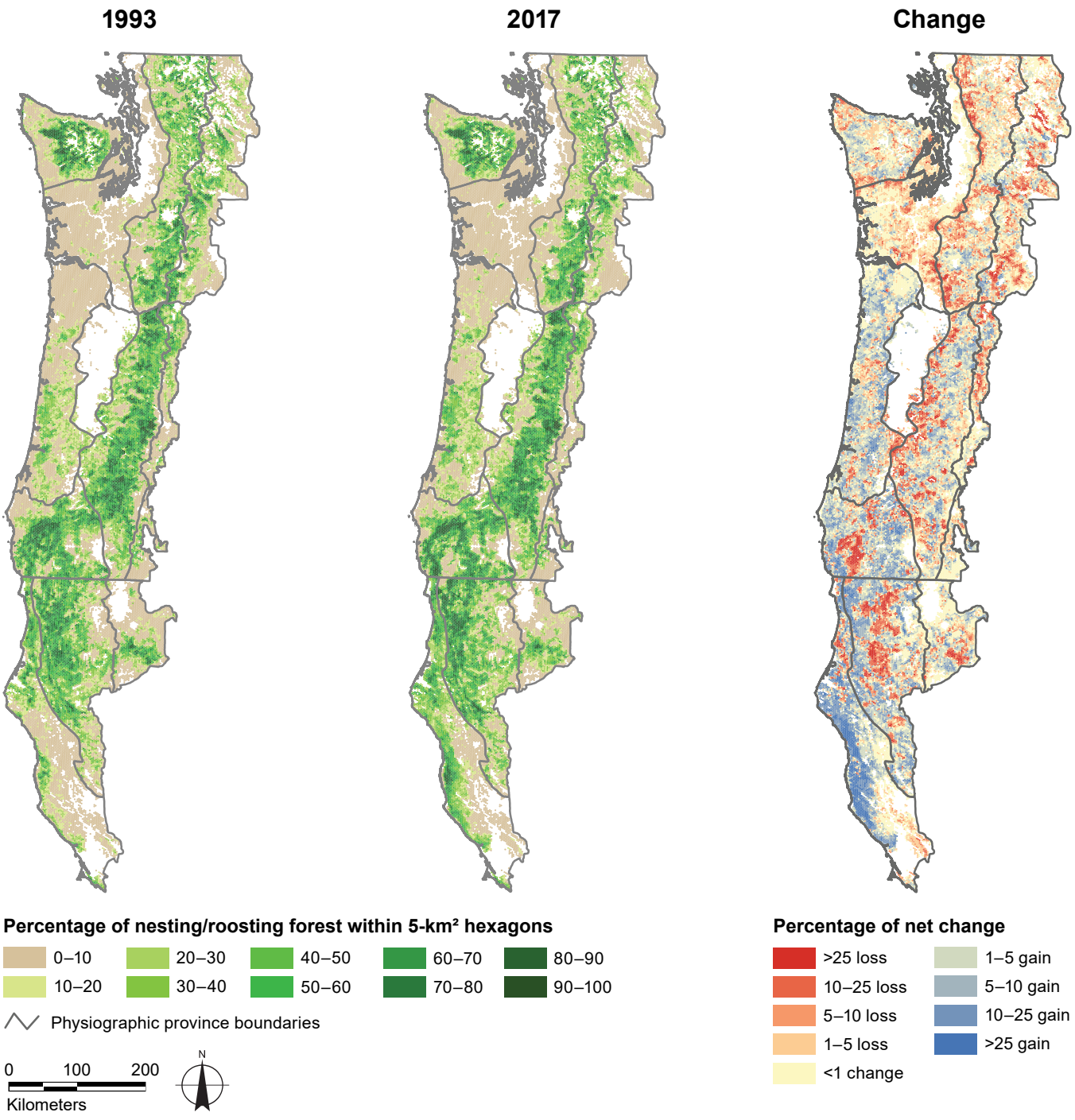


Figure 5—Bookend and change maps of nesting/roosting forest and patterns of change for the first 25 years of Northwest Forest Plan implementation within the range of the northern spotted owl in the United States.

forest of 3 percent on federal lands. The linear trend between bookend years on federal lands was positive, with an average of 12,400 ac (about 0.12 percent) recruited annually. On federally reserved LUAs, the trend was essentially stable with net increase of 0.1 percent (fig. 6).

The 2002 wildfire season caused the largest annual loss of nesting/roosting forest (≈180,000 ac, or ≈1-percent loss), most of this (86 percent) was in reserved LUAs. The period 2009–2012 showed the highest annual gains (about 53,500 ac per year, or 0.6-percent recruitment), with about half of that occurring in reserved LUAs. Most of the gains occurred closer to the Pacific coast and moister physiographic provinces (e.g., coast ranges and western Cascades). Reasons for the net gain were mainly owing to recruitment from old stand-replacing fires that burned in those areas during the mid- to late-1800s.

The physiographic province that experienced the greatest net loss of nesting/roosting forest on federal lands was the Washington Eastern Cascades (fig. 7). The California and Oregon Klamath physiographic provinces experienced the largest gross losses (394,200 and 220,600 ac, respectively) as a result of wildfires, but gains offset losses in both provinces (app. 1). Net gains were seen in 8 of the 12 physiographic provinces with the largest net gains occurring in the Oregon Coast Range and western Cascades (fig. 7). For more details on nesting/roosting forest net change and gross losses, see appendix 1.

Habitat Fragmentation Analysis

Although we estimated a net increase in nesting/roosting forests on federal lands rangewide, these forests have become slightly more fragmented with a rangewide, 2.6-percent increase in the proportion of edge. This varied by physiographic province (fig. 8).

The Oregon western Cascades had the most intact nesting/roosting forest and the western lowlands of Washington had the most fragmented forest. Rangewide, nesting/roosting forest was 5 percent less fragmented on federal reserved LUAs compared to nonreserved forest lands. The most intact reserved allocations were on Washington's Olympic Peninsula, with 30 percent more interior forest on reserved than nonreserved LUAs. The only province with more fragmented nesting/roosting forest on reserved LUAs than nonreserved LUAs was the eastern Cascades of Washington, which increased from 2 to 3.5 percent more fragmented between 1993 and 2017.

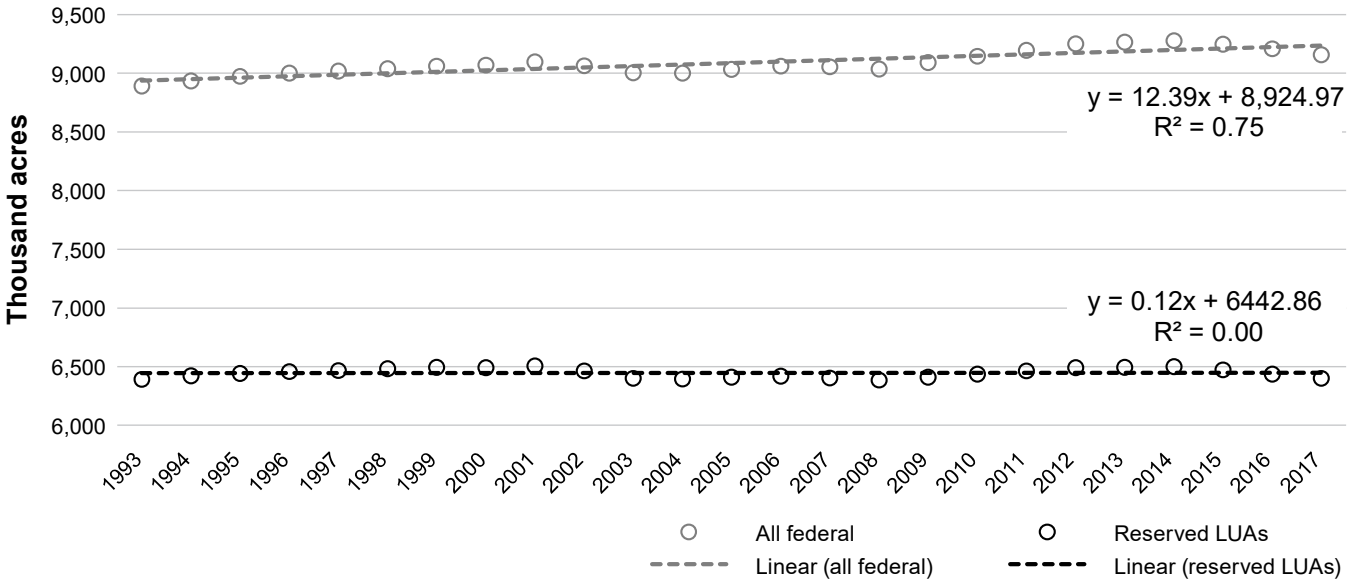


Figure 6—Trends of nesting/roosting forest on federal lands between 1993 and 2017. The *x*-axis values used in the regression are the sequential index of the years starting with 1993 (year 1) and indexed to 2017 (year 25), which represent the first 25 years since the design and implementation of the Northwest Forest Plan. LUAs = land use allocations.

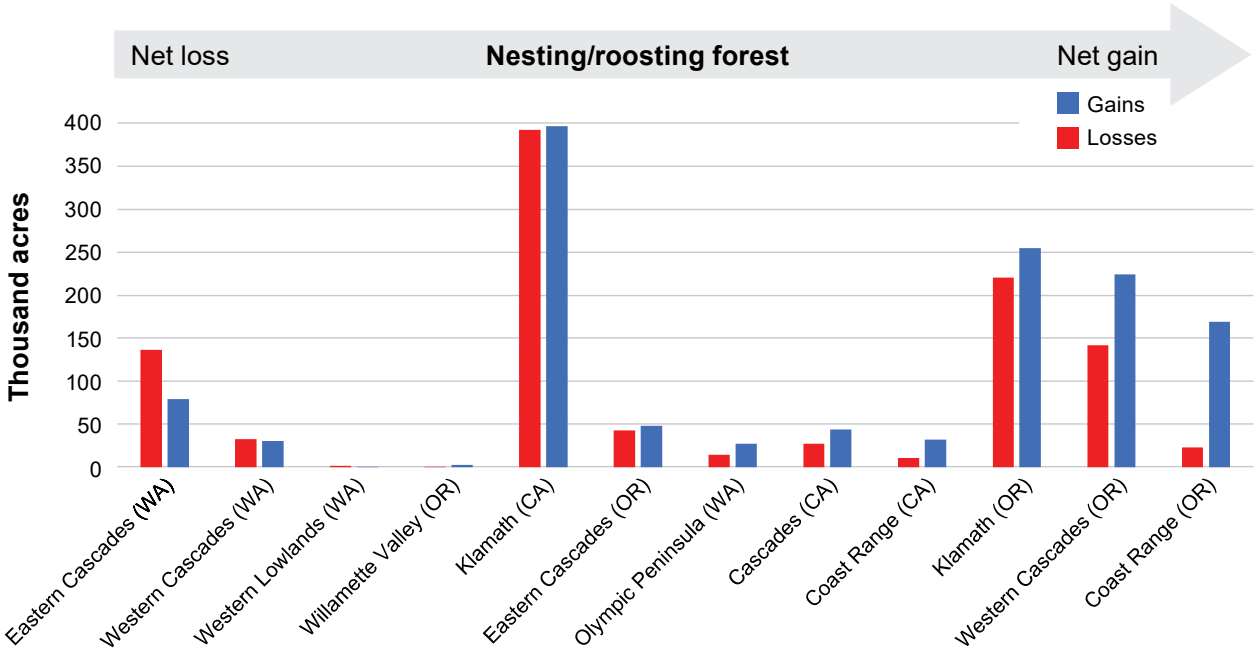


Figure 7—Bookend losses and gains in nesting/roosting forest on federal lands. Physiographic provinces are ordered by net gain (least to most) from left to right.



Figure 8—Bookend changes in nesting/roosting forest spatial patterns by physiographic province.

Dispersal-Capable Landscape Analysis

Rangewide, we report an estimated gross loss of about 1.47 million ac of dispersal forest on federal lands, about 9.4 percent of what was present in 1993 (app. 2). Similar to the pattern of loss for nesting/roosting forest, 69.3 percent of dispersal forest losses occurred on reserved LUAs. On federal lands, wildfires accounted for 67.9 percent (998,300 ac) of dispersal forest losses. Timber harvesting accounted for 23.3 percent (343,200 ac), while insects, disease, and other disturbances accounted for 8.7 percent (128,600 ac). Losses were offset by a 1.63-million-ac gross gain in dispersal forest from forest succession on federal land, resulting in a 1-percent overall net gain; however, a 1.9-percent net decrease remained in the reserved LUAs. The trend in dispersal forest has been positive for all federal lands, with an annual recruitment of about 7,800 ac per year since 1993. The trend on reserved LUAs was negative, with average losses of about 9,700 ac per year (fig. 9).

The physiographic province that experienced the greatest net loss of dispersal forest on federal lands was the Washington Eastern Cascades (fig. 10). All eastern Cascades and Klamath physiographic provinces, which occur in the most fire-prone portions of the range, experienced net losses of dispersal forests largely because of wildfires. Net gains were seen in six physiographic provinces, with the largest net gains occurring in the western Cascade and Coast Ranges (fig. 10). For more details on dispersal forest net change and gross losses, see appendix 2.

Rangewide, we estimated a 15-percent net decrease in dispersal forests on nonfederal lands, and a 5.8-percent net decrease on all lands combined. These losses resulted in a 12.4-percent gross loss in the dispersal-capable landscape, largely because of second-rotation regeneration timber harvesting on bordering nonfederal lands and large wildfires. We detected a 3.4-percent gain caused by forest succession in younger forests along the periphery of some federal forests, but mainly on nonfederal lands within the redwood region of the California Coast Range physiographic province. The result was an overall net decrease of 9 percent of the dispersal-capable landscape since 1993 (fig. 11).

In general, the dispersal-capable landscape continues to recede into federally managed lands in Washington and Oregon. Extremely large wildfires such as the 2002 Biscuit Fire created large internal gaps within federally managed lands. Notable losses of connectivity between physiographic provinces occurred at the pinch point between the Oregon Coast Range and the western Cascades. A connection was also lost within the Oregon Coast Range province, with the northern portion of this province becoming isolated from the southern portions (fig. 11).

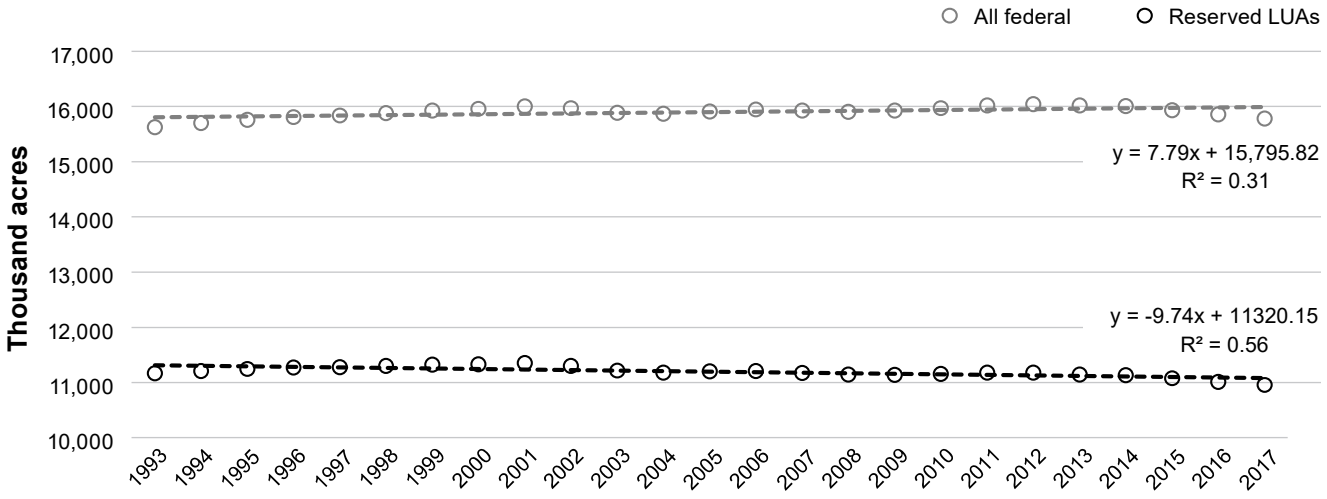


Figure 9—Trends of dispersal forest on federal lands between 1993 and 2017. The *x*-axis values used in the regression are the sequential index of the years starting with 1993 (year 1) and indexed to 2017 (year 25), which represent the first 25 years since the design and implementation of the Northwest Forest Plan. LUAs = land use allocations.

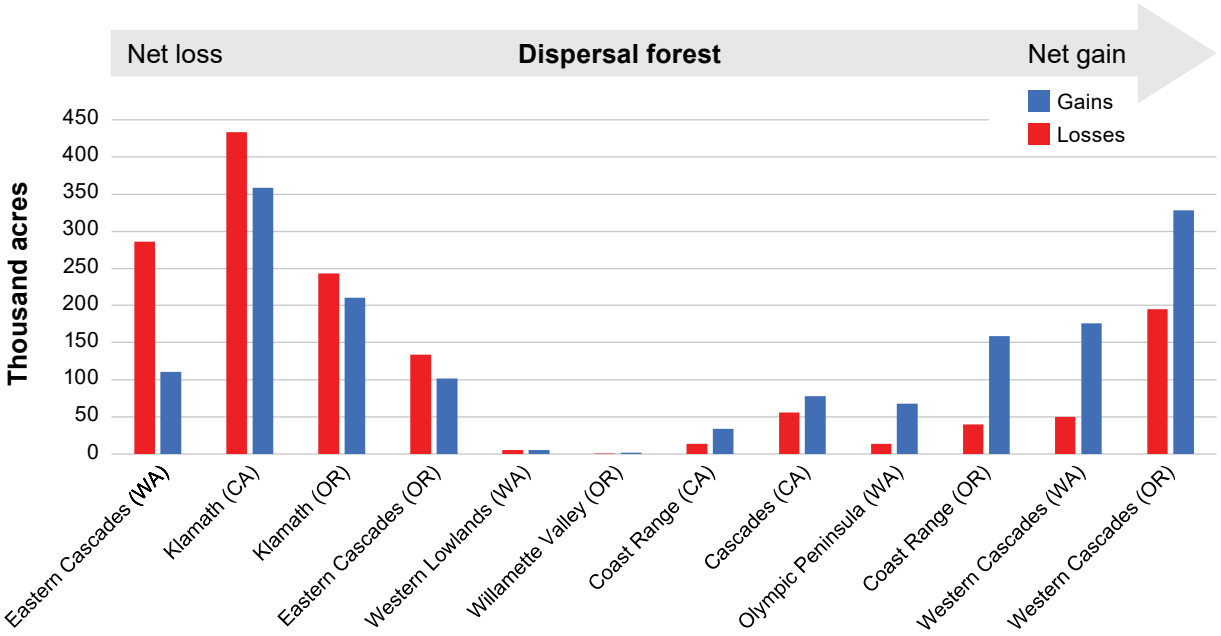


Figure 10—Bookend losses and gains in nesting/roosting forest on federal lands. Physiographic provinces are ordered by net gain (least to most) from left to right.

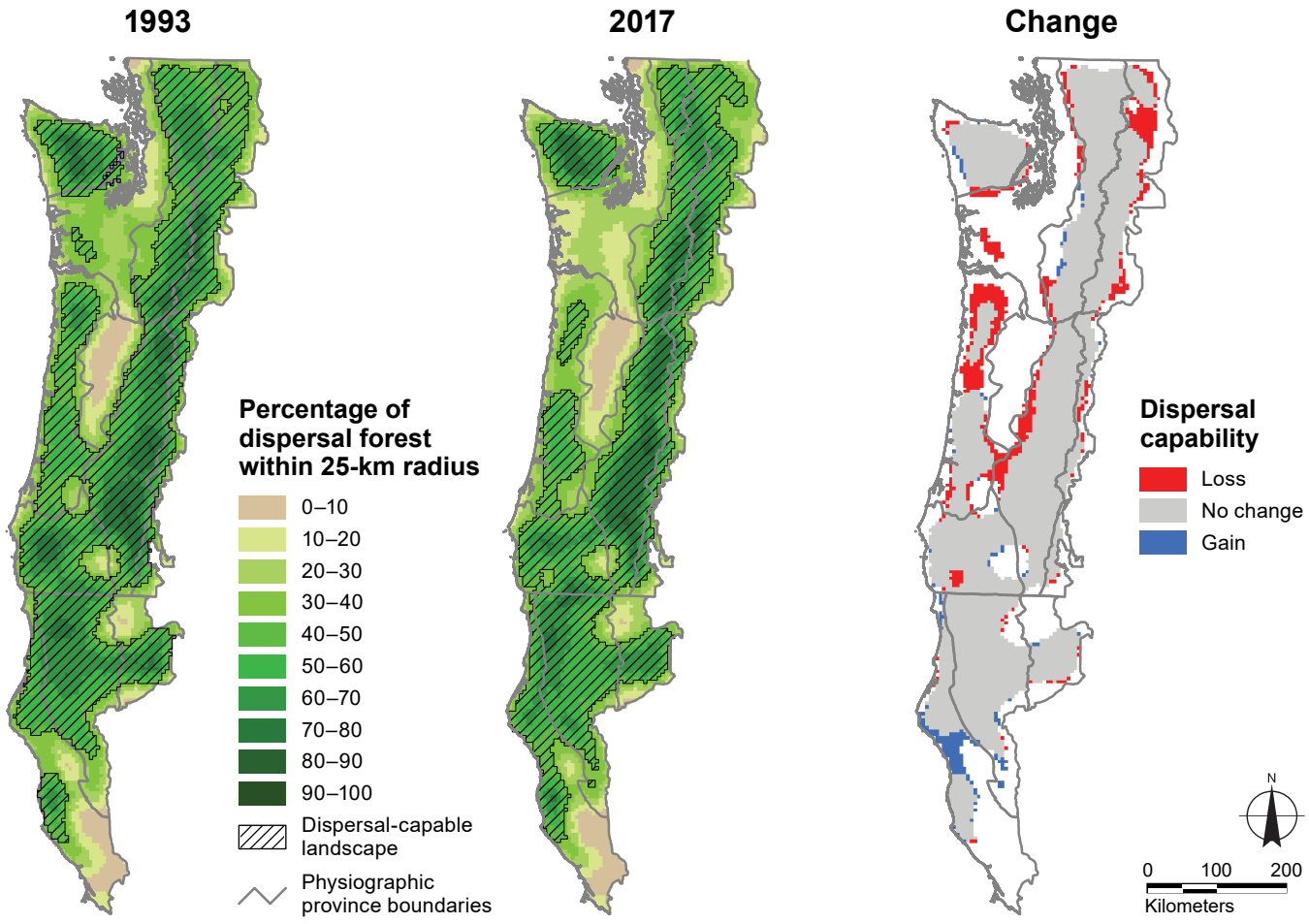


Figure 11—Bookend and change maps of the dispersal-capable landscapes and patterns of change for the first 25 years of Northwest Forest Plan implementation.

Habitat Modeling for Estimating Number of Occupied Territories

Habitat models performed well, with mean testing AUCs ranging from 0.82 to 0.92 and mean Spearman rank correlation coefficients ranging from 0.91 to 0.99 ($P < 0.001$) (table 2).

Our TEROCC point estimates for 1993 and 2017 were generally lower, but with overlapping 95 percent confidence intervals, than those estimated from the most recent meta-analysis (app. 3, Franklin et al. 2021). We suspect that this may be due to the use of an averaged NND based on the NNDs from all study areas within a modeling region for spacing of randomly generated territories. For example, within the Oregon and California Cascades modeling region, the NND for the H.J. Andrews study area is 2 km (1.24 mi) and 3.5 km (2.17 mi) for the southern Cascades study and pair territory estimates for H.J. Andrews were lower for both time periods (app. 3). Changes in TEROCC and Franklin et al. (2021) realized population change estimates had overlapping 95 percent confidence limits (except for the Oregon Klamath study area) and the mean owl pair territory estimates were mostly within the confidence limits of the realized population change (table 3).

On all federal lands at the range scale, habitat carrying capacity increased on federal lands by 3.4 percent, but TEROCC decreased by 61.8 percent (fig. 12). In federal reserved lands, habitat carrying capacity increased by 0.4 percent, but TEROCC decreased by 64.5 percent (fig. 12). On federal lands, the proportion of TEROCC in reserve lands decreased from 70 percent in 1993 to 65 percent in 2017. The opposite trajectories between habitat carrying capacity and TEROCC were mainly due to increased presence of the invasive barred owl. Mean NSO occupancy rates in federal demographic study areas ranged from 46 to 91 percent in 1993 to 7 to 38 percent in 2017 (Franklin et al. 2021). Barred owls displace NSOs from existing and recruited forest habitat. Abundant habitat helps to mitigate the negative effect of barred owls on NSO occupancy but does not reverse it (Franklin et al. 2021, Yackulic et al. 2019).

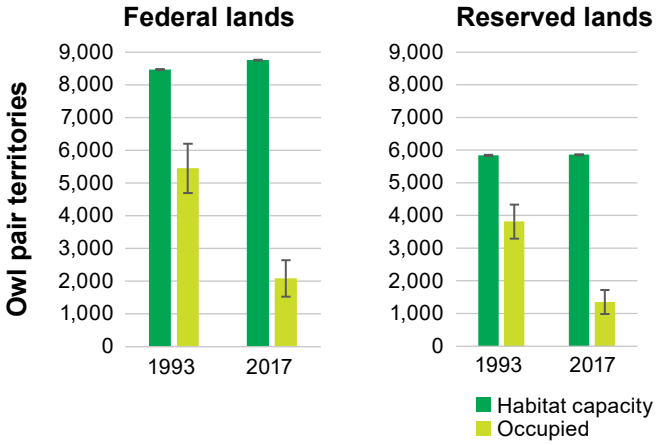


Figure 12—Northern spotted owl pair territory estimates on federal forests for the bookend periods.

Table 2—Habitat modeling results for model calibration and testing statistics

Modeling region	Training sample	Testing sample	RM	Training gain	Testing gain	Testing AUC	Spearman rank
Washington coast and Cascades	250	83	1.00	1.50 (±0.03)	1.52 (±0.05)	0.92 (±0.004)	0.97 (±0.01)
Washington eastern Cascades	87	28	5.00	1.10 (± 0.09)	1.31 (±0.10)	0.90 (± 0.01)	0.91 (±0.02)
Oregon Coast Range	247	82	2.00	1.49 (±0.07)	1.51 (±0.14)	0.91 (±0.01)	0.97 (±0.01)
Oregon and California Cascades	596	198	3.00	0.83 (±0.02)	0.84 (±0.02)	0.84 (±0.004)	0.98 (±0.01)
Oregon and California Klamath	757	252	4.50	0.68 (±0.02)	0.73 (±0.03)	0.82 (±0.004)	0.99 (±0.003)
California coast	175	58	2.50	0.94 (±0.04)	1.03 (±0.099)	0.86 (±0.01)	0.96 (±0.02)

Means with 95 percent confidence intervals are shown in parenthesis.

RM = regularization multiplier setting, AUC = area under the curve.

Table 3—Comparison of population change using the Glenn et al. (2017) method for estimating pair territory densities against realized population change estimates (for all individuals detected regardless of pair status) from the latest population meta-analysis

Demographic study area	Pair territory change (1993–2017)	Realized population change (1995–2017)
	Percentage population decrease (mean and 95% CL)	
Washington Olympic	83.7 (80.4–88.4)	83.9 (74.2–91.1)
Washington Cle Elum	90.4 (86.9–95.5)	84.3 (71.1–93.2)
Oregon Coast Ranges	78.6 (75.4–82.7)	81.1 (73.5–87.0)
Oregon H.J. Andrews	52.1 (47.1–57.9)	63.4 (53.6–71.9)
Oregon Tyee	61.7 (58.6–66.1)	66.2 (53.9–75.7)
Oregon Klamath	47.7 (43.7–53.2)	76.8 (68.2–83.6)
Oregon south Cascades	51.1 (46.8–56.7)	64.6 (51.5–75.1)
Northwest California	47.2 (42.6–53.7)	46.0 (23.4–64.2)

CL = confidence limits.

Source: Franklin et al. 2021.

Discussion

In the early 1970s, the downward trend of old-growth forests resulting from timber harvesting raised concerns for the future of the NSO (Forsman 1975, Gould 1974, Mouat and Schrumpf 1974). Less than two decades later, the owl was listed as threatened under the Endangered Species Act owing to continued chronic habitat loss (USDI FWS 1990). Shortly thereafter, a series of related events led to the design and implementation of the NWFP (FEMAT 1993, Marcot and Thomas 1997), the boundary of which was defined by the NSO geographic range in the United States. A major goal of the NWFP is to stop the downward trend in NSO populations and to maintain and restore forest conditions necessary to support viable populations on federally administered forest lands throughout its range.[2] The recovery of old-forest conditions was anticipated to happen gradually over several decades.

Here we report on monitoring forest structure and composition that are suitable for NSO nesting and roosting; and we demonstrate continued improvements in the process and speed of this monitoring that result in models that performed better than previous monitoring efforts. We expect that future monitoring efforts will improve on our methods to provide near-real-time assessments of status and detailed patterns in annual change. Differing from previous reports, our results indicated a positive trend and net gain in nesting/roosting forest on federal lands that have more than compensated for gross losses caused mainly by wildfires as well as from timber harvesting, insects, disease, and other forest disturbances. Within reserved LUAs, nesting/roosting forest was stable and most of the gains occurred in the nonreserved allocations, contrary to the NWFP assumption that habitat would improve within reserves and decline outside of them. The LSR network was designed (in part) to support NSO metapopulations and dispersal between them across federal lands. As an added measure of assurance for achieving this objective, LSRs were delineated to be large enough to withstand wildfires for up to 50 years (USDA and USDI 1994: apps. J3-8 and 9). In half this time, losses from wildfires have exceeded the anticipated 2.5-percent loss per decade within some LSRs in the fire-prone portions of the range (Davis et al. 2011, Spies et al. 2018). However, some LSRs have remained stable (<1-percent change) and others have shown gains (fig. 13).

There has been a slight increase in the fragmentation of nesting/roosting forests. Not all of it is a result of forest disturbance, it is also owing to the development of younger forests into older forests. These newly recruited nesting/roosting forests tended to occur in small patches, thus increasing the measure of fragmentation. Further, recent studies indicate that interior NSO forest is normally less prone to burning at high severity compared to fragmented (edge) or nonnesting forest types (Lesmeister et al. 2019, 2021b). In addition, it appears to dampen an increasing trend in high-severity wildfire that is occurring in nonnesting forests, and to a lesser extent in edge forests (Lesmeister et al. 2021b). This leads to the conclusion that large patches of interior nesting/roosting forest are

[2] Although the BLM has adopted new resource management plan for BLM land within the range of the NSO, it has retained contributing to the conservation of the NSO as a major objective.

more resilient to wildfires and may serve as fire refugia by normally burning at lower severity than other forest types. Further, these findings highlight the resilience of nesting/roosting forests to wildfire, and these forests are critical in postfire landscapes by providing biological legacies of live and dead large trees as well as logs.

Dispersal forests have increased slightly on federal lands, but losses on nonfederal lands due to timber harvesting

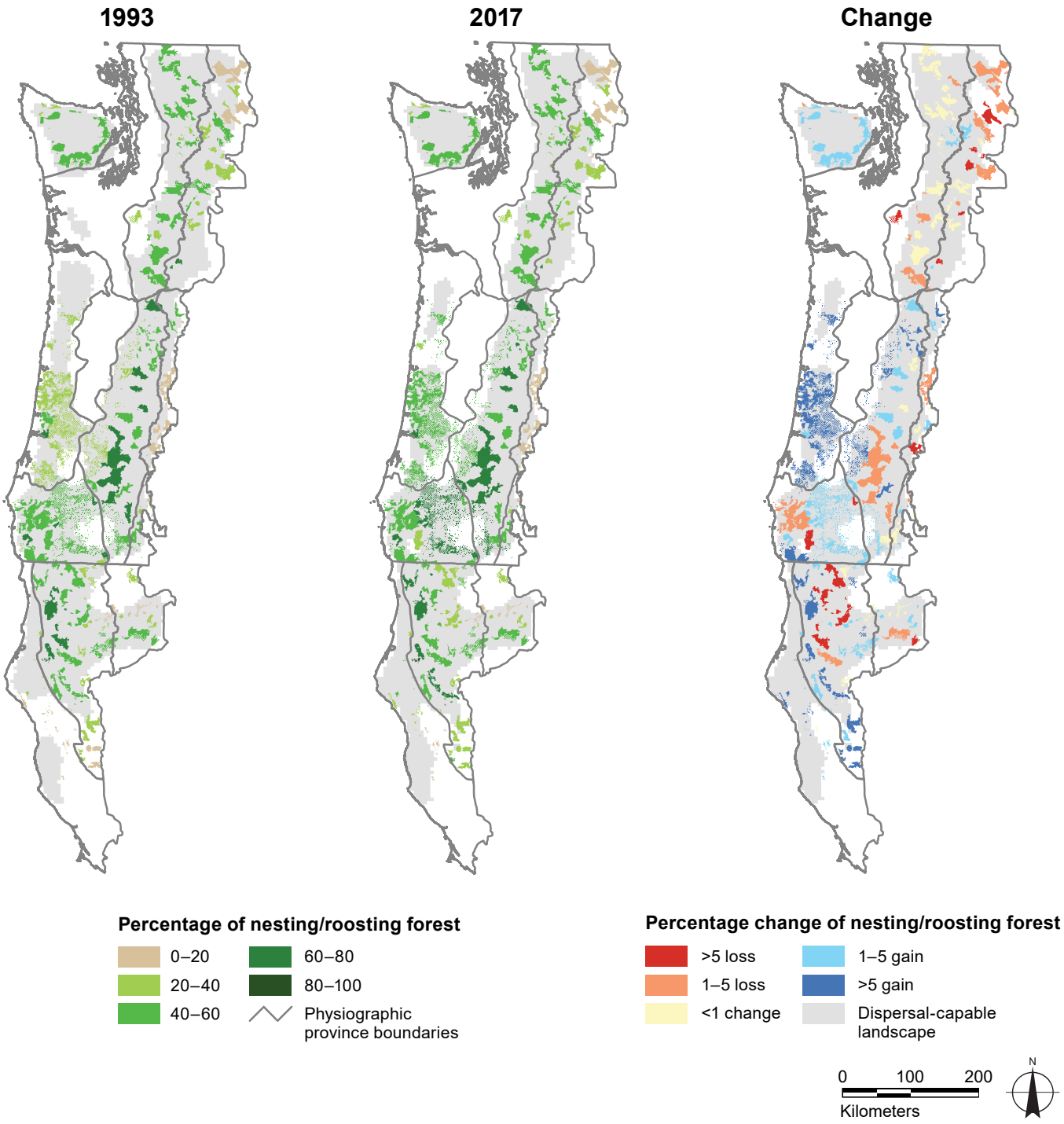


Figure 13—Bookend and change maps of the current large late-successional forest reserve network overlaid on the dispersal-capable landscape maps.

and on federal lands from large wildfires has resulted in a constriction of the dispersal-capable landscape. As a result of past forest management and the ongoing barred owl invasion, NSO populations on federal lands are becoming smaller and more widely dispersed. The decreased, narrowing footprint of dispersal-capable landscapes limits the movement of owls between remnant populations and conceivably makes it harder for recruitment from the floater NSO population (single, nonterritorial birds).

In the previous habitat monitoring report, sufficient time had not yet passed to allow for detectable recruitment of nesting/roosting forest (Davis et al. 2016). Enough time has since passed for old stand-replaced fire patches from the mid- to late-1800s to cross the threshold into suitable nesting/roosting forest conditions. The annual time series maps of nesting/roosting forest allowed us to see this occur as suitable forest pixels began to aggregate as edge-type forest, eventually forming patches of interior forest. More time is needed before we can observe significant recruitment of nesting/roosting forest from the hundreds of thousands of acres of regeneration harvest units that occurred prior to the NSO listing and implementation of the NWFP on federal lands. Given the history of timber harvesting in this region (Gale et al. 2012), this recruitment should begin to peak by around 2040, assuming that setbacks in forest succession do not occur at higher than expected rates as a result of future high-severity wildfires or timber harvest. These assumptions may not fully hold given increased occurrence of wildfires and changes in timber management plans in the region. For example, in 2020, five megafires burned about 812, 977 ac in Oregon and more than 321,236 ac was at high severity.

Despite positive trends in owl forests, NSO populations continue to decline (Franklin et al. 2021), and now the subspecies warrants reclassification to endangered (USDI FWS 2020). The declines have been attributed to continued forest loss and the invasive barred owl that are displacing NSOs from their native habitat. Although increasing amounts of suitable nesting/roosting forest help to mitigate declines in NSO occupancy, it is not expected to reverse the trend by itself (Franklin et al. 2021, Yackulic et al. 2019). The predicted increase in frequency and extent of large wildfires (Davis et al. 2017) will make the NWFP goal of stabilizing NSO habitat and populations more challenging. In addition, the occurrence of large megafires that burn large areas at high severity that results in extensive losses of nesting/roosting forest, as witnessed in 2020, puts isolated populations at risk of rapid extirpation.

Finally, in the short term, climate change is likely to contribute to changes in prey populations and, in the long term, alter future forest species composition, geographic distributions, and extent by the end of the 21st century (Peterson et al. 2014). As the fire-prone footprint expands, fire-susceptible tree species (e.g., *Tsuga heterophylla* (Raf.) Sarg.) may recede and fire-associated species (e.g., *Pinus* spp.) may expand in distribution. Subalpine forests are expected to recede in area, while Douglas-fir forests will likely expand into higher elevations. How these long-term changes unfold remains uncertain, as does the effect on future owl forests.

Conclusion

One of the main goals of the NWFP was to reduce the rate at which owl nesting/roosting forests were being lost on federal lands and to eventually restore them to within a natural range to support viable populations of NSO, especially within the LSR network. A quarter century into the NWFP, the latest monitoring shows that it has been effective at reducing the preceding rate of loss. We also report that recruitment is beginning to occur, but mostly in the nonreserved LUAs.

We estimated rangewide gross losses of nesting/roosting forest on federal lands at 7.9 percent (703,700 ac) from wildfire, 2.9 percent (257,700 ac) from timber harvesting, and 0.9 percent (83,700 ac) from insects, disease, or other natural disturbances. However, we also documented development of about 1.3 million acres through succession, so an overall 3-percent net increase of nesting/roosting forest. All but 0.1 percent of this net gain occurred on nonreserved LUAs. While there was a net gain, a slightly larger proportion of nesting/roosting forest was fragmented, compared to 1993.

Rangewide, the observed rate of loss on federal lands was less than what was anticipated when the NWFP was designed, mostly because of less timber harvest. Losses from wildfire were higher (8.5 vs. 6.25 percent; based on a 2.5-percent loss per decade) than anticipated in federal reserved LUAs at the range scale. Insects and disease

accounted for less than 1 percent of gross losses. Although dispersal forest increased by 1 percent on federal lands, it decreased by 1.9 percent on reserved LUAs. Large losses primarily from timber harvest on surrounding nonfederal lands and large wildfires reduced the footprint of the dispersal-capable landscape by 9 percent. What remains, as of 2017, is more confined to federal forest lands, and the connection between the Oregon Coast Range and the western Cascades through "checkerboard" BLM land has been broken.

Although we observed gains in nesting/roosting forest through mid-2017, there have been four big wildfire seasons (2017, 2018, 2020, and 2021) since the end of this monitoring cycle. Significant challenges remain, as witnessed by the 2020 wildfire season, where decades of forest recruitment can be set back in 1 year by extremely large and severe wildfires—the type that have historically occurred within the infrequent, high-severity fire regime (Spies et al. 2018). Climate change is predicted to increase the extent and frequency of large wildfires, with the largest changes occurring along the western Cascades of Oregon and Washington, which defines the leading front of change (Davis et al. 2017). Changing climates may also cause direct drought-related mortality of large trees that are important nesting/roosting structure (Gutiérrez et al. 2017), as well as large shifts in the forest types that recover (or not) after a stand-replacing event (Halofsky et al. 2020, Peterson et al. 2014). The use of increasing remote sensing and GEE technologies will allow us to monitor NSO forest in near-real time, with annual updates instead of every 5 years. To be successful at managing to maintain and restore nesting/roosting forests into the future, it will be critical for forest managers to track and foresee the "when" and "where" of forest changes that may occur because of climate change. Fire refugia in forested landscapes can be defined as forest stands that remain unburned, burn less frequently, or burn at lower severity than the surrounding landscape (Meddens et al. 2018). Old forest classified as nesting/roosting forest is an important component of fire refugia (Lesmeister et al. 2021b), but further research is needed to identify areas within old forest that could be persistent fire refugia, spatially and temporally, through multiple fires.

Lastly, the long-term goal of the monitoring program to transition to a model-driven, habitat-based approach (phase II) for population monitoring (Lint et al. 1999) is feasible and in progress (Lesmeister et al. 2021a). The gains in nesting/roosting are encouraging, but unfortunately the increases in available forest has not translated into recruitment of new owl pair territories. On the contrary, largely because of the invasion of the barred owl, the number of occupied pair territories has dropped significantly since 1993. A key advantage of phase II monitoring will be the ability to conduct prospective modeling of future change as opposed to being limited to retrospective assessments conducted thus far. As described in the NSO monitoring plan for the NWFP, "the latter leaves us only the option to patch and recover as opposed to the prospective approach, which provides opportunity to set the trajectory for desired outcomes through model-driven insights of the future." (Lint et al. 1999: 21).

Acknowledgments

This report is the result of a large, group effort over many years focused on monitoring the effectiveness of the Northwest Forest Plan. It would not have been possible without the work of many dedicated biologists who annually collected northern spotted owl data used to train and test our forest and habitat models. Wall-to-wall annual time series of forest structure and species composition use maps for model predictor variables would not exist without the hard, dedicated work of Matt Gregory of Oregon State University Department of Forest Ecosystems and Society's Landscape, Ecology, Modeling, Mapping, and Analysis team and Dr. David Bell (USDA Forest Service Pacific Northwest Research Station). The mapping of annual forest disturbances would not have been possible without the USDA Forest Service Rocky Mountain Research Station's Landscape Change and Monitoring System program directed by Dr. Sean Healey.

Metric Equivalents

When you know:	Multiply by:	To find:
Inches	2.54	Centimeters (cm)
Feet (ft)	0.3048	Meters (m)
Acres (ac)	0.405	Hectares (ha)
Miles (mi)	1.61	Kilometers
Trees per acre (trees/ac)	2.47	Trees per hectare (trees/ha)

References

Anthony, R.G.; Forsman, E.D.; Franklin, A.B.; Anderson, D.R.; Burnham, K.P.; White, G.C.; Schwarz, C.J.; Nichols, J.D.; Hines, J.E.; Olson, G.S.; Ackers, S.H.; Andrews, L.S.; Biswell, B.L.; Carlson, P.C.; Diller, L.V.; Dugger, K.M.; Fehring, K.E.; Fleming, T.L.; Gerhardt, R.P.; Gremel, S.A.; Gutierrez, R.J.; Happe, P.J.; Herter, D.R.; Higley, J.M.; Horn, R.B.; Irwin, L.L.; Loschl, P.J.; Reid, J.A.; Sovern, S.G. 2006. Status and trends in demography of northern spotted owls, 1985–2003. Wildlife Monographs. 163(1): 1–48. https://doi.org/10.2193/0084-0173(2006)163[1:SATIDO]2.0.CO;2.

Bell, D.M.; Acker, S.A.; Gregory, M.J.; Davis, R.J.; Garcia, B.A. 2021. Quantifying regional trends in large live tree and snag availability in support of forest management. Forest Ecology and Management. 479: Article 118554. https://doi.org/10.1016/j.foreco.2020.118554.

Bright, B.C.; Hudak, A.T.; Kennedy, R.E.; Braaten, J.D.; Henareh Khalyani, A. 2019. Examining post-fire vegetation recovery with Landsat time series analysis in three western North American forest types. Fire Ecology. 15(8): 1–14. https://doi.org/10.1186/s42408-018-0021-9.

Cohen, W.B.; Yang, Z.; Stehman, S.V.; Schroeder, T.A.; Bell, D.M.; Masek, J.G.; Huang, C.; Meigs, G.W. 2016. Forest disturbance in the conterminous United States from 1985–2012: the emerging dominance of forest decline. Forest Ecology and Management. 360: 242–252. https://doi.org/10.1016/j.foreco.2015.10.042.

Cohen, W.B.; Yang, Z.; Healey, S.P.; Kennedy, R.E.; Gorelick, N. 2018. A LandTrendr multispectral ensemble for forest disturbance detection. Remote Sensing of Environment. 205: 131–140. https://doi.org/10.1016/j.rse.2017.11.015.

Coleman, T.W.; Graves, A.D.; Heath, Z.; Flowers, R.W.; Hanavan, R.P.; Cluck, D.R.; Ryerson, D. 2018. Accuracy of aerial detection surveys for mapping insect and disease disturbances in the United States. Forest Ecology and Management. 430: 321–336. https://doi.org/10.1016/j.foreco.2018.08.020.

Davis, R.J.; Dugger, K.M.; Mohoric, S.; Evers, L.; Aney, W.C. 2011. Northwest Forest Plan—the first 15 years (1994–2008): status and trends of northern spotted owl populations and habitats. Gen. Tech. Rep. PNW-GTR-850. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 147 p. https://doi.org/10.2737/PNW-GTR-850.

Davis, R.J.; Hollen, B.; Hobson, J.; Gower, J.E.; Keenum, D. 2016. Northwest Forest Plan—the first 20 years (1994–2013): status and trends of northern spotted owl habitats. Gen. Tech. Rep. PNW-GTR-929. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 54 p. https://doi.org/10.2737/PNW-GTR-929.

Davis, R.; Yang, Z.; Yost, A.; Belongie, C.; Cohen, W. 2017. The normal fire environment—modeling environmental suitability for large forest wildfires using past, present, and future climate normals. Forest Ecology and Management. 390: 173–186. https://doi.org/10.1016/j.foreco.2017.01.027.

Davis, R.J.; Bell, D.M.; Gregory, M.J.; Yang, Z.; Gray, A.N.; Healey, S.P.; Stratton, A.E. In press. Northwest Forest Plan–the first 25 years (1994–2018): status and trends of late-successional and old-growth forests. Gen. Tech. Rep. PNW-GTR-1004. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/PNW-GTR-1004.

Dugger, K.M.; Wagner, F.; Anthony, R.G.; Olson, G.S. 2005. The relationship between habitat characteristics and demographic performance of northern spotted owls in southern Oregon. Condor. 107(4): 863–878. https://doi.org/10.1093/condor/107.4.863.

Dugger, K.M.; Forsman, E.D.; Franklin, A.B.; Davis, R.J.; White, G.C.; Schwarz, C.J.; Burnham, K.P.; Nichols, J.D.; Hines, J.E.; Yackulic, C.B.; Doherty Jr., P.F.; Bailey, L.L.; Clark, D.A.; Ackers, S.H.; Andrews, L.S.; Augustine, B.; Biswell, B.L.; Blakesley, J.A.; Carlson, P.C.; Clement, M.J.; Diller, L.V.; Glenn, E.M.; Green, A.; Gremel, S.A.; Herter, D.R.; Higley, J.M.; Hobson, J.; Horn, R.B.; Huyvaert, K.P.; McCafferty, C.; McDonald, T.L.; McDonnell, K.; Olson, G.S.; Reid, J.A.; Rockweit, J.; Ruiz, V.; Saenz, J.; Sovern, S.G. 2016. The effects of habitat, climate and barred owls on the long-term population demographics of northern spotted owls. Condor. 118(1): 57–116. https://doi.org/10.1650/CONDOR-15-24.1.

Fielding, A.H.; Bell, J.F. 1997. A review of methods for assessment of prediction errors in conservation presence/absence models. Environmental Conservation. 24(1): 38–49. https://doi.org/10.1017/S0376892997000088.

Forest Ecosystem Management Assessment Team [FEMAT]. 1993. Forest ecosystem management: an ecological, economic, and social assessment. Portland, OR: U.S. Department of Agriculture, U.S. Department of the Interior [and others]. [Irregular pagination].

Forsman, E.D. 1975. Preliminary investigation of the spotted owl in Oregon. Corvallis, OR: Oregon State University. 127 p. M.S. thesis.

Forsman, E.D.; Anthony, R.G.; Reid, J.A.; Loschl, P.J.; Sovern, S.G.; Taylor, M.; Biswell, B.L.; Ellingson, A.; Meslow, E.C.; Miller, G.S.; Swindle, K.A.; Thrailkill, J.A.; Wagner, F.F.; Seaman, D.E. 2002. Natal and breeding dispersal of northern spotted owls. Wildlife Monographs No. 149. Washington, DC: The Wildlife Society. 35 p.

Forsman, E.D.; Anthony, R.G.; Dugger, K.M.; Glenn, E.M.; Franklin, A.B.; White, G.C.; Schwartz, C.J.; Burnham, K.P.; Anderson, D.R.; Nichols, J.D.; Hines, J.E.; Lint, J.B.; Davis, R.J.; Ackers, S.H.; Andrews, L.S.; Biswell, B.L.; Carlson, P.C.; Diller, L.V.; Gremel, S.A.; Herter, D.R.; Higley, J.M.; Horn, R.B.; Reid, J.A.; Rockweit, J.; Schaberl, J.P.; Snetsinger, T.J.; Sovern, S.G. 2011. Population demography of northern spotted owls. Studies in Avian Biology. 40: 1–106.

Fourcade, Y.; Engler, J.O.; Rödder, D.; Secondi, J. 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS ONE. 9(5): e97122. https://doi.org/10.1371/journal.pone.0097122.

Franklin, A.B.; Anderson, D.R.; Gutiérrez, R.J.; Burnham, K.P. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs. 70(4): 539–590. https://doi.org/10.1890/0012-9615(2000)070[0539:CHQAFI]2.0.CO;2.

Franklin, A.B.; Dugger, K.M.; Lesmeister, D.B.; Davis, R.J.; Wiens, J.D.; White, G.C.; Nichols, J.D.; Hines, J.E.; Yackulic, C.B.; Schwarz, C.J.; Ackers, S.H.; Andrews, L.S.; Bailey, L.L.; Bown, R.; Burgher, J.; Burnham, K.P.; Carlson, P.C.; Chestnut, T.; Conner, M.M.; Dilione, K.E.; Forsman, E.D.; Glenn, E.M.; Gremel, S.A.; Hamm, K.A.; Herter, D.R.; Higley, M.; Horn, R.B.; Jenkins, J.M.; Kendall, W.L.; Lamphear, D.W.; McCafferty, C.; McDonald, T.L.; Reid, J.A.; Rockweit, J.T.; Simon, D.C.; Sovern, S.G.; Swingle, J.K.; Wise, H. 2021. Range-wide declines of northern spotted owl populations in the Pacific Northwest: a meta-analysis. Biological Conservation. 259: 109168. https://doi.org/10.1016/j.biocon.2021.109168.

Franklin, J.F.; Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 417 p.

Gale, C.B.; Keegan, C.E., III; Berg, E.C.; Daniels, J.; Christensen, G.A.; Sorenson, C.B.; Morgan, T.A.; Polzin, P. 2012. Oregon's forest products industry and timber harvest, 2008: industry trends and impacts of the Great Recession through 2010. Gen. Tech. Rep. PNW-GTR-868. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 55 p. https://doi.org/10.2737/PNW-GTR-868.

Glenn, E.M.; Lesmeister, D.B.; Davis, R.J.; Hollen, B.; Poopatanapong, A. 2017. Estimating density of a territorial species in a dynamic landscape. Landscape Ecology. 32: 563–579. https://doi.org/10.1007/s10980-016-0467-6.

Gorelick, N.; Hancher, M.; Dixon, M.; Ilyushchenko, S.; Thau, D.; Moore, R. 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. Remote Sensing of Environment. 202: 18–27. https://doi.org/10.1016/j.rse.2017.06.031.

Gould, G.I., Jr. 1974. The status of the spotted owl in California. Unpublished technical report. On file: California Department of Fish and Wildlife, P.O Box 944209, Sacramento, CA 94244-2090. 36 p.

Gutiérrez, R.J.; Manley, P.N.; Stine, P.A., tech. eds. 2017. The California spotted owl: current state of knowledge. Gen. Tech. Rep. PSW-GTR-254. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 294 p. https://doi.org/10.2737/PSW-GTR-254.

Halofsky, J.E.; Peterson, D.L.; Harvey, B.J. 2020. Changing wildfire, changing forests: the effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. Fire Ecology. 16: 4. https://doi.org/10.1186/s42408-019-0062-8.

Healey, S.P.; Cohen, W.B.; Yang, Z.; Brewer, C.K.; Brooks, E.B.; Gorelick, N.; [et al.]. 2018. Mapping forest change using stacked generalization: an ensemble approach. Remote Sensing of Environment. 204: 717–728. https://doi.org/10.1016/j.rse.2017.09.029.

Heithecker, T.D.; Halpern, C.B. 2007. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. Forest Ecology and Management. 248(3): 163–173. https://doi.org/10.1016/j.foreco.2007.05.003.

Herold, N.D.; Koeln, G.; Cunnigham, D. 2003. Mapping impervious surfaces and forest canopy using classification and regression tree (CART) analysis. In: proceedings of the American Society for Photogrammetry and Remote Sensing 2003 annual conference. Anchorage, AK: American Society for Photogrammetry and Remote Sensing. 7 p.

Hirzel, A.H.; Le Lay, G.; Helfer, V.; Randin, C.; Guisan, A. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling. 199(2): 142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017.

Jenkins, J.M.A.; Lesmeister, D.B.; Forsman, E.D.; Dugger, K.M.; Ackers, S.H.; Andrews, L.S.; McCafferty, C.E.; Pruett, M.S.; Reid, J.A.; Sovern, S.G.; Horn, R.B.; Gremel, S.A.; Wiens, J.D.; Yang, Z. 2019. Social status, forest disturbance, and barred owls shape long-term trends in breeding dispersal distance of northern spotted owls. The Condor. 121(4): 1–17. https://doi.org/10.1093/condor/duz055.

Johnson, J. 2016. Aerial forest insect and disease detection surveys in Oregon and Washington 1947–2016. Gen. Tech. Rep. R6-FHP-GTR-0302. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, State and Private Forestry, Forest Health Protection. 298 p.

Landscape Ecology Modeling, Mapping, and Analysis Team [LEMMA]. 2020. Gradient Nearest Neighbor (GNN) raster dataset (version 2020.01). Modeled forest vegetation data using direct gradient analysis and nearest neighbor imputation. https://lemma.forestry.oregonstate.edu/data. (11 April 2022).

Lesmeister, D.B.; Davis, R.J.; Singleton, P.H.; Wiens, J.D. 2018. Northern spotted owl habitat and populations: status and threats In: Spies, T.A.; Stine, P.A.; Gravenmier, R.; Long, J.W.; Reilly, M.J., tech. coords. 2018. Synthesis of science to inform land management within the Northwest Forest Plan area. Gen. Tech. Rep. PNW-GTR-966. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 245–299.

Lesmeister, D.B.; Sovern, S.G.; Davis, R.J.; Bell, D.M.; Gregory, M.J.; Vogeler, J.C. 2019. Mixed-severity wildfire and habitat of an old-forest obligate. Ecosphere. 10(4): e02696. https://doi.org/10.1002/ecs2.2696.

Lesmeister, D.B.; Appel, C.L.; Davis, R.J.; Yackulic, C.B.; Ruff, Z.J. 2021a. Simulating the effort necessary to detect changes in northern spotted owl (*Strix occidentalis caurina*) populations using passive acoustic monitoring. Res. Pap. PNW-RP-618. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 55 p.

Lesmeister, D.B.; Davis, R.J.; Sovern, S.G.; Yang, Z. 2021b. Northern spotted owl nesting forests as fire refugia: a 30-year synthesis of large wildfires. Fire Ecology. 17: 32. https://doi.org/10.1186/s42408-021-00118-z.

Lint, J.B., tech. coord. 2005. Northwest Forest Plan—the first 10 years (1994–2003): status and trends of northern spotted owl populations and habitat. Gen. Tech. Rep. PNW-GTR-648. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 176 p. https://doi.org/10.2737/PNW-GTR-648.

Lint, J.; Noon, B.; Anthony, R.; Forsman, E.; Raphael, M.; Collopy, M.; Starkey, E. 1999. Northern spotted owl effectiveness monitoring plan for the Northwest Forest Plan. Gen. Tech. Rep. PNW-GTR-440. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 43 p. https://doi.org/10.2737/PNW-GTR-440.

Marcot, B.G.; Thomas, J.W. 1997. Of spotted owls, old growth, and new policies: a history since the Interagency Scientific Committee report. Gen. Tech. Rep. PNW-GTR-408. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 34 p. https://doi.org/10.2737/PNW-GTR-408.

Meddens, A.J.H.; Kolden, C.A.; Lutz, J.A.; Smith, A.M.S.; Cansler, C.A.; Abatzoglou, J.T.; Meigs, G.W.; Downing, W.M.; Krawchuk, M.A. 2018. Fire refugia: what are they, and why do they matter for global change? BioScience. 68(12): 944–954. https://doi.org/10.1093/biosci/biy103.

Merow, C.; Smith, M.J.; Silander, J.A., Jr. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography. 36(10): 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x.

Miller, J.D.; Thode, A.E. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR). Remote Sensing of Environment. 109(1): 66–80. https://doi.org/10.1016/j.rse.2006.12.006.

Mouat, D.A.; Schrumpf, B.J. 1974. Second-year projects and activities of the Environmental Remote Sensing Applications Laboratory (ERSAL). Annual progress report. Corvallis, OR: Oregon State University.

Mulder, B.S.; Noon, B.R.; Spies, T.A.; Raphael, M.G.; Palmer, C.J.; Olsen, A.R.; Reeves, G.H.; Welsh, H.H., tech. coords. 1999. The strategy and design of the effectiveness monitoring program for the Northwest Forest Plan. Gen. Tech. Rep. PNW-GTR-437. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 138 p. https://doi.org/10.2737/PNW-GTR-437.

Ohmann, J.L.; Gregory, M.J. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, U.S.A. Canadian Journal of Forest Research. 32: 725–741. https://doi.org/10.1139/x02-011.

Omernik, J.M. 1987. Ecoregions of the conterminous United States (map supplement) [1:750,000]. Annals of the Association of American Geographers. 77(1): 118–125.

Peterson, D.L.; Kerns, B.K.; Dodson, E.K. 2014. Climate change effects on vegetation in the Pacific Northwest: a review and synthesis of the scientific literature and simulation model projections. Gen. Tech. Rep. PNW-GTR-900. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 183 p. https://doi.org/10.2737/PNW-GTR-900.

Phillips, S.J.; Anderson, R.P.; Dudik, M.; Shapire, R.E.; Blair, M.E. 2017. Opening the black box: an open-source release of Maxent. Ecography. 40(7): 887–893. https://doi.org/10.1111/ecog.03049.

Phillips, S.J.; Anderson, R.P.; Shapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling. 190(3–4): 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Phillips, S.J.; Dudik, M.; Elith, J.; Graham, C.H.; Lehmann, A.; Leathwick, J. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications. 19(1): 181–197. https://doi.org/10.1890/07-2153.1.

Phillips, S.J.; Dudík, M.; Shapire, R.E. 2021. Maxent software for modeling species niches and distributions (Version 3.4.1). http://biodiversityinformatics.amnh.org/open_source/maxent. (31 January 2021).

PRISM. 2015. PRISM Climate Group. http://prism.oregonstate.edu. (12 February 2015).

QGIS. 2021. QGIS geographic information system. QGIS Association. http://www.qgis.org. (27 January 2022).

Reilly, M.J.; Dunn, C.J.; Meigs, G.W.; Spies, T.A.; Kennedy, R.E.; Bailey, J.D.; Briggs, K. 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). Ecosphere. 8(3): 1–28. https://doi.org/10.1002/ecs2.1695.

Soille, P.; Vogt, P. 2009. Morphological segmentation of binary patterns. Pattern Recognition Letters. 30(4): 456–459. https://doi.org/10.1016/j.patrec.2008.10.015.

Sovern, S.G.; Forsman, E.D.; Dugger, K.M.; Taylor, M. 2015. Roosting habitat use and selection by northern spotted owls during natal dispersal. The Journal of Wildlife Management. 79(2): 254–262. https://doi.org/10.1002/jwmg.834.

Spies, T.A.; Stine, P.A.; Gravenmier, R.; Long, J.W.; Reilly, M.J., tech. coords. 2018. Synthesis of science to inform land management within the Northwest Forest Plan area. Gen. Tech. Rep. PNW-GTR-966. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 1020 p. 3 vol. https://doi.org/10.2737/PNW-GTR-966.

Thomas, J.W.; Forsman, E.D.; Lint, J.B.; Meslow, E.C.; Noon, B.R.; Verner, J. 1990. A conservation strategy for the northern spotted owl: report of the Interagency Scientific Committee to address the conservation of the northern spotted owl. Portland, OR: U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management, Fish and Wildlife Service, National Park Service. 427 p. https://doi.org/10.5962/bhl.title.124040.

U.S. Department of Agriculture, Forest Service [USDA FS]. 2021. Landscape Change Monitoring System Data Explorer [Online]. https://apps.fs.usda.gov/lcms-viewer. (10 April 2022).

U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management [USDA and USDI]. 1994. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. Volumes 1–2 and Record of Decision. Portland, OR.

U.S. Department of the Interior, Bureau of Land Management [USDI BLM]. 2016a. Northwestern and coastal Oregon record of decision and approved resource management plan, Coos Bay, Eugene, Salem Districts, and Swiftwater Field Office of Roseburg District. Portland, OR. 320 p.

U.S. Department of the Interior, Bureau of Land Management [USDI BLM]. 2016b. Southwestern Oregon record of decision and approved resource management plan, Klamath Falls Field Office of Lakeview District, Medford District, and South River Field Office of Roseburg District. Portland, OR. 332 p.

U.S. Department of the Interior, Fish and Wildlife Service [USDI FWS]. 1990. Endangered and threatened wildlife and plants: determination of threatened status for the northern spotted owl. Federal Register. 55: 26114–26194.

U.S. Department of the Interior, Fish and Wildlife Service [USDI FWS]. 2020. Endangered and threatened wildlife and plants: 12-month finding for the northern spotted owl. Federal Register 85: 81144–81152.

Vogelmann, J.E.; Howard, S.M.; Yang, L.; Larson, C.R.; Wylie, B.K.; Van Driel, J.N. 2001. Completion of the 1990's national land cover data set for the conterminous United States. Photogrammetric Engineering and Remote Sensing. 67(6): 650–662.

Yackulic, C.B.; Bailey, L.L.; Dugger, K.M.; Davis, R.J.; Franklin, A.B.; Forsman, E.D.; Ackers, S.H.; Andrews, L.S.; Diller, L.V.; Gremel, S.A.; Hamm, K.A.; Herter, D.R.; Higley, J.M.; Horn, R.B.; McCafferty, C.; Reid, J.A.; Rockweit, J.T.; Sovern, S.G. 2019. The past and future roles of competition and habitat in the range-wide occupancy dynamics of northern spotted owls. Ecological Applications. 29(3): e01861. https://doi.org/10.1002/eap.1861.

Appendix 1—Bookend Map Area Estimates of Nesting/Roosting Forests

Table A1-1—Bookend map area estimates of nesting/roosting forests on federal lands and explained losses from Landscape Change Monitoring System (LCMS) disturbance maps

State and physiographic province	Nesting/roosting forest area estimates from bookend maps				LCMS disturbance explanation for losses					
	1993	2017	Net area change	Net percent change	Harvest	Wildfire	Insect	Other	Total explained loss	Percentage loss from 1993
	Thousand acres			*Percent*	*Thousand acres*					*Percent*
Washington:										
Olympic Peninsula	719.0	732.3	13.3	1.9	3.6	3.4	0.3	6.7	14.1	-2.0
Western Lowlands	12.3	10.9	-1.4	-11.1	1.8	0.0	0.0	0.0	1.8	-14.4
Western Cascades	1,382.4	1,380.2	-2.2	-0.2	14.9	5.8	1.8	10.2	32.7	-2.4
Eastern Cascades	730.4	673.5	-56.9	-7.8	31.3	75.2	22.7	7.4	136.7	-18.7
Total	2,844.1	2,797.0	-47.1	-1.7	51.6	84.4	24.9	24.2	185.2	-6.5
Oregon:										
Coast Range	413.6	559.4	145.8	35.3	22.9	0.2	0.0	0.1	23.3	-5.6
Willamette Valley	6.2	8.8	2.6	42.0	0.5	0.0	0.0	0.0	0.5	-8.6
Western Cascades	2,251.2	2,333.7	82.5	3.7	68.5	68.0	2.1	3.3	141.8	-6.3
Klamath	1,087.6	1,121.6	34.0	3.1	40.3	178.6	0.3	1.4	220.6	-20.3
Eastern Cascades	283.9	288.9	5.0	1.7	19.6	20.0	2.7	1.0	43.4	-15.3
Total	4,042.5	4,312.3	269.8	6.7	151.9	266.8	5.1	5.8	429.6	-10.6
California:										
Coast Range	106.8	128.5	21.7	20.3	2.6	7.7	0.0	0.3	10.6	-9.9
Klamath	1,722.9	1,727.2	4.3	0.2	40.6	329.3	7.5	14.9	392.4	-22.8
Cascades	174.2	190.7	16.5	9.4	11.0	15.5	0.8	0.1	27.4	-15.7
Total	2,003.9	2,046.4	42.4	2.1	54.2	352.5	8.3	15.3	430.3	-21.5
NWFP total	8,890.5	9,155.7	265.1	3.0	257.7	703.7	38.3	45.3	1,045.1	-11.8

NWFP = Northwest Forest Plan.

Table A1-2—Bookend map area estimates of nesting/roosting forests on federal reserved lands and explained losses from Landscape Change Monitoring System (LCMS) disturbance maps

State and physiographic province	Nesting/roosting forest area estimates from bookend maps				LCMS disturbance explanation for losses					
	1993	2017	Net area change	Net percent change	Harvest	Wildfire	Insect	Other	Total explained loss	Percentage loss from 1993
	Thousand acres			*Percent*	*Thousand acres*					*Percent*
Washington:										
Olympic Peninsula	692.5	700.0	7.5	1.1	2.9	3.4	0.3	6.7	13.3	-2.0
Western Lowlands	12.3	10.9	-1.4	-11.1	1.8	0.0	0.0	0.0	1.8	-14.4
Western Cascades	1,112.4	1,101.9	-10.4	-0.9	7.9	5.7	1.8	10.2	25.6	-2.4
Eastern Cascades	525.4	467.5	-57.9	-11.0	14.4	62.6	19.2	7.2	103.4	-18.7
Total	2,342.6	2,280.4	-62.2	-2.7	26.9	71.7	21.3	24.1	144.0	-6.1
Oregon:										
Coast Range	372.7	483.1	110.4	29.6	15.3	0.2	0.0	0.1	15.6	-4.2
Willamette Valley	1.7	2.0	0.3	19.7	0.1	0.0	0.0	0.0	0.1	-8.2
Western Cascades	1,353.2	1,354.5	1.3	0.1	16.8	53.5	1.5	3.2	75.0	-5.5
Klamath	791.7	771.1	-20.6	-2.6	19.0	154.6	0.2	1.3	175.0	-22.1
Eastern Cascades	177.5	175.8	-1.6	-0.9	5.1	13.1	1.8	0.9	20.9	-11.8
Total	2,696.8	2,786.6	89.8	3.3	56.3	221.4	3.4	5.6	286.7	-10.6
California:										
Coast Range	98.5	117.1	18.6	18.9	2.2	7.6	0.0	0.3	10.1	-10.3
Klamath	1,142.2	1,099.7	-42.5	-3.7	14.6	233.7	6.6	14.7	269.6	-23.6
Cascades	111.4	114.7	3.3	3.0	4.3	11.0	0.4	0.1	15.8	-14.2
Total	1,352.1	1,331.6	-20.5	-1.5	21.1	252.3	7.0	15.1	295.5	-21.9
NWFP total	6,391.4	6,398.6	7.1	0.1	104.3	545.4	31.7	44.8	726.2	-11.4

NWFP = Northwest Forest Plan.

Table A1-3—Bookend map area estimates of nesting/roosting forests on nonfederal lands and explained losses from Landscape Change Monitoring System (LCMS) disturbance maps

State and physiographic province	Nesting/roosting forest area estimates from bookend maps				LCMS disturbance explanation for losses					
	1993	2017	Net area change	Net percent change	Harvest	Wildfire	Insect	Other	Total explained loss	Percentage loss from 1993
	Thousand acres			*Percent*	*Thousand acres*					*Percent*
Washington:										
Olympic Peninsula	151.7	137.7	-14.0	-9.2	74.2	0.0	0.5	0.1	74.7	-49.2
Western Lowlands	222.4	135.0	-87.4	-39.3	152.8	0.0	0.3	0.0	153.1	-68.8
Western Cascades	407.2	272.8	-134.4	-33.0	164.5	0.4	0.3	0.0	165.2	-40.6
Eastern Cascades	285.7	219.2	-66.5	-23.3	122.9	13.9	5.5	0.1	142.4	-49.8
Total	1,067.0	764.7	-302.3	-28.3	514.4	14.4	6.5	0.2	535.5	-50.2
Oregon:										
Coast Range	277.9	325.2	47.3	17.0	264.8	0.3	0.4	0.0	265.5	-95.5
Willamette Valley	82.7	76.8	-5.9	-7.2	48.8	0.0	0.1	0.0	48.9	-59.0
Western Cascades	448.7	295.4	-153.3	-34.2	339.4	2.2	0.5	0.0	342.0	-76.2
Klamath	340.3	365.0	24.7	7.3	188.7	13.7	0.4	0.1	202.9	-59.6
Eastern Cascades	98.4	68.9	-29.5	-30.0	46.9	9.5	0.7	0.1	57.2	-58.2
Total	1,248.0	1,131.2	-116.7	-9.4	888.6	25.6	2.0	0.3	916.5	-73.4
California:										
Coast Range	681.6	1,050.6	369.1	54.2	232.0	9.0	0.1	0.0	241.1	-35.4
Klamath	315.6	381.6	66.0	20.9	87.5	23.3	0.6	0.1	111.5	-35.3
Cascades	164.4	143.6	-20.7	-12.6	75.4	9.8	1.0	0.0	86.2	-52.5
Total	1,161.5	1,575.8	414.3	35.7	395.0	42.0	1.8	0.1	438.9	-37.8
NWFP total	3,476.5	3,471.8	-4.7	-0.1	1,797.9	82.0	10.3	0.6	1,890.8	-54.4

NWFP = Northwest Forest Plan.

Table A1-4—Bookend map area estimates of nesting/roosting forests on all lands and explained losses from Landscape Change Monitoring System (LCMS) disturbance maps

State and physiographic province	Nesting/roosting forest area estimates from bookend maps				LCMS disturbance explanation for losses					
	1993	2017	Net area change	Net percent change	Harvest	Wildfire	Insect	Other	Total explained loss	Percentage loss from 1993
	Thousand acres			*Percent*	*Thousand acres*					*Percent*
Washington:										
Olympic Peninsula	870.7	870.1	-0.7	-0.1	77.8	3.4	0.8	6.7	88.8	-10.2
Western Lowlands	234.7	145.9	-88.8	-37.8	154.5	0.0	0.3	0.0	154.9	-66.0
Western Cascades	1,789.6	1,653.0	-136.5	-7.6	179.4	6.2	2.1	10.2	198.0	-11.1
Eastern Cascades	1,016.1	892.7	-123.4	-12.1	154.3	89.2	28.2	7.5	279.1	-27.5
Total	3,911.1	3,561.7	-349.4	-8.9	566.0	98.8	31.4	24.4	720.7	-18.4
Oregon:										
Coast Range	691.5	884.6	193.1	27.9	287.8	0.5	0.4	0.1	288.8	-41.8
Willamette Valley	89.0	85.6	-3.3	-3.8	49.3	0.0	0.1	0.0	49.4	-55.5
Western Cascades	2,699.9	2,629.1	-70.8	-2.6	407.8	70.2	2.5	3.3	483.8	-17.9
Klamath	1,427.8	1,486.5	58.7	4.1	229.1	192.2	0.7	1.5	423.5	-29.7
Eastern Cascades	382.3	357.7	-24.6	-6.4	66.5	29.5	3.5	1.2	100.6	-26.3
Total	5,290.5	5,443.6	153.1	2.9	1,040.4	292.4	7.1	6.1	1,346.1	-25.4
California:										
Coast Range	788.4	1,179.1	390.8	49.6	234.6	16.6	0.1	0.3	251.7	-31.9
Klamath	2,038.5	2,108.8	70.3	3.4	128.2	352.6	8.1	14.9	503.9	-24.7
Cascades	338.6	334.3	-4.3	-1.3	86.4	25.3	1.8	0.1	113.6	-33.5
Total	3,165.4	3,622.2	456.8	14.4	449.2	394.6	10.1	15.4	869.2	-27.5
NWFP total	12,367.0	12,627.5	260.5	2.1	2,055.7	785.7	48.6	45.9	2,935.9	-23.7

NWFP = Northwest Forest Plan.

Appendix 2—Bookend Map Area Estimates of Dispersal Forests

Table A2-1—Bookend map area estimates of dispersal forests on federal lands and explained losses from Landscape Change Monitoring System (LCMS) disturbance maps

State and physiographic province	Nesting/roosting forest area estimates from bookend maps				LCMS disturbance explanation for losses					
	1993	2017	Net area change	Net percent change	Harvest	Wildfire	Insect	Other	Total explained loss	Percentage loss from 1993
	Thousand acres			*Percent*	*Thousand acres*					*Percent*
Washington:										
Olympic Peninsula	1,109.7	1,164.1	54.4	4.9	3.8	3.9	0.5	5.3	13.5	-1.2
Western Lowlands	58.8	59.0	0.2	0.3	5.5	0.0	0.0	0.0	5.5	-9.4
Western Cascades	2,286.0	2,411.6	125.6	5.5	19.2	9.2	5.3	16.5	50.2	-2.2
Eastern Cascades	1,927.0	1,751.5	-175.6	-9.1	39.1	205.3	28.0	14.1	286.4	-14.9
Total	5,381.5	5,386.2	4.7	0.1	67.6	218.3	33.8	35.9	355.7	-6.6
Oregon:										
Coast Range	911.3	1,030.1	118.8	13.0	39.4	0.3	0.0	0.1	39.9	-4.4
Willamette Valley	12.7	14.0	1.3	10.3	0.7	0.0	0.0	0.0	0.7	-5.2
Western Cascades	3,350.1	3,483.8	133.7	4.0	67.5	112.5	7.4	7.5	194.9	-5.8
Klamath	1,436.9	1,403.9	-33.0	-2.3	41.5	200.1	0.3	1.4	243.4	-16.9
Eastern Cascades	1,015.8	983.9	-31.9	-3.1	41.7	72.4	14.0	5.4	133.5	-13.1
Total	6,726.8	6,915.8	189.0	2.8	190.8	385.2	21.8	14.4	612.3	-9.1
California:										
Coast Range	189.4	209.9	20.5	10.8	3.5	9.6	0.0	0.3	13.5	-7.1
Klamath	2,703.8	2,629.4	-74.5	-2.8	44.7	367.2	7.8	13.1	432.9	-16.0
Cascades	620.9	643.5	22.6	3.6	36.6	17.8	1.2	0.2	55.8	-9.0
Total	3,514.2	3,482.7	-31.4	-0.9	84.8	394.7	9.0	13.6	502.1	-14.3
NWFP total	15,622.5	15,784.7	162.2	1.0	343.2	998.3	64.7	63.9	1,470.0	-9.4

NWFP = Northwest Forest Plan.

Table A2-2—Bookend map area estimates of dispersal forests on federal reserved lands and explained losses from Landscape Change Monitoring System (LCMS) disturbance maps

State and physiographic province	Nesting/roosting forest area estimates from bookend maps				LCMS disturbance explanation for losses					
	1993	2017	Net area change	Net percent change	Harvest	Wildfire	Insect	Other	Total explained loss	Percentage loss from 1993
	Thousand acres			*Percent*	*Thousand acres*					*Percent*
Washington:										
Olympic Peninsula	1,036.8	1,074.7	37.9	3.7	2.4	3.9	0.5	5.3	12.1	-1.2
Western Lowlands	58.5	58.6	0.1	0.2	5.5	0.0	0.0	0.0	5.5	-9.4
Western Cascades	1,872.4	1,930.4	58.1	3.1	9.9	9.1	5.2	16.5	40.8	-2.2
Eastern Cascades	1,505.7	1,332.0	-173.7	-11.5	15.9	172.6	24.1	13.8	226.5	-15.0
Total	4,473.3	4,395.8	-77.6	-1.7	33.8	185.6	29.9	35.6	284.9	-6.4
Oregon:										
Coast Range	746.5	829.7	83.2	11.1	25.2	0.2	0.0	0.1	25.6	-3.4
Willamette Valley	2.8	2.9	0.1	3.6	0.2	0.0	0.0	0.0	0.2	-8.9
Western Cascades	2,030.0	2,026.3	-3.8	-0.2	17.8	91.3	5.8	7.3	122.3	-6.0
Klamath	1,006.3	942.0	-64.4	-6.4	17.9	170.1	0.2	1.3	189.4	-18.8
Eastern Cascades	683.0	629.8	-53.1	-7.8	12.8	54.6	9.9	5.0	82.2	-12.0
Total	4,468.6	4,430.6	-37.9	-0.8	73.9	316.2	15.9	13.8	419.7	-9.4
California:										
Coast Range	165.5	184.0	18.5	11.2	2.5	8.4	0.0	0.3	11.2	-6.8
Klamath	1,790.5	1,676.2	-114.3	-6.4	13.7	254.4	6.8	12.9	287.8	-16.1
Cascades	267.8	268.5	0.7	0.3	5.2	9.9	0.4	0.2	15.6	-5.8
Total	2,223.7	2,128.7	-95.1	-4.3	21.4	272.7	7.2	13.4	314.7	-14.2
NWFP total	11,165.6	10,955.1	-210.6	-1.9	129.1	774.4	53.0	62.8	1,019.3	-9.1

NWFP = Northwest Forest Plan.

Table A2-3—Bookend map area estimates of dispersal forests on nonfederal lands and explained losses from Landscape Change Monitoring System (LCMS) disturbance maps

State and physiographic province	Nesting/roosting forest area estimates from bookend maps				LCMS disturbance explanation for losses					
	1993	2017	Net area change	Net percent change	Harvest	Wildfire	Insect	Other	Total explained loss	Percentage loss from 1993
	Thousand acres			*Percent*	*Thousand acres*					*Percent*
Washington:										
Olympic Peninsula	576.2	520.4	-55.7	-9.7	296.6	0.0	1.1	0.1	297.8	-51.7
Western Lowlands	1,939.6	1,412.1	-527.6	-27.2	1,110.0	0.1	2.3	0.0	1,112.4	-57.4
Western Cascades	1,072.4	923.6	-148.8	-13.9	465.9	0.7	0.6	0.0	467.2	-43.6
Eastern Cascades	888.6	719.4	-169.2	-19.0	312.4	44.3	7.6	0.2	364.4	-41.0
Total	4,476.8	3,575.5	-901.3	-20.1	2,185.0	45.0	11.5	0.3	2,241.9	-50.1
Oregon:										
Coast Range	1,883.1	1,378.1	-505.0	-26.8	1,169.7	0.8	1.9	0.0	1,172.4	-62.3
Willamette Valley	234.0	182.2	-51.8	-22.1	107.9	0.0	0.1	0.0	108.1	-46.2
Western Cascades	969.0	695.9	-273.1	-28.2	588.5	6.1	0.8	0.1	595.5	-61.5
Klamath	665.9	604.4	-61.6	-9.2	313.6	16.5	0.6	0.2	330.9	-49.7
Eastern Cascades	328.2	260.5	-67.7	-20.6	148.9	26.4	2.7	0.3	178.3	-54.3
Total	4,080.3	3,121.2	-959.1	-23.5	2,328.6	49.8	6.2	0.5	2,385.2	-58.5
California:										
Coast Range	1,874.2	1,994.3	120.1	6.4	259.2	22.2	0.2	0.0	281.7	-15.0
Klamath	586.5	641.8	55.2	9.4	126.0	33.6	0.9	0.1	160.6	-27.4
Cascades	497.0	457.2	-39.8	-8.0	126.2	14.5	2.0	0.0	142.8	-28.7
Total	2,957.7	3,093.3	135.6	4.6	511.4	70.4	3.2	0.1	585.1	-19.8
NWFP total	11,514.8	9,790.0	-1,724.8	-15.0	5,025.1	165.2	20.9	1.0	5,212.1	-45.3

NWFP = Northwest Forest Plan.

Table A2-4—Bookend map area estimates of dispersal forests on all lands and explained losses from Landscape Change Monitoring System (LCMS) disturbance maps

State and physiographic province	Nesting/roosting forest area estimates from bookend maps				LCMS disturbance explanation for losses					
	1993	2017	Net area change	Net percent change	Harvest	Wildfire	Insect	Other	Total explained loss	Percentage loss from 1993
	Thousand acres			*Percent*	*Thousand acres*					*Percent*
Washington:										
Olympic Peninsula	1,685.9	1,684.5	-1.3	-0.1	300.5	3.9	1.6	5.4	311.3	-18.5
Western Lowlands	1,998.4	1,471.1	-527.4	-26.4	1,115.5	0.1	2.3	0.0	1,117.9	-55.9
Western Cascades	3,358.4	3,335.2	-23.2	-0.7	485.1	9.9	5.9	16.6	517.5	-15.4
Eastern Cascades	2,815.6	2,470.9	-344.7	-12.2	351.5	249.5	35.6	14.3	650.9	-23.1
Total	9,858.3	8,961.7	-896.6	-9.1	2,252.6	263.4	45.4	36.2	2,597.6	-26.3
Oregon:										
Coast Range	2,794.4	2,408.3	-386.1	-13.8	1,209.1	1.0	1.9	0.1	1,212.2	-43.4
Willamette Valley	246.8	196.3	-50.5	-20.5	108.6	0.0	0.1	0.0	108.8	-44.1
Western Cascades	4,319.1	4,179.7	-139.4	-3.2	656.0	118.6	8.2	7.6	790.4	-18.3
Klamath	2,102.8	2,008.2	-94.6	-4.5	355.1	216.7	1.0	1.5	574.3	-27.3
Eastern Cascades	1,344.0	1,244.5	-99.6	-7.4	190.6	98.7	16.7	5.7	311.8	-23.2
Total	10,807.1	10,036.9	-770.1	-7.1	2,519.5	435.0	28.0	15.0	2,997.4	-27.7
California:										
Coast Range	2,063.6	2,204.2	140.6	6.8	262.7	31.9	0.3	0.3	295.1	-14.3
Klamath	3,290.4	3,271.1	-19.2	-0.6	170.7	400.9	8.8	13.2	593.5	-18.0
Cascades	1,117.9	1,100.7	-17.2	-1.5	162.8	32.3	3.2	0.2	198.5	-17.8
Total	6,471.9	6,576.1	104.2	1.6	596.2	465.1	12.2	13.7	1,087.2	-16.8
NWFP total	27,137.3	25,574.7	-1,562.6	-5.8	5,368.3	1,163.5	85.5	64.9	6,682.2	-24.6

NWFP = Northwest Forest Plan.

Appendix 3—Estimating Northern Spotted Owl Pair Territories

Modeling parameters used to estimate owl pair territories following methods in Glenn et al. (2017) relied primarily on demographic data from population meta-analyses information from Dugger et al. (2016) and Franklin et al. (2021). Demographic parameters were averaged when more than one study area occurred within a modeling region (table A3-2).

Table A3-1—Data summary from demographic studies that informed the models

Demographic study areas	½ median nearest neighbor distance[1]	Occupancy rate (1993)[2]	Occupancy rate (2018)[2]	Number of territories (Thiessen polygons)[2,3]
	Kilometers	*Mean (95% CL)*	*Mean (95% CL)*	*1993/2017*
OLY	1.75	0.77 (0.64–0.90)	0.12 (0.07–0.18)	98
RAI[4]	1.50	0.85 (0.72–0.98)	0.11 (0.05–0.16)	NA
CLE	1.75	0.65 (0.53–0.77)	0.07 (0.03–0.11)	92
COA	1.25	0.72 (0.63–0.81)	0.15 (0.11–0.19)	172
HJA	1.00	0.91 (0.81–1.00)	0.27 (0.21–0.33)	11/185
TYE	1.00	0.46 (0.39–0.54)	0.17 (0.13–0.22)	160
CAS	1.75	0.70 (0.61–0.80)	0.23 (0.18–0.29)	113/169
KLA	1.25	0.68 (0.58–0.78)	0.20 (0.16–0.25)	91/158
NWC	0.75	0.76 (0.63–0.88)	0.38 (0.28–0.48)	99
GDR[4]	0.60	0.97 (0.92–1.00)	0.35 (0.27–0.44)	NA

[1] From Dugger et al. (2016, table 3).

[2] From Franklin et al. (2021).

[3] Two numbers for study area expansions between 1993 and 2017.

[4] Not a Northwest Forest Plan monitoring program demographic study area.

OLY = Olympic (WA), RAI = Mt. Rainier (WA), CLE- = Cle Elum (WA), COA = Coast Ranges (OR), HJA = H.J. Andrews (OR), TYE = Tyee (OR), CAS = South Cascades (OR), KLA = Klamath (OR), NWC = Northwest (CA), GDR = Green Diamond Resources (CA). CL = confidence limits.

Table A3-2—Modeling parameters used to generate estimates of owl pair territories

Modeling region	Demographic study areas	Minimum spacing	Occupancy rate (1993)	Occupancy rate (2017)
		Kilometers	*Mean (95% CL)*	*Mean (95% CL)*
WA Coast and Western Cascades	OLY, RAI	3.2	0.81 (0.68–0.94)	0.12 (0.06–0.17)
WA Eastern Cascades	CLE	3.8	0.65 (0.53–0.77)	0.07 (0.03–0.11)
OR Coast Range	COA, TYE	2.4	0.59 (0.51–0.67)	0.16 (0.12–0.20)
OR and CA Cascades	HJA, CAS	2.8	0.80 (0.71–0.90)	0.25 (0.20–0.31)
OR and CA Klamath Mountains	KLA, NWC	2.0	0.48 (0.40–0.55)	0.29 (0.22–0.37)
CA Coast Range	GDR	1.2	0.97 (0.92–1.00)	0.35 (0.27–0.44)

WA = Washington, OR = Oregon, CA = California, OLY = Olympic (WA), RAI = Mount Rainier (WA), CLE- = Cle Elum (WA), COA = Coast Ranges (OR), HJA = H.J. Andrews (OR), TYE = Tyee (OR), CAS = South Cascades (OR), KLA = Klamath (OR), NWC = Northwest (CA), GDR = Green Diamond Resources (CA), CL = confidence limits.

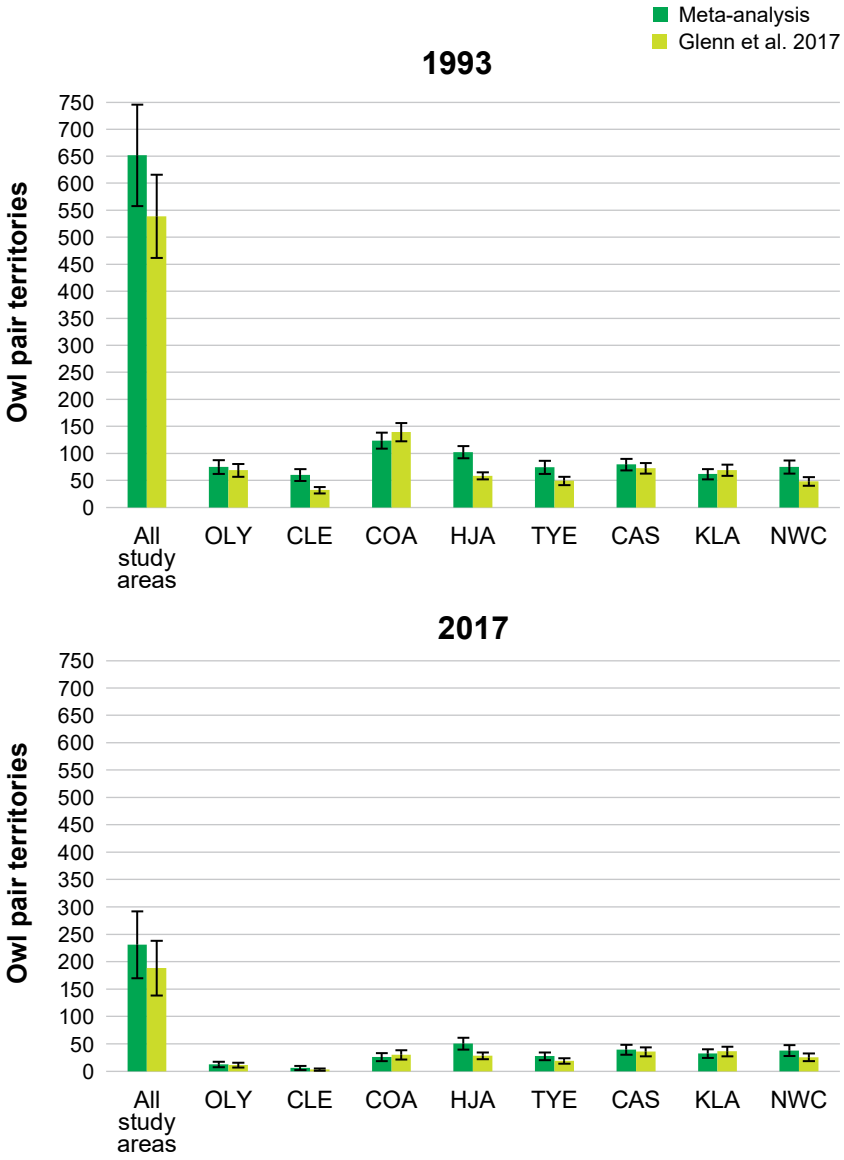


Figure A3-1—Comparison (means and 95% confidence limits) of owl occupied owl territory estimates for the bookend time periods using the Glenn et al. (2017) method to occupancy analysis estimates from the last population meta-analysis applied to the number of Theisen polygons on each demographic study area (Franklin et al. 2021). OLY = Olympic (WA), CLE = Cle Elum (WA), COA = Coast Ranges (OR), HJA = H.J. Andrews (OR), TYE = Tyee (OR), CAS = South Cascades (OR), KLA = Klamath (OR), NWC = Northwest (CA).

Pacific Northwest Research Station

Website	https://www.fs.usda.gov/pnw
Telephone	(503) 808-2100
Publication requests	(503) 808-2138
FAX	(503) 808-2130
E-mail	sm.fs.pnw_pnwpubs@usda.gov
Mailing address	Publications Distribution Pacific Northwest Research Station USDA Forest Service 1220 SW 3rd Avenue Portland, OR 97204

Federal Recycling Program
Printed on Recycled Paper

Pacific Northwest Research Station
USDA Forest Service
1220 SW 3rd Ave., Suite 1400
Portland, OR 97204

Official Business
Penalty for Private Use, $300



United States
Department of
Agriculture

Forest Service

**Northern
Research Station**

Research Paper NRS-15

Differences Between Standing and Downed Dead Tree Wood Density Reduction Factors: A Comparison Across Decay Classes and Tree Species

**Mark E. Harmon
Christopher W. Woodall
Becky Fasth
Jay Sexton
Misha Yatkov**

Abstract

Woody detritus or dead wood is an important part of forest ecosystems and has now become a routine facet of forest monitoring and inventory. Biomass and carbon estimates of dead wood depend on knowledge of species- and decay class- specific density or density reduction factors. While some progress has been made in determining these parameters for dead and downed trees (DD), there are very few estimates of these key parameters for standing dead trees (SD). In this study we evaluated indicators of decay to relate subjective SD and DD decay classifications then compared SD and DD density and density reduction factors by decay class for a total of 19 tree species at nine sites in the United States and Russia. A set of preliminary decay reduction factors for SD trees by species and decay class was developed for tree species inventoried by the U.S. Department of Agriculture's Forest Inventory and Analysis (FIA) program. Results indicate that SD density declined with decay class for all examined species. For six of the examined species, SD tree density could be assumed equal to that of DD tree density. The most common situation (13 species) was for SD density to be higher than for DD density. The likely cause of these differences was the drier microenvironment of SD which slows decomposition relative to that of DD. By applying these results, a new set of SD density reduction factors was developed for 260 species inventoried by FIA in forests of the United States. Comparison of biomass estimates using this study's proposed SD density reduction factors with existing SD volume estimates based solely on undecayed wood density indicated a possible biomass overestimate of 16.5 percent for Minnesota. Given the size of the potential biases involved and the uncertainty associated with decay reduction factors developed in this study, additional work to develop a multispecies SD decay class system and further empirical sampling of SD tree density is recommended.

Cover Photo

Standing dead tree on the shores of Octopus Lake, Boundary Waters Canoe Area Wilderness, Superior National Forest, Minnesota, USA. Christopher W. Woodall, U.S. Forest Service.

Manuscript received for publication 19 April 2011

Published by:

U.S. FOREST SERVICE
11 CAMPUS BLVD SUITE 200
NEWTOWN SQUARE PA 19073

August 2011

For additional copies:

U.S. Forest Service
Publications Distribution
359 Main Road
Delaware, OH 43015-8640
Fax: (740)368-0152
Email: nrspubs@fs.fed.us

Visit our homepage at: **http://www.nrs.fs.fed.us/**

INTRODUCTION

Woody detritus or dead wood is an important part of forest ecosystems, providing habitats and food sources, a store of carbon, nutrients, and water, as well as influencing geomorphic processes (Franklin et al. 1987, Harmon et al. 1986, Triska and Cromack 1980). In particular, standing dead trees provide structural complexity and enhance biodiversity in many forest ecosystems (Jonsell et al. 1998, Kruys et al. 1999, Nilsson et al. 2001). Therefore, dead wood is increasingly being included in ecological studies and environmental assessments (Woodall et al. 2009), with the number of publications on this subject rapidly growing. Both downed (DD) and standing dead (SD) wood store carbon and are important components of forest carbon dynamics, but also release carbon via decomposition and combustion in fires. However, given the contrasting microenvironments that SD and DD trees inhabit, their decay dynamics and attributes may vary (Aakala et al. 2008, Aakala 2010, Lee 1998, Vanderwel et al. 2006). Accurate estimates of standing dead tree carbon stocks are important for monitoring carbon flux, for characterizing processes such as respiration and combustion losses, and for validating simulation models that are used to project how carbon dynamics will change in the future.

It is difficult to develop accurate estimates of dead wood biomass for several reasons. First, until recently there have been few systematic, regional-scale dead wood inventories, resulting in highly uncertain dead wood population estimates (Harmon et al. 2001). However, regional-scale inventories of dead wood are becoming more common (Woodall et al. 2009). For example, the Forest Inventory and Analysis (FIA) program of the U.S. Forest Service now conducts a national inventory of woody material including fine woody detritus (FWD) and DD (for more details see Woodall and Monleon 2008). Second, given the size and actively decomposing nature of dead trees, direct measurements of biomass during forest inventories are not possible. Instead, the volume of individual DD pieces is estimated from fixed-area plot or line-intersect transect estimators (Woodall and Monleon 2008). Biomass of DD is then often estimated by multiplying volume by an estimate of density specific to a dead wood piece's individual attributes (e.g., species and stage of decay). Density reduction factors may be defined as the ratio of the decayed density (current mass/volume) of a piece of dead wood compared to its undecayed density (initial live tree mass/volume; Miles and Smith 2009). The development of DD species- and decay class-specific density and decay reduction values for the FIA program has offered the promise of substantially reducing the uncertainty associated with DD mass/carbon population estimates resulting from large-scale inventories (Harmon et al. 2008). Unfortunately, there are very few decay class- or species-

The Authors

MARK E. HARMON is a Richardson Chair and professor in forest science with the Department of Forest Science, Oregon State University, Corvallis, OR.

CHRISTOPHER W. WOODALL is research forester with the U.S. Forest Service, Northern Research Station's Forest Inventory and Analysis unit, St, Paul MN.

BECKY FASTH is a senior research assistant with the Department of Forest Science, Oregon State University, Corvallis, OR.

JAY SEXTON is a senior research assistant with the Department of Forest Science, Oregon State University, Corvallis, OR.

MISHA YATKOV is a Ph.D. candidate with the Department of Forest Science, Oregon State University, Corvallis, OR.

specific estimates of density or decay reduction factors for SD trees. The lack of these estimates is likely due to the danger in felling snags during sampling and the historical lack of emphasis on SD biomass/carbon estimates during traditional forest inventories focused on estimating live tree growing stock volume on timberlands.

Several assumptions regarding wood density influence biomass estimates of SD trees. In the case of the FIA program, it is currently assumed that the density of SD trees is the same as that of live trees. While this seems unlikely, in some situations (e.g., extremely slow decomposition in arid environments) this assumption may be accurate. Alternately, (e.g., Smithwick et al. 2002) the density of SD trees for a given decay class may be assumed to be similar to that of DD wood. While this would seem to be a more realistic assumption, it has yet to be tested across a wide range of tree species and environments. The uncertainty associated with SD tree density is likely to have major impacts on biomass, carbon, and fuel estimates, but without knowledge of how SD tree wood density changes through its decay process, the effect of this uncertainty cannot be quantified.

OBJECTIVES

Given that deadwood inventories are rapidly becoming a common component of forest resource inventories around the world, there is a need to refine the constants used in biomass estimation procedures for both SD and DD. Our objective was to determine SD species- and decay-class specific density and density reduction factors for forest tree species in the United States by linking empirical SD data from a subset of study species with that of DD of those same species to develop constants that can then be applied to other SD species. The broad concept was to use SD:DD density relationships to utilize currently available DD density information to provide an initial approximation of SD density attributes for forest tree species in the United States.

Harmon et al. (2008) developed a set of density reduction factors, including estimates of uncertainty, for DD and FWD based on a thorough literature review and unpublished data. Our approach for this study was to sample SD and DD for 19 tree species in temperate forests of the northern hemisphere. As the decay classification system for both SD and DD trees are qualitative (i.e., visual assessments of wood condition and structure) and separate, the two classification systems need to be linked in order to propose SD to DD wood density relationships by decay class. First, indicators of decay were evaluated for SD and DD decay classes to ensure decay classification system compatibility. Second, the density of SD and DD was compared for the same decay classes and species. These ratios were then used to estimate SD density and density reduction factors for species that have not been sampled across the United States. Finally, to initially assess the impact of wood density decay reduction factors on SD population estimates, a SD tree inventory in Minnesota was used to calculate state SD biomass using no decay reduction factor and using factors developed in previous objectives.

MATERIALS AND METHODS

Study Areas

To ensure our study acquired a robust estimate of SD to DD, we sampled five study sites in the United States and four in Russia representing a range of species and climates in North America and Russia (Table 1). Given the similarity between the temperate and boreal forests of North America and Russia, it was felt that the additional statistical rigor resulting from the combination of data outweighed the loss of some regional specificity. As study objectives focus on tree species in the United States along with greater diversity among the study sites (e.g., species composition), study site locations in the United States were kept separate and identified by unique abbreviations in subsequent tables, while Russian study sites were pooled with the abbreviation "RUS." Site descriptions for Russian locations are based on information from Yatskov (2000).

Cascade Head Experimental Forest (CHE), Oregon

Cascade Head is located on the north-central coast of Oregon, 8 km north of Lincoln City. It lies entirely within the Hebo Ranger District of the Siuslaw National Forest. The site is in the Oregon Coast Range ecoregion and the forests are representative of the sitka spruce-western hemlock (*Picea sitchensis* (Bong.) Carrière -*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir (*Pseudotsuga*

Table 1.—Site name, location, and climate description for areas sampled

Site Name	Climate	Temperature
Cascade Head EF, Oregon (CHE)	Very wet	Moderate
Fraser EF, Colorado (FEF)	Dry	Cool
Chapel Hill, North Carolina (NCB)	Moderate	Moderate
Marcell EF, Minnesota (MEF)	Moderate	Cold
Kenai Peninsula, Alaska (AK)	Dry	Cold
St. Petersburg, Russia (RUS)	Moderate	Cool
Krasnoyarsk, Russia (RUS)	Dry	Cold
Irkutsk, Russia (RUS)	Dry	Cold
Khabarovsk, Russia (RUS)	Moderate	Cold

menziesii (Mirb.) Franco) zones of the region. Soils, derived primarily from tuffaceous siltstones, are fine textured, moderately well drained, and deep (up to 100+ cm). Because of the Pacific Ocean influence, CHE has a moderate and very wet climate. Mean annual temperature is 10 °C with minimal seasonal variation. Average yearly rainfall is 2489 mm, although fog drip through the forest canopy can add 500 mm or more precipitation a year (Greene and Acker 1999).

Fraser Experimental Forest (FEF), Colorado

Fraser Experimental Forest is located in the heart of the central Rocky Mountains, about 80 km from Denver. FEF includes subalpine forests typical of the area, with Engelmann spruce (*Picea engelmannii* Parry x Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) predominating at higher elevations, and lodgepole pine (*Pinus contorta* var. *latifolia* (Douglas ex Louden var. latifolia Engelm. ex S. Watson)) predominating at lower elevations and on drier upper slopes. Soils are generally derived from gneiss and schist and typically contain angular gravel and stone with very little silt or clay. These soils are very permeable and can store considerable water during snowmelt. Climate varies strongly with elevation. Overall, the climate is cool and dry with long, cold winters and short, cool summers. Mean annual temperature at the Fraser Forest headquarters is 0.5 °C and mean annual precipitation over the entire FEF is 737 mm. (Adams et al. 2004).

Chapel Hill (NCB), North Carolina

The study was conducted at the North Carolina Botanical Garden, a 242-ha tract of oak-hickory-pine forest in Chapel Hill, North Carolina. The area sampled in this project was dominated by mixed hardwoods including *Liriodendron tulipifera* L. on the moist lower slopes and mixed hardwoods with pine (*Pinus taeda* L. and *Pinus echinata* Mill.) on the dryer mid and upper slopes. It is an area defined by undulating topography, soils of poor to good quality, and a temperate climate. Soils of the study area include Wedowee sandy loam and Goldston slaty silt loam (Dunn 1977). The average annual temperature is 14.6 °C and the average annual precipitation is 1220 mm. Precipitation is uniformly distributed throughout the year. The elevation ranges from 103 to 150 m (Fasth et al., in press).

Marcell Experimental Forest (MEF), Minnesota

The Marcell Experimental Forest is an 890-ha tract of land in the Chippewa National Forest, located 40 km north of Grand Rapids, Minnesota. Vegetation in the upland topography includes jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) among other species. Mineral soils of the area are derived from glacial processes that occurred during and after the Wisconsinan glaciation. Soils are mainly loamy sands covered with fine sandy loam derived from eolean loess after glacial melt. The climate is subhumid continental, with wide and rapid diurnal and seasonal temperature fluctuations. The average annual temperature is 3 °C and the average annual precipitation is 785 mm with 75 percent occurring in the snow-free period (mid-April to early November) (Adams et al. 2004).

Kenai Peninsula (AK), Alaska

The study was conducted on the Kenai Peninsula of Alaska on Federal lands including the Chugach National Forest as well as on State owned lands. The maritime

climate of this study site supports temperate, coniferous rainforest. The drier and colder climate inland from the coastal mountains supports forests dominated by white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Miller) Britt), and paper birch (*Betula papyrifera* Marsh). A fertile hybrid between white spruce and Sitka spruce (Lutz spruce, *Picea x lutzii* Little) is a common tree in maritime and mountainous areas of the Kenai Peninsula. The topography of the study area varies from lowlands to foothills. The lowlands of the Kenai Peninsula are a glaciated surface with gentle relief and a mean elevation of approximately 300 m. Throughout most of this lowland glacial till of Wisconsin age is overlain by deep glacial lake and fluvial sediments and is mantled with loess. The Alaska Climate Research Center (ACRC) climatic summaries indicate the study area has a mean annual temperature of approximately 1.1 °C and annual precipitation of 630 mm (Harmon et al. 2005).

St. Petersburg, Russia (RUS)

The region of northwestern Russia has a cool maritime climate with cool wet summers and long cold winters. Major forest tree species include silver birch (*Betula pendula* Roth.), Norway spruce (*Picea abies* (L.) Karst.), and Eurasian aspen (*Populus tremula* L.). The mean annual temperature of July is 16.5 °C, while the mean temperature of January is 8.5 °C with an annual mean of 3.4 °C. The mean annual precipitation is 708 mm.

Krasnoyarsk, Russia (RUS)

This region of central Siberia has a moderately cold and continental climate. It belongs to the Angara province of the southern taiga and is dominated by Russian larch-Scots pine (*Larix siberica* Ledeb. and *Pinus sylvestris* L.) forests. The vegetation period lasts 126 days with a frost-free period of 110 days. The mean temperature of July is 16 °C, while the mean temperature of January is -25 °C, and the overall mean annual temperature is -3.2 °C. The mean annual precipitation is 361 mm.

Irkutsk, Russia (RUS)

This region of Eastern Siberia has sites located in the area of strictly continental climate with permafrost. Forests were primarily comprised of Scots pine (*Pinus sylvestris*). In mountainous areas Siberian larch (*Larix siberica*), Siberian white pine (*Pinus siberica* Ledeb.), and Siberian spruce (*Picea obovata* Ledeb.) were common, and were associated with small amounts of Siberian fir (*Abies siberica* Ledeb.). The mean temperature of July is 17 °C and mean temperature of January is -20 °C with an overall mean annual temperature of -0.6 °C and a mean annual precipitation of 216 mm.

Khabarovsk, Russia (RUS)

This region is part of the Far East and has a continental climate that promotes the growth of a wide range of plant species, including Korean white pine (*Pinus koraiensis* Sieb. et Zucc.), Dahurian larch (*Larix dahurica* Turcz.) spruce (*Picea obovata* and *Picea ajanensis* Fisch.), true fir (*Abies siberica*), and yellow birch (*Betula costata* Trautv.). The vegetation period lasts 174 days in lowlands and 158 days in mountainous areas. The mean temperature of July is 17 °C, while mean temperature of January is -24 °C, with an overall annual mean of -1.9 °C. The mean annual precipitation is 909 mm.

Linking SD and DD Decay Classifications through Indicators of Decay

To accurately estimate DD and SD population attributes such as biomass or carbon, the FIA program assigns each sampled DD and SD individual to a decay class. To facilitate linkage of DD and SD decay classes, indicators of decay were developed in this study that were assessed for each study dead wood piece. For both DD and SD, there were five decay classes that span a spectrum of decay from fresh mortality to nearly complete decay. Decay classes are largely qualitative based on the physical appearance and structural integrity of individual dead wood pieces (USDA 2007, Woundenberg et al. 2010). For SD trees the five decay classes were defined as:

Class 1: All limbs and branches are present; the top of the crown is still present; all bark remains; sapwood is intact, with minimal decay; heartwood is sound and hard.

Class 2: There are few limbs and no fine branches; the top may be broken; a variable amount of bark remains; sapwood is sloughing with advanced decay; heartwood is sound at base but beginning to decay in the outer part of the upper bole.

Class 3: Only limb stubs exist; the top is broken; a variable amount of bark remains; sapwood is sloughing; heartwood has advanced decay in upper bole and is beginning at the base.

Class 4: Few or no limb stubs remain; the top is broken; a variable amount of bark remains; sapwood is sloughing; heartwood has advanced decay at the base and is sloughing in the upper bole.

Class 5: No evidence of branches remains; the top is broken; <20 percent of the bark remains; sapwood is gone; heartwood is sloughing throughout.

For DD trees the five decay classes were defined as:

Class 1: Sound, freshly fallen, intact logs with no rot, no conks present indicating a lack of decay, original color of wood, no invading roots, fine twigs attached with tight bark.

Class 2: Sound log sapwood partly soft but can't be pulled apart by hand, original color of wood, no invading roots, many fine twigs are gone and remaining fine twigs have peeling bark.

Class 3: Heartwood is still sound with piece supporting its own weight, sapwood can be pulled apart by hand or is missing, wood color is reddish-brown or original color, roots may be invading sapwood, only branch stubs are remaining which cannot be pulled out of log.

Class 4: Heartwood is rotten with piece unable to support own weight, rotten portions of piece are soft and/or blocky in appearance, a metal pin can be pushed into heartwood, wood color is reddish or light brown, invading roots may be found throughout the log, branch stubs can be pulled out.

Class 5: There is no remaining structural integrity to the piece with a lack of circular shape as rot spreads out across ground, rotten texture is soft and can become powder when dry, wood color is red-brown to dark brown, invading roots are present throughout, branch stubs and pitch pockets have usually rotten down.

Based on decades of research into the ecological role of detritus in forest ecosystems, we hypothesized that the differences between SD and DD would be greatest for intermediate decay classes (i.e., 2 and 3). Given the lack of time in decay class 1, decay reductions are likely minimal for both SD and DD. For decay classes 4 and 5, which are based on structural strength, it is likely that SD and DD are similar given that structural strength of wood is highly dependent on density. We also hypothesized that the wood density of SD and DD would diverge more in dry climates than in humid ones due to moisture limitations in dry climates that inhibit SD decomposition. Since SD falls and becomes DD, the input of decayed SD-related wood might influence the overall density of DD. Since decay classes are largely based on exterior appearances, it is likely that SD in dry climates will be denser than DD for a given decay class because the exterior of SD will continue to degrade (e.g., bark loss, fragmentation of twigs, etc) whereas the interior will remain relatively sound. Conversely, in very wet environments, fragmentation of bark and cover of mosses and other bryophytes are likely to make the exterior of DD look decayed despite the slow rate of decomposition of DD in very wet environments. Based on these hypotheses, a variety of indicators of decay were visually assessed for both SD and DD in this study (Table 2). Similarities in indicators of decay among SD and DD pieces sampled in this study will suggest appropriate linkage between the SD and DD decay classification systems and subsequent development of SD decay reduction factors based on extensive DD woody decay information.

FIELD AND LABORATORY

Decay Classes and Indicators of Decay

At each study site we sampled SD and DD covering the full range of decomposition stages, which necessitated the felling of SD trees. To sample indicators of decay, selected SD or DD pieces were categorized into one of five decay classes based on visual characteristics linked to the degree of decomposition that was noted in the previous section: the presence of leaves, twigs, branches, percent bark cover on branches and bole, sloughing of wood, collapsing and spreading of DD or SD (indicating the transition from intact elliptical forms to degraded

Table 2.—Decay indicators used to determine decay classes for standing and downed dead trees

Code	Indicator question
Foliage	Is foliage present?
Twigs	Are twigs present?
Branches	Are branches present?
Bark_br	Is there bark present on the branches?
Bark_bole	Is there bark present on the bole?
Moss	Is there moss present?
Lichens	Are there lichens present?
Beetles	Is there evidence of beetle presence?
Woodborer	Is there evidence of woodborer presence?
Conks	Are there conks present?
Whiterot	Is there white rot present?
Brownrot	Is there brown rot present?
Casehard	Does the bole exhibit case hardening?
SW_friable	Is the sapwood crushable by hand?
HW_friable	Is the heartwood crushable by hand?
Ants	Is there evidence of ants present?
SW slough	Is the sapwood sloughing?
Collapse	Has the bole shape collapsed?
Scatter	Is the bole scattered in the ground?
Stub_move	Do the branch stubs move in the bole?

shapes), friability or crushability of wood, color of wood, and mobility of branch stubs (Triska and Cromack 1980, Graham and Cromack 1982, Sollins 1982, Harmon and Sexton 1996). In addition to visual and structural indicators of decay used by the FIA program, biological indicators (Table 2) of decomposition, such as moss cover, presence of fungal fruiting bodies, and the presence of insect galleries, were also noted. In addition, at most sites we sampled live trees to determine densities of undecayed wood and bark. Dimensions recorded for each tree sampled included length, base and top diameters, and current d.b.h. The decay classes of both SD and DD used in this study align with the same decay classes used by the FIA program. Please refer to USDA (2010), Woodall et al. (2010), and Woudenberg et al. (2010) for details regarding the SD and DD decay classification systems used by FIA.

Wood Density and Density Reduction Factors

To measure wood density of SD and DD, samples were divided into four sections of similar length. Short pieces (e.g., in more advanced decay classes) were divided into two or three sections. For each section, end diameters and length were recorded. From the end of each section, a disk (a cross section 5 to 10 cm thick) was cut with a chainsaw to determine wood and bark density. To determine disk volume, for each cross-section disk we recorded the outermost diameter, outer wood diameter, mean longitudinal thickness, circumference covered by bark, radial thickness of bark, and mean radial depth of decay. Bark was separated from wood and the total wet weight of each tissue was determined. Lengths of bark and wedge-shaped wood subsamples of ~100 g taken from each disk using a hammer and chisel were weighed. Dry weights were recorded after oven drying at 55 °C to a constant weight (within 0.01 g). For disks that had not been dried and weighed, dry weights of wood and bark were calculated from total wet weights of these tissues and the ratio of dry-to-wet weight determined from subsamples. The density of the bark and wood for each disk was calculated as the ratio of its dry weight to undecayed volume (g/cm^3). Mean bark density and mean wood density for each tree were calculated by averaging the density of all the cross-section values of each tissue for each tree. Recorded values of percent bark cover for the whole tree and bark circumferential length for each disk were used to determine the proportion of total tree volume that was bark. Total density per tree was calculated as the summation of each tissue density multiplied by the proportion of total tree volume applicable to that tissue. An average density for each tree species, decay class, and position (i.e., SD or DD) was calculated using total tree density. Trees were also categorized as either hardwood (i.e., angiosperm) or softwood (i.e., gymnosperm) and total density per tree was averaged across each category for each decay class and position. Finally, an average of total density was calculated for all trees by decay class and position.

The density reduction factor was calculated as the ratio of the average current density to average undecayed density for each species, category, or combination and by each decay class and position (i.e., SD versus DD) to indicate the relative rate that tree density declined for each scenario.

Statistical Analysis

We used analysis of variance (ANOVA) to test how the dependent variable density reduction factor varied by the independent variables taxa (i.e., species or hardwood/softwood), decay class, and position. The following model was fit:

$$Y_{khij} = m + \alpha_k + \beta_h + d_i + a_j + da_{ij} + \varepsilon_{khij}$$

where:

m is the overall mean value of Y_{khij}, the average density reduction factor of the jth decay class in the ith position in region k and stand h

α_k is the random effect of the region k that was sampled, that adds variability to the value of Y, k=region name, $\alpha_{k\,h} \sim N(0, \sigma^2_b)$, α_k and $\alpha_{k'}$ are independent

β_h is the random effect of stand h that was sampled, that adds variability to the value of Y, h=stand name, $\beta_h \sim N(0, \sigma^2_b)$, β_h and $\beta_{h'}$ are independent

d_i is the effect of the ith level of the independent variable position, i=SD or DD

a_j is the effect of the jth level of the independent variable decay, j= 1, 2, 3, 4

da_{ij} is the interaction of position and decay

ε_{khij} is the random error term that adds variability to the value of Y, $\varepsilon_{khij} \sim N(0, \sigma^2)$ and ε_{khij} and $\varepsilon_{khi'j'}$ are independent.

When comparing softwoods and hardwoods, species was added as an additional random variable in the model. In the case of all species combined, the variables species and type (softwood or hardwood) were added as additional random variables. Residuals from the models were fairly symmetric and there was no indication of increasing variance with decreasing mean. Therefore, assumptions of normality and constant variance of residuals appeared to be adequately met. Through ANOVA testing, three results were postulated: 1) No significant difference between DD and SD density reduction factors by decay classes. This would indicate that decay occurred with similar patterns for dead wood in standing or lying positions; 2) The main effects of position and decay class would both be significant when the density reduction diverged early in the decomposition process (i.e., between class 0 and 1). This might suggest that one position started with a lower density than the other; 3) A significant interaction of position and decay class. This would indicate that one position was decaying to a lesser extent than the other and that density reduction factors were diverging. We tested these hypotheses at three separate levels: individual species, softwoods versus hardwoods, and for all species combined.

To examine why DD and SD might have different densities and density reduction factors, we compared indicators of decay (Table 2) between the two positions. We computed the relative frequency that indicators were present for two positions and the three taxonomic levels described above to examine which characteristics might be associated with differences in dependent variables.

All statistical tests based on the model outlined above were performed by the MIXED procedure of SAS (SAS Institute Inc.) using the LSMEANS statement which computes least squares means of fixed effects and corresponding *t* and *F* tests. Statistical tests were significant if $0.05 > P > 0.01$ and highly significant if $P < \text{or} = 0.01$. We emphasize that a minimal amount of replication was conducted within species, study sites, and decay classes. Replication was limited by the difficulty in finding study sites with a full representation of DD and SD decay classes. Furthermore, the felling of SD trees is extremely hazardous to the sawyer. We have expressed the high levels of uncertainty in Appendix C. The results presented in this study should be considered preliminary to guide future research and promote refined SD population estimation (i.e., use of decay reduction factors in biomass/carbon estimates).

Development of Standing Dead (SD) Databases

We used the findings of the current study to estimate decayed density and the density reduction factors of SD for tree species inventoried by the FIA program. For the species that we sampled, we used the observed densities and density reduction factors. For the species that we did not sample, we calculated decayed density and density reduction factors using ratios of the species we sampled and the estimated values for DD from Harmon et al. (2008). Specifically, for decay classes 1 to 3 we multiplied the SD to DD ratio for either hardwoods or softwoods (depending on the species) by the DD density or density reduction factor. For decay class 4, there were few species sampled. We therefore used the average SD to DD ratio of all species sampled. For decay class 5, as no species were sampled given the scarcity of these trees, this study suggests future research or assuming decay class 4 wood density results can be extrapolated to decay class 5.

To provide an estimate of uncertainty, we used one of the following methods:

A. Species that had been sampled for SD density. We used standard error of the observed values of decayed density or the density reduction factor.

B. Species lacking sampling to determine decayed SD density. The uncertainty (U) in the decayed SD density for this set of species was estimated by:

$$U_{\text{Decayed SD}} = \sqrt{(\text{Den}_{DD}^2)(U_{DD}^2) + (R^2)(U_R^2)}$$

where U_{DD} is the uncertainty in DD (Harmon et al. 2008), Den_{DD} is the mean DD density, and U_R is the uncertainty in R, the mean SD to DD density ratio. This formula accounts for the fact that uncertainty for decayed SD density is a function of two uncertainties. Our formula assumed no correlation between the uncertainties. Uncertainty was estimated for each decay class of SD. For decay classes 1 to 3 we used R values associated with either hardwoods or softwoods and applied them to appropriate taxa. For decay class 4 there were few observations, so we used values for all the taxa sampled.

A similar uncertainty estimate was made for density reduction factors using the average density reduction factor and associated uncertainty for DD.

RESULTS

Decay Indicators

All Species

The relative frequency of decay indicators (Table 2) as DD and SD decomposed was surprisingly similar (Figure 1). In terms of physical indicators (presence of parts, shape, friability) prior to reaching decay class 4, DD and SD were quite comparable and go through a similar progression from one decay class to the next. Decay class 4 DD and SD differed in terms of structural integrity indicators. This is a logical result as SD that lacks physical integrity tends to fall and form DD. The nearly entire lack of bark in decay class 4 SD, as compared to DD, is related to vertical orientation, as even loose bark can remain on the surface of DD. Across all species and study sites, the means of SD bark cover (percent of piece covered by bark) were 91.62, 65.55, 38.91, and 21.11 for decay classes 1 through 4, respectively.

In terms of biological indicators (presence of moss, lichens, insects, and fungi), the major difference between SD and DD appeared to be the abundance of moss. DD tended to have higher presence of moss than SD, which would be consistent with the wetter microclimate associated with DD versus SD. Conversely, lichens were slightly more abundant on SD than DD, which is consistent with a drier microclimate associated more with SD than DD. DD also had a greater tendency to support fungal fruiting bodies, whereas SD had a greater tendency to support wood borers. The former may indicate a more favorable decomposition environment; the latter may be an artifact related to greater moss cover and decay state in DD hiding evidence of wood borers. For further evaluation of these moss/lichen results we suggest consulting the abundance of literature regarding lichen substrate preferences.

We observed little bark cover in both class 2 and 3 SD for some species, making the characteristic less useful as an indicator than for DD. Two characteristics proved

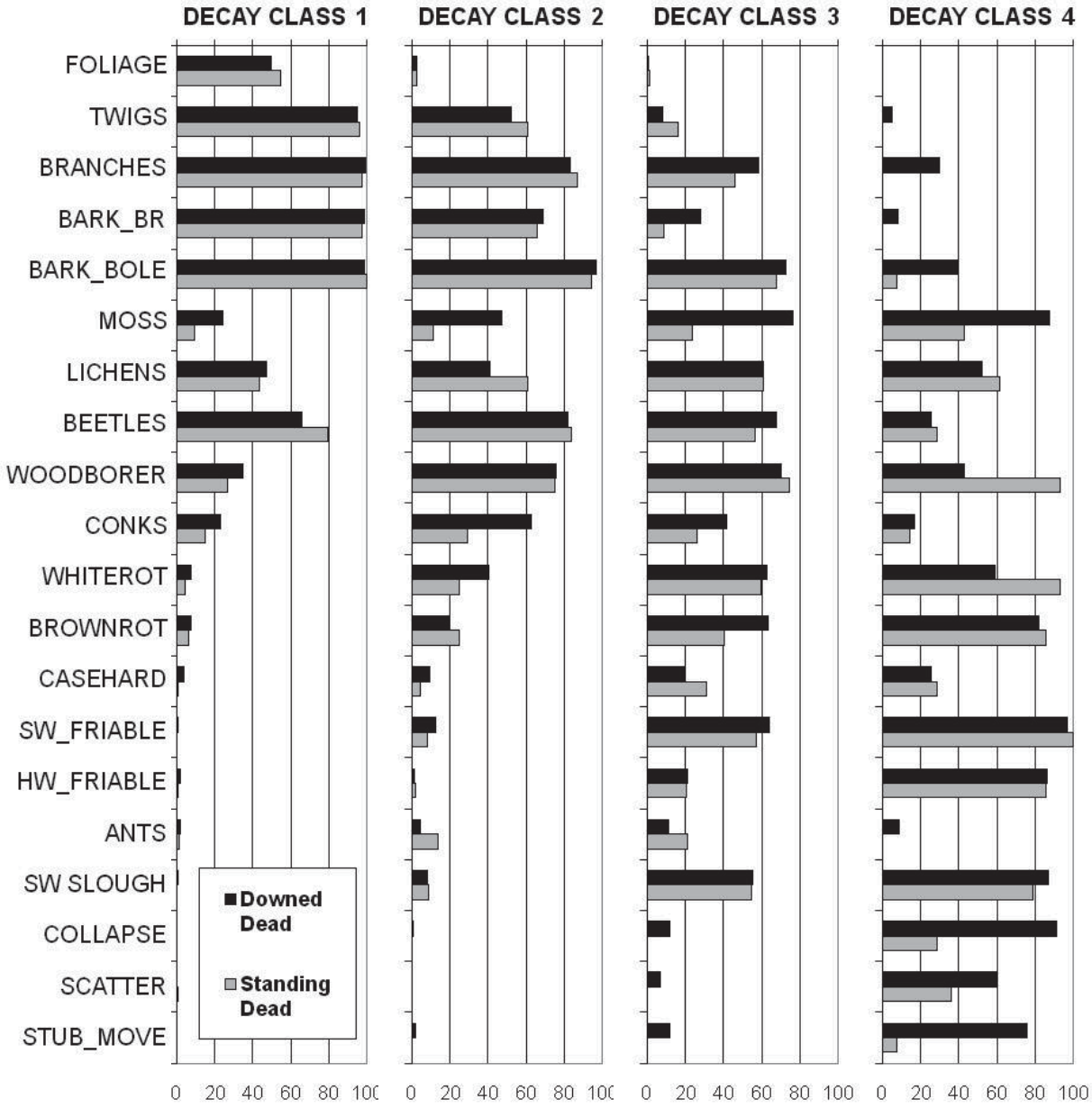


Figure 1.—Percent frequency of abundance for physical indicators of decay class for standing dead and downed dead trees

useful in distinguishing these two decay classes when SD had little bark cover. First, decay class 3 SD tended to have more lichens than decay class 2 SD. This is likely related to the older surface having more time to accumulate lichens. Second, the wood of decay class 3 SD tended to take on what might be described as a "ropey" texture. This is caused by a weakening of the outer wood layers causing cracks that look similar to the strands in a rope often associated with white-rot fungus. Findings by Aakala et al. (2008) indicate that the surface appearance of standing dead trees can remain static for long periods of time, thus the presence/absence of surface biological indicators may not fully indicate internal decay dynamics. Barring destructive sampling, standard forest inventory field crew must continue to rely on qualitative SD appearance to determine decay classification.

Hardwoods versus Softwoods

While the overall relationship between external characteristics and decay classes were similar for hardwoods and softwoods, there were some notable differences (Figure 2). In terms of physical indicators,

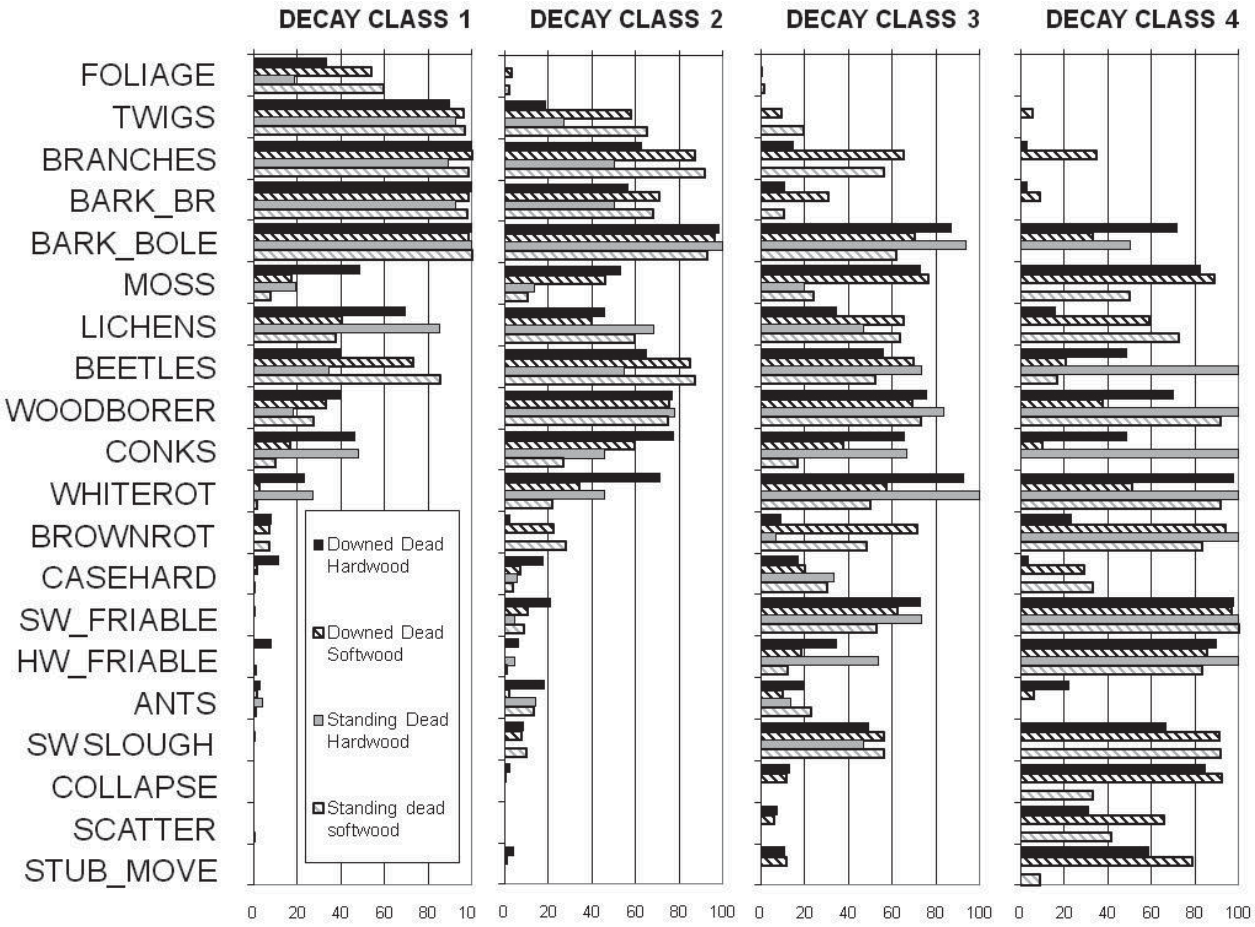


Figure 2.—Percent frequency of abundance for physical indicators of decay class for hardwood and softwood standing and downed dead trees

hardwoods appeared to lose twigs and branches to a higher degree than softwoods as decay class increased. Conversely, softwoods lost bark on the bole to a higher degree than hardwoods, although this was likely related to the presence of birch (*Betula* sp.), a genus well known for bark retention. For the biological indicators, hardwoods were more likely to have white-rot fungus, whereas softwoods were more likely to have brown-rot fungus, at least in decay classes 2 and 3. In decay class 1, hardwood SD were more likely to have lichens and mosses present than softwoods, but this likely stems from the difference of these tree taxa to support epiphytes in general.

Overall, indicators of decay were not evaluated in this study as an in-depth discourse on SD and DD decay dynamics and ecology, rather as a qualitative means to assure differentiation between decay classes and alignment with FIA sampling protocols. Results indicated adequate decay class differentiation, linkage between SD and DD decay classification systems, and FIA sampling protocol alignment allowing subsequent development of wood density estimates for SD tree species in U.S. forests based on relatively extensive DD wood density information.

Wood Density

As expected, SD wood density declined with decay class (Appendix A). The initial, undecayed tree densities for the 19 species studied ranged from 0.31 to 0.54 g/cm^3 (Table 3). The overall mean initial density was 0.39 g/cm^3. Decay class 3, the most advanced decay class common to SD and DD, had densities that ranged from 0.16 to 0.34 g/cm^3 for DD and 0.21 to 0.46 g/cm^3 for SD. Decay class 3 density for all species of DD averaged 0.26 g/cm^3 and averaged 0.35 g/cm^3 for SD indicating that SD contain less decay than logs (Table 4). This is

Table 3.—Undecayed wood density by tree species code, scientific name, and location of sample collection (U.S. study site or general Russian location)

Code	Scientific name	Location	Undecayed Density (g/cm^3)
PILU	*Picea x lutzii*	AK	0.36
PICO	*Pinus contorta*	FEF	0.40
PIBA2	*Pinus banksiana*	MEF	0.42
POTR	*Populus tremuloides*	MEF	0.39
LITU	*Liriodendron tulipifera*	NCB	0.41
PINE	*Pinus species*	NCB	0.49
TSHE	*Tsuga heterophylla*	CHE	0.44
ABSI	*Abies siberica*	RUS	0.31
BECO	*Betula costata*	RUS	0.54
BEPE	*Betula pendula*	RUS	0.48
LADA	*Larix daurica*	RUS	0.46
LASI	*Larix sibirica*	RUS	0.49
PIAB	*Picea abies*	RUS	0.37
PIAJ	*Picea ajanensis*	RUS	0.36
PIOB	*Picea obovata*	RUS	0.38
PIKO	*Pinus koraiensis*	RUS	0.35
PISI2	*Pinus sibirica*	RUS	0.34
PISY	*Pinus sylvestris*	RUS	0.38
POTR2	*Populus tremula*	RUS	0.35

Table 4.—Average density (g/cm^3) for standing dead (SD) to downed dead (DD) trees and associated ratio (SD/DD average density) for all species and sites combined by decay class

Decay class	SD (g/cm^3)	n	DD (g/cm^3)	n	SD/DD Ratio
1	0.40 (0.00)	175	0.40 (0.00)	185	1.00
2	0.38 (0.00)	189	0.33 (0.00)	292	1.15
3	0.35 (0.01)	78	0.26 (0.00)	391	1.35
4	0.25 (0.03)	14	0.15 (0.00)	246	1.67
5			0.11 (0.00)	174	

Note: Values are means with standard errors in parentheses. “n” is the number of SD or DD.

consistent with the notion that SD must retain some sound wood to remain upright. Aakala’s (2010) study in *Picea abies* forests in northern Europe found a range of SD decayed density ranging from 0.14 to 0.47 g/cm^3.

Hardwoods tended to have slightly higher initial density than softwoods, but the opposite was true after extensive decay (Table 5). For example, the mean initial, undecayed density for hardwoods and softwoods was 0.40 and 0.38 g/cm^3, respectively. However, decay class 3 hardwood DD and SD had mean densities of 0.23 and 0.24 g/cm^3, whereas softwood DD and SD had mean densities of 0.27 and 0.38 g/cm^3, respectively.

Density Reduction Factors

Individual species

Density reduction factors for decay class 3 ranged from 0.34 to 0.80 and from 0.44 to 1.11 for DD and SD, respectively (Appendix B). Statistical analysis showed five species with highly significant interactions and two with significant interactions between position and decay class (*P*-values: *Larix sibirica* 0.00; *Pinus contorta* 0.00; *Picea lutzii* 0.00; *Pinus* species 0.01; *Pinus sibirica* 0.01; *Pinus banksiana* 0.05; *Pinus koraiensis* 0.05). Of these seven species, four were in the genus *Pinus*. This interaction indicated that SD for these species retained a higher density than DD and that these differences increased as decay proceeded. Aakala (2010) found similar results in *Picea abies* forests of northern Europe, with the wood density of SD significantly higher than DD. Furthermore, in our study three species (two hardwood and one softwood) had highly significant decay class and position main effects, but no significant interaction between the two factors. This result may indicate that early in the decay process, DD and SD diverge, with DD undergoing an initial rapid period of decomposition and SD subject to a lag. Four species (three hardwoods and one softwood) showed only decay class as a highly significant factor in density reduction (*P*-values: *Betula pendula* 0.00; *Tsuga heterophylla* 0.00; *Populus tremula* 0.00; *Populus tremuloides* 0.00). This would indicate that decay progresses similarly in SD and DD for these species. Two species showed only position as a highly significant factor in density reduction, but this was likely an artifact related to the few decay classes sampled for these species.

Hardwoods versus softwoods

Compared to hardwoods, softwoods, on average, are more likely to have a greater divergence in SD and DD decay reduction factors as decay progresses (Table 6). For example, the mean density reduction factors for decay class 3 hardwood DD and SD were 0.51 and 0.54,

Table 5.—Average density (g/cm^3) for standing dead (SD) and downed dead (DD) trees and associated ratio (SD/DD average density) by hardwood/softwood and decay class

Type	Decay class	SD (g/cm^3)	n	DD (g/cm^3)	n	Ratio SD/DD
Hardwood	1	0.46 (0.01)	37	0.43 (0.01)	51	1.07
	2	0.36 (0.01)	31	0.33 (0.01)	58	1.09
	3	0.24 (0.02)	14	0.23 (0.01)	60	1.04
	4	0.20 (0.03)	2	0.13 (0.01)	55	1.54
	5			0.11 (0.01)	31	
Softwood	1	0.38 (0.00)	138	0.38 (0.00)	134	1.00
	2	0.39 (0.00)	158	0.34 (0.00)	234	1.15
	3	0.38 (0.01)	64	0.27 (0.00)	331	1.41
	4	0.26 (0.03)	12	0.15 (0.00)	191	1.73
	5			0.11 (0.00)	143	

Note: Values are means with standard errors in parentheses. “n” is the number of SD or DD.

Table 6.—Average density reduction factor (decayed density/undecayed density) for standing dead (SD) and downed dead (DD) trees and associated ratio (SD/DD density reduction factor) by hardwood/softwood and decay class

Type	Decay class	SD	n	DD	n	Ratio SD/DD
Hardwood	1	0.99 (0.01)	37	0.95 (0.01)	51	1.04
	2	0.80 (0.02)	31	0.74 (0.02)	58	1.08
	3	0.54 (0.04)	14	0.51 (0.03)	60	1.06
	4	0.43 (0.05)	2	0.29 (0.02)	55	1.48
	5			0.22 (0.02)	31	
Softwood	1	0.97 (0.01)	138	0.93 (0.01)	134	1.04
	2	1.00 (0.01)	158	0.87 (0.01)	234	1.15
	3	0.92 (0.03)	64	0.70 (0.01)	331	1.33
	4	0.55 (0.06)	12	0.40 (0.01)	191	1.38
	5			0.29 (0.01)	143	

Note: Values are means with standard errors in parentheses. “n” is the number of SD or DD.

respectively. In contrast, the mean density reduction factors for decay class 3 softwood DD and SD were 0.70 and 0.92, respectively. For softwood species collectively, there was a highly significant interaction between position and decay class effects. For hardwood species, decay class was a highly significant factor in density reduction. This indicates that DD density factors could be substituted for SD ones in hardwoods, but not for softwoods.

All species combined

The density reduction factors for all decay class 3 DD and SD was 0.67 and 0.86, respectively (Table 7). There was a highly significant interaction between position and decay class in the reduction factor, which may be due to softwood species being over represented in the data set.

Standing Dead Databases

Of 260 species considered by the FIA inventory, eight (3 percent) have had some SD decay classes sampled. For sampled species, the uncertainty of SD density was approximately 3 to 14 percent of the mean estimate. In contrast for species in which SD density had to be estimated from the DD database produced by Harmon et al. (2008), the uncertainty is approximately 20 to 100

Table 7.—Average density reduction factor for standing dead (SD) and downed dead (DD) trees and associated ratio (SD/DD density reduction factor) for all sites/ species combined by decay class

Decay class	SD	n	DD	n	Ratio SD/ DD
1	0.97 (0.01)	175	0.94 (0.01)	185	1.03
2	0.97 (0.01)	189	0.84 (0.01)	292	1.15
3	0.86 (0.03)	78	0.67 (0.01)	391	1.28
4	0.53 (0.06)	14	0.38 (0.01)	246	1.39
5			0.28 (0.01)	174	

Note: Values are means with standard errors in parentheses. "n" is the number of SD or DD.

percent of the mean estimate, the latter for decay class 4 SD. This indicates that actual sampling of SD density could reduce the uncertainties with this material at least an order of magnitude.

Implications of Density Reduction on Population Estimates

The implications of assumptions of SD density can be potentially profound in terms of biomass estimates. Using FIA's forest inventory of the state of Minnesota (2005-2009), we explored the impact of three plausible scenarios for estimating total SD biomass (i.e., SD wood density assumptions): 1) SD wood density equals live tree wood density; 2) SD and DD wood density are equal; and 3) SD wood density based on this study's newly created SD density reduction factors. To convert that volumetric estimate to one of biomass, the three SD wood density assumptions were evaluated. Assuming that SD wood density was equal to live trees gives a total SD biomass estimate of 32.98 million Mg. By assuming that SD and DD wood density are equal, the estimated biomass was 24.38 million Mg, or 26 percent less. Using the new estimates of SD wood density provided an estimated biomass of 27.52 million Mg or 16.5 percent less than the assumption of undecayed density.

DISCUSSION

SD inhabit a very different environment than DD, with the former usually being drier. Given that the response of decomposition to moisture shows an optimum range (i.e., woody tissues can be too dry or too wet to decompose readily), the position supporting the fastest decomposition can change with macroclimate (Harmon 2009). This might lead to consistent differences in the density of SD versus DD. In very humid environments, DD and SD both may retain moisture and hence the density of SD and DD might remain similar. This may explain our results from Cascade Head, the wettest site examined. In very dry environments SD decay may be limited relative to that of DD and that could lead to an increasing difference as decay class increases. Specific to sites in this study, but possibly not pertinent to all forest conditions across the United States, softwoods tended to grow in drier climates and microsites than hardwoods, which may explain why many softwoods exhibited an increasing difference in density as decay classes increased. In environments with intermediate moisture, SD may be slightly drier than DD. This could lead to a relatively short lag in decomposition that would result in a constant difference between decay classes in terms of density. While our observations are consistent with these hypotheses, other factors could be causing the patterns observed and more SD:DD comparisons in a wider range of environments would be helpful in determining the mechanisms explaining these phenomena. Differences in the density of SD versus DD may also be related to the physical limits of strength of woody tissues. That is, SD have to be fully self supporting, and once their strength decreases past a threshold they will collapse to form DD. In contrast, DD with minimal structural strength can collapse, but remain as DD. This may lead to an apparent abundance of higher wood density SD trees as less sound SD fall to become DD. However, SD do not necessarily have to decompose throughout to fall. For example, SD in dry environments fall after root systems decompose, adding relatively sound wood to the DD pool. When this occurs the density of DD might increase due to this input of relatively sound SD wood. Therefore, the difference in wood density between SD and DD are likely to be controlled by a number of interacting factors. Care should be taken not to infer rates of decay with assigned decay classes. Differences in wood density were quantitively determined between SD and DD qualitative decay classes in this study. Rates of decay are only inferred as initial hypotheses for future research.

There is an emerging abundance of research discussing the dynamics of SD and DD decay and subsequent

effects on biomass/residence times (Aakala et al. 2008, Aakala 2010, Kruys et al. 2002, Vanderwel et al. 2006, Zielonka 2006,). Moving beyond initial characterizations of SD and DD decay dynamics on intensively monitored study sites towards estimates of SD wood density by decay class for all forest tree species in the United States is a tremendous change in study scope. However, the immediate need to develop and document SD decay reduction factors for most forest tree species in the United States to meet mandated carbon stock reports requires a timely assimilation of the best available science. Given the lack of information on SD decayed wood density for hundreds of tree species in the United States, several approaches were considered. First, SD tree density can be assumed to be similar to undecayed tree density. For some environments in which decomposition is very slow, this might be acceptable. However, in our analysis we did not find a single species in which density did not decline with decay class. Second, SD tree density could be assumed equal to that of DD tree density. This would be appropriate for 6 of the 19 species we examined. The most common situation in our study (13 of 19 species) was for either position or a position X decay class interaction to be significant.

To create the needed SD decay reduction factors for all tree species in the United States, decay classes in this study were aligned with those used by FIA using this study's indicators of decay. FIA's SD decay classes 1 and 2 were quite similar to the classes 1 and 2 assessed in this study. Given the more highly decayed nature of SD decay classes 3 and 4, FIA's SD decay classes 3 and 4 seem to span the characteristics of decay class 3 SD trees with some overlap into decay class 4. The FIA SD decay class 5 would seem to be similar to this study's SD decay class 4. Based on this finding, it is suggested that the decay reductions for SD decay class 4 be used as an approximation for SD decay class 5 until such time that empirical information refines SD decay class 5 attributes or a model is suggested to extrapolate decay class 4 attributes to decay class 5 pieces. Furthermore, given the potential safety hazard of felling decay class 5 SD trees, this assumption may be the most practical. In general, these are gross approximations and, given the fact that the FIA system is based on Douglas-fir with unspecified modifications for other species, it would be logical to develop a SD decay class system based on a wider range of species better aligned with the DD system.

While it is important to eventually determine density and density reduction factors for SD and DD of the major species encountered in inventories, in the short-term one is forced to make assumptions when species or positions have not been sampled. Whether considering individual species, hardwoods and softwoods, or all samples combined, the ranges of density reduction factors for SD were consistently higher compared to DD. This indicates generally less reduction in density as decay progresses in SD than DD. Softwood species tended to exhibit this pattern more strongly than hardwood species, sometimes even increasing in density. There were exceptions to this pattern in the statistical analysis (insignificant effect of position), but inspection of the charted data indicated that these cases had samples for only decay classes 1 and 2, were hardwood species, or were located in a warm and wet climate. The assumption with the strongest support at this time is that softwoods tend to have a greater divergence in SD and DD density reduction factors than hardwoods. However, additional sampling of species, hardwoods in particular, is required to confirm if this is actually the case.

Irrespective of the findings of this study, SD wood density at some point in its decay process will become substantially less than that of living trees. The selection of density reduction factors can have a profound effect on resulting population estimates (e.g., SD carbon in a state). This study found substantial variation in SD biomass population estimates for Minnesota when using undecayed density versus reduced wood density values. The differences in estimates depend strongly on the dominance of hardwoods versus softwoods. When only softwood species were considered, the difference between the assumption of live tree wood density and the SD densities that we estimated was 2.5 percent. In contrast, when only hardwood species were considered the difference between these two methods was 22 percent. Therefore, the potential biases contained in current SD estimates are likely to vary substantially. This analysis is considered preliminary for illustrative purposes as structural reductions for decay were not incorporated into the estimation procedures.

CONCLUSIONS

To provide accurate, unbiased estimates of the biomass and carbon stocks of SD trees, it is necessary to have species- and decay class-specific estimates of either density or density reduction factors. Empirically sampling the wood density of SD by species and decay class across the forests of the United States is currently restricted by the inherent costs and felling hazards involved. As an approach to estimate preliminary SD wood density reduction factors, this study established relationships between SD and DD such that extensive DD woody density studies could be used to suggest SD wood density attributes. This study suggests a new set of SD decay specific density and density reduction factors for many tree species in the United States that may be used to refine FIA's SD population estimation procedures. Given the size of the uncertainty involved with the SD wood decay attributes proposed in this study, additional work to develop a multispecies SD decay class system and to better characterize differences between SD and DD trees is recommended.

ACKNOWLEDGMENTS

This work was funded by a joint venture agreement between the U.S. Forest Service Forest Inventory and Analysis and Oregon State University (09-JV-11242305-025).

Special thanks are extended to Shawn Fraver, Ph.D., and Brad Oberle, Ph.D., who provided abundant constructive criticism that improved the quality of this documentation.

The cooperation of numerous experimental forest staff at locations in the United States and Russia were critical to this study's success. In particular, Randy Kolka, Ph.D. and his staff at the Marcell Experimental Forest were especially helpful with facilitating the field work. We would also like to thank Peter White, Ph.D. of the North Carolina Botanical Garden for the use of facilities and his many students whose efforts made this project possible.

LITERATURE CITED

Aakala, T. 2010. **Coarse woody debris in late-successional *Picea abies* forests in northern Europe: Variability in quantities and models of decay class dynamics**. Forest Ecology and Management. 260: 770-779.

Aakala, T.; Kuuluvainen, T.; Gauthier, S.; DeGrandpre, L. 2008. **Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec**. Forest Ecology and Management. 255: 410-420.

Adams, M.B.; Loughry, L.; Plaugher, L., comps. 2004. **Experimental Forests and Ranges of the USDA Forest Service**. Gen. Tech. Rep. NE-321. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 178 p.

Dunn, J. 1977. **Soil survey of Orange County, NC**. Raleigh, NC: U.S. Department of Agriculture, Soil Conservation Service. 93 p.

Fasth, B.; Harmon, M.E.; Sexton, J.; White, P.S. 2011. In press. **Decomposition of fine woody debris in a deciduous forest in North Carolina**. Journal of the Torrey Botanical Society.

Franklin, J.F.; Shugart, H.H.; Harmon, M.E. 1987. **Tree death as an ecological process**. BioScience. 37(8): 550-556.

Graham, R.L.; Cromack, K. 1982. **Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park**. Canadian Journal of Forest Research. 12: 511-521.

Greene, S.; Acker, S. 1999. **Growth and Yield Permanent Plots at the Cascade Head Experimental Forest**. Available at http://andrewsforest.oregonstate.edu/pubs/webdocs/reports/permplot/psp3.cfm?topnav=55 (Accessed June 13, 2011).

Harmon, M.E. 2009. **Woody detritus mass and its contribution to carbon dynamics of old-growth forests: The temporal context**. In: Wirth, C.; Gleixner, G.; Heimann, M. eds. Old-growth forests: Function, fate and value. New York. Springer-Verlag Ecological Studies. 207: 159-189.

Harmon, M.E.; Sexton, J. 1996. **Guidelines for measurements of woody detritus in forest ecosystems**. US LTER Publication No. 20. Seattle, WA: U.S. LTER Network Office, University of Washington, College of Forest Resources, Seattle, WA. 73 p.

Harmon, M.E.; Fasth, B.; Yatskov, M.; Sexton, J. 2005. **The fate of beetle-killed spruce on the Kenai Peninsula: A preliminary report**. Gen. Tech. Rep. R10-TP-134. Anchorage, AK: U.S. Department of Agriculture, Forest Service State and Private Forestry. 23 p.

Harmon, M.E.; Woodall, C.W.; Fasth, B.; Sexton, J. 2008. **Woody detritus density and density reduction factors for tree species in the United States: a synthesis**. Gen. Tech. Rep. NRS-29. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 84 p.

Harmon, M.E.; Franklin, J.F.; Swanson, F.J.; Sollins, P.; Lattin, J.D.; Anderson, N.H.; Gregory, S.V.; Cline, S.P.; Aumen, N.G.; Sedell, J.R.; Lienkaemper, G.W.; Cromack, K. Jr.; Cummins, K.W. 1986. **The ecology of coarse woody debris in temperate ecosystems**. Recent Advances in Ecological Research. 15: 133-302.

Harmon, M. E.; Krankina, O.N.; Yatskov, M.; Matthews, E. 2001. **Predicting broad-scale carbon stores of woody detritus from plot-level data**. In: Lai, R.; Kimble, J.; Stewart, B.A.; Assessment methods for soil carbon, New York: CRC Press: 533-552.

Jonsell, M.; Weslien, J.; Ehnstrom, B. 1998. **Substrate requirements of red-listed saproxylic invertebrates in Sweden**. Biodiversity Conservation. 7: 749-764.

Kruys, N.; Fries, C.; Jonsson, B.G.; Lamas, T.; Stahl, G. 1999. **Wood inhabiting cryptograms on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests**. Canadian Journal of Forest Research. 29: 178-186.

Kruys, N.; Jonsson, B.G.; Stahl, G. 2002. **A stage-based matrix model for decay-class dynamics of woody debris**. Ecological Applications. 12: 773-781.

Lee, P. 1998. **Dynamics of snags in aspen-dominated midboreal forests**. Forest Ecology and Management. 105: 263-272.

Miles, P.D.; Smith, W.B. 2009. **Specific gravity and other properties of wood and bark for 156 tree species found in North America**. Res. Note. NRS-38. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 35 p.

Nilsson, S.G.; Hedin, J.; Niklasson, M. 2001. **Biodiversity and its assessment in boreal and nemoral forests**. Scandinavian Journal of Forest Research. 3(suppl): 10-26.

Smithwick, E.A.H.; Harmon, M.E.; Remillard, S.M.; Acker, S.A.; Franklin, J.F. 2002. **Potential upper bounds of carbon stores in forests of the Pacific Northwest**. Ecological Applications. 12: 1303-1317.

Sollins, P. 1982. **Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington**. Canadian Journal of Forest Research. 12: 18-28.

Triska, F.J.; Cromack,K. 1980. **The role of wood debris in forests and streams**. In: Waring, R.H., ed. Forests: fresh perspectives from ecosystem analysis. proceedings 40th biology colloquium. Corvallis, OR: Oregon State University Press: 171-190.

U.S. Department of Agriculture, Forest Service. 2007. **Forest Inventory and Analysis national core field guide, volume I: Field data collection procedures for phase 2 plots, version 4.0**. Washington, DC: U.S. Department of Agriculture Forest Service, Forest Inventory and Analysis, Washington, D.C.:

Available at: http://www.fia.fs.fed.us/library/ (Accessed December 2010).

Vanderwel, M.; Malcolm, J.R.; Smith, S.M. 2006. **An integrated model for snag and downed woody debris decay class transitions**. Forest Ecology and Management. 234: 48-59.

Woodall, C.W., Monleon, V.J. 2008. **Sampling protocol, estimation, and analysis procedures for the down woody materials indicator of the FIA program**. Gen. Tech. Rep. NRS-22. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 68 p.

Woodall, C.W.; Rondeux, J.; Verkerk, P.J.; Ståhl, G. 2009. **Estimating dead wood during national forest inventories: A review of inventory methodologies and suggestions for harmonization**. Environmental Management. 44: 624-631.

Woodall, C.W.; Conkling, B.L.; Amacher, M.C.; Coulston, J.W.; Jovan, S.; Perry, C.H.; Schulz, B.; Smith, G.C.; Will-Wolf, S. 2010. **The Forest Inventory and Analysis Database Version 4.0: Description and users manual for Phase 3**. Gen. Tech. Rep. NRS-61. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 180 p.

Woudenberg, S.W.; Conkling, B.L.; O'Connell, B.M.; LaPoint, E.B.; Turner, J.A.; Waddell, K.L. 2010. **The Forest Inventory and Analysis database: Database description and users manual version 4.0 for Phase 2**. Gen. Tech. Rep. RMRS-GTR- 245. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 339 p.

Yatskov, M.A. 2000. **A chronosequence of wood decomposition in the boreal forests of Russia**. Corvallis, OR: Oregon State University. 168 p. M.S. thesis.

Zielonka, T. 2006. **Quantity and decay stages of coarse woody debris in old-growth subalpine forests of western Carpathians, Poland**. Canadian Journal of Forest Research. 36: 2614-2622.

Appendix A

Average density (g/cm^3) for standing dead (SD) and downed dead (DD) trees and their associated ratio (SD/DD average density) for all study species

Species code	Decay class	SD (g/cm^3)	n	DD (g/cm^3)	n	Ratio SD/DD
ABSI	1	0.30 (0.02)	7			
ABSI	2	0.33 (0.02)	4	0.30 (0.02)	4	1.10
ABSI	3	0.32 ()	1	0.25 (0.03)	7	1.28
ABSI	4			0.20 (0.02)	10	
ABSI	5			0.17 (0.02)	7	
BECO	1	0.54 (0.01)	5	0.50 (0.01)	8	1.08
BECO	2			0.33 (0.04)	3	
BECO	3	0.24 (0.00)	2	0.18 (0.01)	8	1.33
BECO	4			0.12 (0.00)	2	
BECO	5			0.08 (0.00)	2	
BEPE	1	0.48 (0.01)	21	0.47 (0.01)	25	1.02
BEPE	2	0.39 (0.01)	19	0.37 (0.01)	28	1.05
BEPE	3	0.27 (0.03)	6	0.25 (0.02)	29	1.08
BEPE	4	0.20 (0.03)	2	0.15 (0.01)	41	1.33
BEPE	5			0.11 (0.01)	29	
LADA	1	0.44 (0.01)	2	0.46 (0.01)	13	0.96
LADA	2	0.46 (0.03)	8	0.39 (0.02)	13	1.18
LADA	3			0.33 (0.02)	14	
LADA	4			0.19 (0.01)	9	
LADA	5			0.11 (0.02)	4	
LASI	1	0.45 (0.01)	12	0.46 (0.01)	16	0.98
LASI	2	0.46 (0.02)	11	0.40 (0.01)	13	1.15
LASI	3	0.46 (0.01)	12	0.34 (0.02)	16	1.35
LASI	4			0.15 (0.01)	16	
LASI	5			0.11 (0.01)	16	
LITU	0			0.40 (0.00)	2	
LITU	1	0.37 (0.01)	6	0.31 (0.05)	3	1.19
LITU	2	0.35 (0.01)	5	0.28 (0.02)	9	1.25
LITU	3			0.20 (0.03)	5	
LITU	4			0.11 (0.02)	3	
PIAB	1	0.37 (0.03)	4	0.33 (0.01)	5	1.12
PIAB	2	0.37 (0.02)	5	0.27 (0.01)	6	1.37
PIAB	3			0.21 (0.02)	7	
PIAB	4			0.13 (0.05)	3	
PIAJ	1	0.38 (0.01)	8	0.34 (0.01)	11	1.12
PIAJ	2	0.39 (0.01)	3	0.32 (0.02)	11	1.22
PIAJ	3	0.36 ()	1	0.24 (0.02)	15	1.50
PIAJ	4			0.15 (0.02)	10	
PIAJ	5			0.12 (0.01)	6	
PIBA2	1	0.39 (0.02)	7	0.39 (0.01)	5	1.00
PIBA2	2	0.38 (0.01)	5	0.36 (0.01)	7	1.06
PIBA2	3	0.32 (0.04)	6	0.22 (0.02)	6	1.45
PIBA2	4			0.12 (0.01)	7	
PICO	1	0.39 (0.00)	27	0.37 (0.01)	18	1.05
PICO	2	0.41 (0.01)	8	0.36 (0.01)	15	1.14

continued

Appendix A.—continued

Species code	Decay class	SD (g/cm^3)	n	DD (g/cm^3)	n	Ratio SD/DD
PICO	3	0.40 (0.00)	7	0.32 (0.02)	15	1.25
PICO	4			0.17 (0.01)	7	
PICO	5			0.16 (0.01)	9	
PIKO	1	0.36 (0.00)	4	0.35 (0.01)	8	1.03
PIKO	2	0.34 (0.02)	5	0.32 (0.01)	10	1.06
PIKO	3	0.33 (0.02)	3	0.24 (0.01)	12	1.38
PIKO	4			0.16 (0.01)	4	
PIKO	5			0.13 (0.03)	2	
PILU	0			0.38 (0.01)	11	
PILU	1	0.38 (0.01)	21	0.36 (0.01)	7	1.06
PILU	2	0.38 (0.01)	69	0.34 (0.01)	92	1.12
PILU	3	0.40 (0.02)	17	0.26 (0.01)	153	1.54
PILU	4			0.13 (0.01)	58	
PILU	5			0.08 (0.00)	52	
PINE	1	0.37 (0.02)	5	0.37 (0.03)	5	1.00
PINE	2	0.36 (0.02)	4	0.27 (0.02)	9	1.33
PINE	3	0.35 (0.05)	5	0.19 (0.02)	8	1.84
PINE	4	0.35 (0.03)	6	0.19 (0.03)	7	1.84
PINE	5			0.22 ()	1	
PIOB	1	0.36 (0.02)	4	0.37 (0.01)	10	0.97
PIOB	2	0.39 (0.01)	4	0.33 (0.02)	10	1.18
PIOB	3			0.25 (0.01)	14	
PIOB	4			0.13 (0.01)	13	
PIOB	5			0.10 (0.01)	8	
PISI2	1	0.33 (0.01)	8	0.33 (0.01)	8	1.00
PISI2	2	0.34 (0.00)	7	0.30 (0.01)	8	1.13
PISI2	3	0.30 (0.00)	2	0.23 (0.02)	8	1.30
PISI2	4			0.14 (0.01)	8	
PISI2	5			0.10 (0.01)	8	
PISY	1	0.37 (0.01)	23	0.36 (0.01)	20	1.03
PISY	2	0.36 (0.01)	19	0.32 (0.01)	31	1.13
PISY	3	0.31 (0.03)	4	0.27 (0.01)	47	1.15
PISY	4			0.18 (0.01)	32	
PISY	5			0.12 (0.01)	29	
POTR	1	0.37 (0.02)	5	0.36 (0.01)	7	1.03
POTR	2	0.29 (0.02)	6	0.28 (0.02)	6	1.04
POTR	3	0.21 (0.03)	5	0.16 (0.01)	7	1.31
POTR	4			0.07 (0.01)	6	
POTR2	1			0.35 (0.01)	8	
POTR2	2	0.25 ()	1	0.29 (0.02)	12	0.86
POTR2	3	0.24 ()	1	0.25 (0.02)	11	0.96
POTR2	4			0.14 (0.01)	3	
TSHE	1	0.39 (0.01)	6	0.42 (0.01)	8	0.93
TSHE	2	0.36 (0.02)	6	0.35 (0.03)	5	1.03
TSHE	3	0.29 (0.02)	6	0.28 (0.02)	9	1.04
TSHE	4	0.17 (0.02)	6	0.17 (0.03)	7	1.00
TSHE	5			0.12 ()	1	

Note: Values are means with standard errors in parentheses. “n” is the number of SD or DD.

Appendix B

Average density reduction factor for standing dead (SD) and downed dead (DD) trees and their associated ratio (SD/DD decay reduction factor) for all study species

Species code	Decay class	SD	n	DD	n	Ratio SD/DD
ABSI	1	0.95 (0.06)	7			
ABSI	2	1.06 (0.06)	4	0.97 (0.05)	4	1.09
ABSI	3	1.03 ()	1	0.79 (0.08)	7	1.30
ABSI	4			0.66 (0.07)	10	
ABSI	5			0.55 (0.08)	7	
BECO	1	1.00 (0.01)	5	0.93 (0.01)	8	1.08
BECO	2			0.62 (0.07)	3	
BECO	3	0.44 (0.01)	2	0.34 (0.02)	8	1.29
BECO	4			0.22 (0.01)	2	
BECO	5			0.16 (0.00)	2	
BEPE	1	1.01 (0.01)	21	0.98 (0.02)	25	1.03
BEPE	2	0.81 (0.03)	19	0.77 (0.02)	28	1.05
BEPE	3	0.56 (0.07)	6	0.53 (0.04)	29	1.06
BEPE	4	0.43 (0.05)	2	0.30 (0.03)	41	1.43
BEPE	5			0.23 (0.02)	29	
LADA	1	0.88 (0.01)	2	0.90 (0.02)	13	0.98
LADA	2	0.92 (0.05)	8	0.77 (0.03)	13	1.19
LADA	3			0.66 (0.04)	14	
LADA	4			0.37 (0.03)	9	
LADA	5			0.22 (0.05)	4	
LASI	1	0.92 (0.02)	12	0.94 (0.03)	16	0.98
LASI	2	0.95 (0.03)	11	0.82 (0.02)	13	1.16
LASI	3	0.95 (0.02)	12	0.70 (0.04)	16	1.36
LASI	4			0.30 (0.02)	16	
LASI	5			0.22 (0.02)	16	
LITU	0			0.97 (0.00)	2	
LITU	1	0.91 (0.03)	6	0.76 (0.12)	3	1.20
LITU	2	0.85 (0.02)	5	0.68 (0.04)	9	1.25
LITU	3			0.48 (0.07)	5	
LITU	4			0.28 (0.05)	3	
PIAB	1	1.01 (0.09)	4	0.88 (0.03)	5	1.15
PIAB	2	1.01 (0.04)	5	0.73 (0.03)	6	1.38
PIAB	3			0.57 (0.05)	7	
PIAB	4			0.36 (0.12)	3	
PIAJ	1	1.07 (0.02)	8	0.97 (0.03)	11	1.10
PIAJ	2	1.11 (0.02)	3	0.92 (0.05)	11	1.21
PIAJ	3	1.03 ()	1	0.68 (0.06)	15	1.51
PIAJ	4			0.43 (0.05)	10	
PIAJ	5			0.34 (0.02)	6	
PIBA2	1	0.95 (0.04)	7	0.95 (0.03)	5	1.00
PIBA2	2	0.92 (0.03)	5	0.87 (0.03)	7	1.06
PIBA2	3	0.78 (0.09)	6	0.53 (0.04)	6	1.47
PIBA2	4			0.29 (0.03)	7	
PICO	1	0.98 (0.01)	27	0.95 (0.02)	18	1.03
PICO	2	1.04 (0.03)	8	0.92 (0.02)	15	1.13

continued

Appendix B.—continued

Species code	Decay class	SD	n	DD	n	Ratio SD/DD
PICO	3	1.02 (0.01)	7	0.80 (0.05)	15	1.28
PICO	4			0.43 (0.03)	7	
PICO	5			0.42 (0.02)	9	
PIKO	1	0.92 (0.01)	4	0.90 (0.02)	8	1.02
PIKO	2	0.88 (0.05)	5	0.81 (0.03)	10	1.09
PIKO	3	0.86 (0.05)	3	0.62 (0.03)	12	1.39
PIKO	4			0.41 (0.03)	4	
PIKO	5			0.34 (0.07)	2	
PILU	0			1.06 (0.03)	11	
PILU	1	1.06 (0.02)	21	1.01 (0.04)	7	1.05
PILU	2	1.06 (0.02)	69	0.93 (0.01)	92	1.14
PILU	3	1.11 (0.04)	17	0.73 (0.02)	153	1.52
PILU	4			0.37 (0.01)	58	
PILU	5			0.23 (0.01)	52	
PINE	1	0.76 (0.05)	5	0.75 (0.06)	5	1.01
PINE	2	0.74 (0.03)	4	0.55 (0.04)	9	1.35
PINE	3	0.72 (0.09)	5	0.40 (0.03)	8	1.80
PINE	4	0.72 (0.07)	6	0.39 (0.06)	7	1.85
PINE	5			0.46 ()	1	
PIOB	1	0.97 (0.04)	4	0.98 (0.03)	10	0.99
PIOB	2	1.03 (0.03)	4	0.87 (0.05)	10	1.18
PIOB	3			0.66 (0.03)	14	
PIOB	4			0.35 (0.03)	13	
PIOB	5			0.26 (0.02)	8	
PISI2	1	0.86 (0.02)	8	0.85 (0.02)	8	1.01
PISI2	2	0.89 (0.01)	7	0.77 (0.03)	8	1.16
PISI2	3	0.78 (0.01)	2	0.58 (0.04)	8	1.34
PISI2	4			0.36 (0.03)	8	
PISI2	5			0.27 (0.02)	8	
PISY	1	0.99 (0.02)	23	0.96 (0.02)	20	1.03
PISY	2	0.98 (0.02)	19	0.87 (0.02)	31	1.13
PISY	3	0.83 (0.08)	4	0.71 (0.02)	47	1.17
PISY	4			0.48 (0.04)	32	
PISY	5			0.33 (0.02)	29	
POTR	1	0.97 (0.04)	5	0.93 (0.03)	7	1.04
POTR	2	0.75 (0.05)	6	0.72 (0.04)	6	1.04
POTR	3	0.54 (0.07)	5	0.41 (0.03)	7	1.32
POTR	4			0.18 (0.01)	6	
POTR2	1			0.95 (0.02)	8	
POTR2	2	0.66 ()	1	0.78 (0.05)	12	0.85
POTR2	3	0.63 ()	1	0.66 (0.07)	11	0.95
POTR2	4			0.36 (0.03)	3	
TSHE	1	0.90 (0.03)	6	0.96 (0.02)	8	0.94
TSHE	2	0.83 (0.04)	6	0.80 (0.06)	5	1.04
TSHE	3	0.66 (0.05)	6	0.64 (0.05)	9	1.03
TSHE	4	0.38 (0.05)	6	0.40 (0.06)	7	0.95
TSHE	5			0.27 ()	1	

Note: Values are means with standard errors in parentheses. “n” is the number of SD or DD.

Appendix C

Standing dead tree absolute density and its uncertainty for each decay class by species present in the U.S. FIA inventory

Genus	Species	Code	den0	den1	unc1	cod1	den2	unc2	cod2	den3	unc3	cod3	den4	unc4	cod4
Abies	*amabilis*	ABAM	0.400	0.356	0.020	B	0.382	0.014	B	0.301	0.060	B	0.239	0.336	C
Abies	*balsamea*	ABBA	0.340	0.356	0.024	B	0.414	0.014	B	0.412	0.058	B	0.286	0.336	C
Abies	*bracteata*	ABBR	0.360	0.367	0.024	B	0.354	0.029	B	0.301	0.060	B	0.239	0.336	C
Abies	*concolor*	ABCO	0.370	0.337	0.012	B	0.319	0.013	B	0.172	0.057	B	0.232	0.336	C
Abies	*fraseri*	ABFR	0.340	0.367	0.024	B	0.354	0.029	B	0.301	0.060	B	0.239	0.336	C
Abies	*grandis*	ABGR	0.350	0.338	0.010	B	0.338	0.013	B	0.320	0.057	B	0.239	0.336	C
Abies	*lasiocarpa*	ABLA	0.310	0.367	0.014	B	0.331	0.025	B	0.331	0.057	B	0.255	0.336	C
Abies	*magnifica*	ABMA	0.360	0.473	0.012	B	0.435	0.023	B	0.213	0.057	B	0.240	0.336	C
Abies	*magnifica* var. *shastensis*	ABMA2	0.360	0.367	0.024	B	0.354	0.029	B	0.301	0.060	B	0.239	0.336	C
Abies	*procera*	ABPR	0.370	0.364	0.010	B	0.309	0.012	B	0.334	0.057	B	0.252	0.336	C
Abies	*species*	ABIE	0.340	0.367	0.024	B	0.354	0.029	B	0.301	0.060	B	0.239	0.336	C
Acacia	*species*	ACSP2	0.600	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Acer	*barbatum*	ACBA	0.540	0.568	0.048	B	0.415	0.053	B	0.295	0.087	B	0.297	0.336	C
Acer	*glabrum*	ACGL	0.440	0.568	0.048	B	0.415	0.053	B	0.295	0.087	B	0.297	0.336	C
Acer	*grandidentatum*	ACGR	0.440	0.568	0.048	B	0.415	0.053	B	0.295	0.087	B	0.297	0.336	C
Acer	*macrophyllum*	ACMA	0.440	0.568	0.048	B	0.415	0.053	B	0.295	0.087	B	0.297	0.336	C
Acer	*negundo*	ACNE	0.440	0.568	0.048	B	0.415	0.053	B	0.295	0.087	B	0.297	0.336	C
Acer	*nigrum*	ACNI	0.520	0.568	0.048	B	0.415	0.053	B	0.295	0.087	B	0.297	0.336	C
Acer	*pensylvanicum*	ACPE	0.440	0.568	0.048	B	0.415	0.053	B	0.295	0.087	B	0.297	0.336	C
Acer	*rubrum*	ACRU	0.490	0.462	0.030	B	0.286	0.047	B	0.208	0.085	B	0.297	0.336	C
Acer	*saccharinum*	ACSA2	0.440	0.568	0.048	B	0.415	0.053	B	0.295	0.087	B	0.297	0.336	C
Acer	*saccharum*	ACSA	0.560	0.720	0.028	B	0.497	0.052	B	0.340	0.085	B	0.306	0.336	C
Acer	*species*	ACER	0.490	0.568	0.048	B	0.415	0.053	B	0.295	0.087	B	0.297	0.336	C
Acer	*spicatum*	ACSP	0.440	0.568	0.048	B	0.415	0.053	B	0.295	0.087	B	0.297	0.336	C
Aesculus	*californica*	AECA	0.380	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Aesculus	*species*	AESP	0.330	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Ailanthus	*altissima*	AIAL	0.370	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Aleurites	*fordii*	ALFO	0.470	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Alnus	*rubra*	ALRU	0.370	0.409	0.021	B	0.359	0.047	B	0.207	0.084	B	0.181	0.336	C
Alnus	*species*	ALSP	0.370	0.409	0.092	B	0.359	0.096	B	0.207	0.098	B	0.181	0.337	C
Amelanchier	*species*	AMSP	0.660	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C

continued

Appendix C.—continued

Genus	Species	Code	den0	den1	unc1	cod1	den2	unc2	cod2	den3	unc3	cod3	den4	unc4	cod4
Arbutus	*menziesii*	ARME	0.580	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Asimina	*triloba*	ASTR	0.470	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Betula	*alleghaniensis*	BEAL	0.550	0.615	0.049	B	0.443	0.115	B	0.200	0.084	B	0.286	0.336	C
Betula	*lenta*	BELE	0.600	0.673	0.049	B	0.462	0.061	B	0.297	0.087	B	0.286	0.337	C
Betula	*lutea*	BELU	0.600	0.674	0.035	B	0.424	0.049	B	0.246	0.085	B	0.286	0.337	C
Betula	*nigra*	BENI	0.560	0.615	0.049	B	0.443	0.115	B	0.278	0.088	B	0.286	0.337	C
Betula	*occidentalis*	BEOC	0.530	0.615	0.049	B	0.443	0.115	B	0.278	0.088	B	0.286	0.337	C
Betula	*papyrifera*	BEPA	0.480	0.497	0.032	B	0.443	0.115	B	0.370	0.095	B	0.286	0.337	C
Betula	*papyrifera* var. *commutata*	BEPA2	0.480	0.615	0.049	B	0.443	0.115	B	0.278	0.088	B	0.286	0.337	C
Betula	*populifolia*	BEPO	0.450	0.615	0.049	B	0.443	0.115	B	0.278	0.088	B	0.286	0.337	C
Betula	*species*	BESP	0.480	0.615	0.049	B	0.443	0.115	B	0.278	0.088	B	0.286	0.337	C
Bumelia	*lanuginosa*	BULA	0.470	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Calocedrus	*decurrens*	CADE3	0.370	0.421	0.046	B	0.309	0.019	B	0.328	0.058	B	0.262	0.336	C
Carpinus	*caroliniana*	CACA	0.580	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Carya	*aquatica*	CAAQ	0.610	0.635	0.041	B	0.450	0.053	B	0.250	0.085	B	0.291	0.337	C
Carya	*cordiformis*	CACO	0.600	0.647	0.050	B	0.404	0.052	B	0.261	0.085	B	0.291	0.337	C
Carya	*glabra*	CAGL	0.660	0.635	0.041	B	0.450	0.053	B	0.250	0.085	B	0.291	0.337	C
Carya	*illinoensis*	CAIL	0.600	0.635	0.041	B	0.450	0.053	B	0.250	0.085	B	0.291	0.337	C
Carya	*laciniosa*	CALA	0.620	0.635	0.041	B	0.450	0.053	B	0.250	0.085	B	0.291	0.337	C
Carya	*myristicaeformis*	CAMY	0.560	0.635	0.041	B	0.450	0.053	B	0.250	0.085	B	0.291	0.337	C
Carya	*ovata*	CAOV	0.640	0.584	0.044	B	0.527	0.061	B	0.323	0.086	B	0.291	0.337	C
Carya	*species*	CASP	0.620	0.671	0.029	B	0.459	0.045	B	0.205	0.084	B	0.291	0.336	C
Carya	*texana*	CATE	0.540	0.635	0.041	B	0.450	0.053	B	0.250	0.085	B	0.291	0.337	C
Carya	*tomentosa*	CATO	0.640	0.637	0.041	B	0.409	0.046	B	0.250	0.085	B	0.291	0.337	C
Castanea	*dentata*	CADE	0.400	0.382	0.027	B	0.383	0.046	B	0.268	0.085	B	0.356	0.338	C
Castanea	*ozarkensis*	CAOZ	0.400	0.382	0.087	B	0.383	0.102	B	0.268	0.107	B	0.356	0.338	C
Castanea	*pumila*	CAPU	0.400	0.382	0.087	B	0.383	0.102	B	0.268	0.107	B	0.356	0.338	C
Castanopsis	*species*	CAST	0.420	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Catalpa	*species*	CATA	0.380	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Celtis	*laevigata*	CELA	0.470	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Celtis	*occidentalis*	CEOC	0.490	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Celtis	*species*	CESP	0.490	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C

continued

Appendix C.—continued

Genus	Species	Code	den0	den1	unc1	cod1	den2	unc2	cod2	den3	unc3	cod3	den4	unc4	cod4
Cercis	*canadensis*	CECA	0.580	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Cercocarpus	*intricatus*	CEIN	1.000	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Cercocarpus	*ledifolius*	CELE	1.000	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Cercocarpus	*montanus*	CEMO	1.000	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Chamaecyparis	*lawsoniana*	CHLA	0.390	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Chamaecyparis	*nootkatensis*	CHNO	0.420	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Chamaecyparis	*thyoides*	CHTH	0.310	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Cladrastis	*lutea*	CLLU	0.520	0.528	0.125	B	0.485	0.112	B	0.462	0.102	B	0.356	0.338	C
Cornus	*florida*	COFL	0.640	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Cornus	*nuttallii*	CONU	0.580	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Cornus	*species*	COSP	0.640	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Cotinus	*obovaus*	COOB	0.470	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Crataegus	*species*	CRSP	0.620	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Cupressus	*species*	CUSP	0.440	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Diospyros	*virginiana*	DIVI	0.640	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Eucalyptus	*species*	EUSP	0.670	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Fagus	*grandifolia*	FAGR	0.560	0.604	0.038	B	0.330	0.046	B	0.175	0.084	B	0.403	0.336	C
Fraxinus	*americana*	FRAM	0.550	0.504	0.039	B	0.315	0.048	B	0.333	0.085	B	0.356	0.338	C
Fraxinus	*latifolia*	FRLA	0.500	0.504	0.113	B	0.349	0.094	B	0.313	0.114	B	0.356	0.338	C
Fraxinus	*nigra*	FRNI	0.450	0.504	0.113	B	0.349	0.094	B	0.313	0.114	B	0.356	0.338	C
Fraxinus	*pennsylvanica*	FRPE	0.530	0.504	0.113	B	0.349	0.094	B	0.313	0.114	B	0.356	0.338	C
Fraxinus	*profunda*	FRPR	0.540	0.504	0.113	B	0.349	0.094	B	0.313	0.114	B	0.356	0.338	C
Fraxinus	*quadrangulata*	FRQU	0.530	0.504	0.113	B	0.349	0.094	B	0.313	0.114	B	0.356	0.338	C
Fraxinus	*species*	FRSP	0.540	0.504	0.113	B	0.349	0.094	B	0.313	0.114	B	0.356	0.338	C
Gleditsia	*aquatica*	GLAQ	0.600	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Gleditsia	*triacanthos*	GLTR	0.600	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Gordonia	*lasianthus*	GOLA	0.370	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Gymnocladus	*dioicus*	GYDI	0.500	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Halesia	*species*	HASP	0.320	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Ilex	*opaca*	ILOP	0.500	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Juglans	*cinerea*	JUCI	0.360	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Juglans	*species*	JUSP	0.510	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Julglans	*nigra*	JUNI	0.510	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C

continued

Appendix C.—continued

Genus	Species	Code	den0	den1	unc1	cod1	den2	unc2	cod2	den3	unc3	cod3	den4	unc4	cod4
Juniperus	*monosperma*	JUMO	0.450	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Juniperus	*occidentalis*	JUOC	0.440	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Juniperus	*species*	JUSP2	0.440	0.528	0.125	B	0.485	0.112	B	0.462	0.102	B	0.356	0.338	C
Larix	*laricina*	LALA	0.490	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Larix	*lyallii*	LALY	0.480	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Larix	*occidentalis*	LAOC	0.480	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Larix	*species*	LASP	0.440	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Liquidambar	*styraciflua*	LIST	0.460	0.477	0.022	B	0.364	0.045	B	0.239	0.084	B	0.356	0.338	C
Liriodendron	*tulipifera*	LITU	0.410	0.370	0.010	A	0.350	0.010	A	0.213	0.084	B	0.237	0.336	C
Lithocarpus	*densiflorus*	LIDE	0.580	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Maclura	*pomifera*	MAPO	0.760	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Magnolia	*acuminata*	MAAC	0.450	0.451	0.024	B	0.439	0.055	B	0.263	0.085	B	0.356	0.338	C
Magnolia	*species*	MASP	0.450	0.451	0.101	B	0.439	0.114	B	0.263	0.106	B	0.356	0.338	C
Malus	*species*	MASP2	0.610	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Melia	*azedarach*	MEAZ	0.470	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Morus	*alba*	MOAL	0.590	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Morus	*rubra*	MORU	0.590	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Morus	*species*	MOSP	0.590	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Nyssa	*aquatica*	NYAQ	0.460	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Nyssa	*ogeche*	NYOG	0.460	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Nyssa	*sylvatica*	NYSY	0.460	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Olneya	*tesota*	OLTE	1.000	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Ostrya	*virginiana*	OSVI	0.630	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Oxydendrum	*arboreum*	OXAR	0.500	0.555	0.058	B	0.447	0.046	B	0.354	0.086	B	0.356	0.338	C
Paulownia	*tomentosa*	PATO	0.380	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Persea	*borbonia*	PEBO	0.510	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Picea	*abies*	PIAB	0.370	0.370	0.030	A	0.370	0.020	A	0.398	0.065	B	0.260	0.336	C
Picea	*breweriana*	PIBR	0.330	0.389	0.024	B	0.359	0.017	B	0.398	0.065	B	0.260	0.336	C
Picea	*engelmannii*	PIEN	0.330	0.389	0.024	B	0.297	0.013	B	0.398	0.065	B	0.197	0.336	C
Picea	*glauca*	PIGL2	0.370	0.389	0.024	B	0.359	0.017	B	0.398	0.065	B	0.260	0.336	C
Picea	*lutzii*	PILU	0.360	0.380	0.010	A	0.380	0.010	A	0.400	0.020	A	0.254	0.336	C
Picea	*mariana*	PIMA	0.380	0.389	0.024	B	0.359	0.017	B	0.398	0.065	B	0.260	0.336	C
Picea	*pungens*	PIPU	0.380	0.389	0.024	B	0.359	0.017	B	0.398	0.065	B	0.260	0.336	C

continued

Appendix C.—continued

Genus	Species	Code	den0	den1	unc1	cod1	den2	unc2	cod2	den3	unc3	cod3	den4	unc4	cod4
Picea	*rubens*	PIRU	0.380	0.402	0.025	B	0.359	0.017	B	0.449	0.067	B	0.260	0.336	C
Picea	*sitchensis*	PISI	0.370	0.406	0.010	B	0.392	0.014	B	0.373	0.057	B	0.323	0.336	C
Picea	*species*	PICE	0.380	0.389	0.024	B	0.359	0.017	B	0.398	0.065	B	0.260	0.336	C
Pinus	*albicaulis*	PIAL	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*aristata*	PIAR	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*arizonica*	PIAR2	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*attenuata*	PIAT	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*balfouriana*	PIBA	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*banksiana*	PIBA2	0.420	0.390	0.020	A	0.380	0.010	A	0.320	0.040	A	0.284	0.336	C
Pinus	*clausa*	PICL	0.460	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*contorta*	PICO	0.400	0.390	0.001	A	0.415	0.015	A	0.400	0.001	A	0.284	0.336	C
Pinus	*coulteri*	PICO2	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*discolor*	PIDI	0.500	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*echinata*	PIEC	0.470	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*edulis*	PIED	0.500	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*elliotti*	PIEL	0.540	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*engelmannii*	PIEN2	0.370	0.364	0.015	B	0.373	0.017	B	0.398	0.060	B	0.284	0.336	C
Pinus	*flexilis*	PIFL	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*glabra*	PIGL	0.410	0.389	0.021	B	0.359	0.017	B	0.398	0.060	B	0.260	0.336	C
Pinus	*jeffreyi*	PIJE	0.370	0.361	0.014	B	0.412	0.019	B	0.308	0.058	B	0.344	0.336	C
Pinus	*lambertiana*	PILA	0.340	0.365	0.017	B	0.307	0.012	B	0.220	0.057	B	0.205	0.336	C
Pinus	*leiophylla*	PILE	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*monophylla*	PIMO	0.500	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*monticola*	PIMO3	0.350	0.341	0.010	B	0.348	0.012	B	0.437	0.057	B	0.284	0.336	C
Pinus	*muricata*	PIMU	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*nigra*	PINI	0.410	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*palustris*	PIPA	0.540	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*ponderosa*	PIPO	0.380	0.335	0.010	B	0.383	0.013	B	0.469	0.058	B	0.217	0.336	C
Pinus	*pungens*	PIPU2	0.490	0.389	0.021	B	0.359	0.017	B	0.398	0.060	B	0.260	0.336	C
Pinus	*radiata*	PIRA	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*resinosa*	PIRE	0.410	0.337	0.019	B	0.373	0.017	B	0.383	0.060	B	0.252	0.336	C
Pinus	*rigida*	PIRI	0.470	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*sabiniana*	PISA	0.370	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C

continued

Appendix C.—continued

Genus	Species	Code	den0	den1	unc1	cod1	den2	unc2	cod2	den3	unc3	cod3	den4	unc4	cod4
Pinus	*serotina*	PISE	0.510	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*strobiformis*	PIST2	0.350	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*strobus*	PIST	0.340	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Pinus	*sylvestris*	PISY	0.380	0.370	0.010	A	0.360	0.010	A	0.310	0.030	A	0.284	0.336	C
Pinus	*taeda*	PITA	0.470	0.382	0.011	B	0.352	0.012	B	0.325	0.057	B	0.324	0.336	C
Pinus	*virginiana*	PIVI	0.450	0.364	0.015	B	0.373	0.017	B	0.388	0.060	B	0.284	0.336	C
Planera	*aquatica*	PLAQ	0.530	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Platanus	*occidentalis*	PLOC	0.460	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Populus	*alba*	POAL	0.370	0.374	0.085	B	0.464	0.119	B	0.314	0.115	B	0.269	0.337	C
Populus	*angustifolia*	POAN	0.340	0.374	0.085	B	0.464	0.119	B	0.314	0.115	B	0.269	0.337	C
Populus	*balsamifera*	POBA	0.310	0.374	0.085	B	0.464	0.119	B	0.314	0.115	B	0.269	0.337	C
Populus	*deltoides*	PODE	0.370	0.374	0.085	B	0.464	0.119	B	0.314	0.115	B	0.269	0.337	C
Populus	*fremontii*	POFR	0.340	0.374	0.085	B	0.464	0.119	B	0.314	0.115	B	0.269	0.337	C
Populus	*grandidentata*	POGR	0.360	0.356	0.031	B	0.464	0.119	B	0.313	0.086	B	0.269	0.337	C
Populus	*heterophylla*	POHE	0.370	0.374	0.085	B	0.464	0.119	B	0.314	0.115	B	0.269	0.337	C
Populus	*sargentii*	POSA	0.370	0.374	0.085	B	0.464	0.119	B	0.314	0.115	B	0.269	0.337	C
Populus	*species*	POSP	0.370	0.392	0.033	B	0.464	0.119	B	0.315	0.086	B	0.269	0.336	C
Populus	*tremuloides*	POTR	0.390	0.370	0.020	A	0.290	0.020	A	0.210	0.030	A	0.269	0.337	C
Prosopis	*species*	PRSP	0.580	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Prunus	*americana*	PRAM	0.470	0.518	0.044	B	0.460	0.052	B	0.295	0.112	B	0.356	0.338	C
Prunus	*nigra*	PRNI	0.470	0.518	0.044	B	0.460	0.052	B	0.295	0.112	B	0.356	0.338	C
Prunus	*pensylvanica*	PRPE	0.360	0.425	0.024	B	0.371	0.045	B	0.227	0.084	B	0.356	0.338	C
Prunus	*serotina*	PRSE	0.470	0.612	0.047	B	0.549	0.050	B	0.363	0.090	B	0.356	0.338	C
Prunus	*species*	PRSP2	0.470	0.518	0.044	B	0.460	0.052	B	0.295	0.112	B	0.356	0.338	C
Prunus	*virginiana*	PRVI	0.360	0.518	0.044	B	0.460	0.052	B	0.295	0.112	B	0.356	0.338	C
Pseudotsuga	*menziesii*	PSME	0.450	0.382	0.011	B	0.354	0.013	B	0.216	0.057	B	0.207	0.336	C
Quercus	*agrifolia*	QUAG	0.700	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*alba*	QUAL	0.600	0.601	0.028	B	0.426	0.045	B	0.352	0.085	B	0.282	0.336	C
Quercus	*arizonica, grisea*	QUAR	0.700	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*bicolor*	QUBI	0.640	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*chrysolepis*	QUCH	0.700	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*coccinea*	QUCO	0.600	0.605	0.037	B	0.552	0.049	B	0.464	0.085	B	0.405	0.336	C
Quercus	*douglasii*	QUDO	0.510	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C

continued

Appendix C.—continued

Genus	Species	Code	den0	den1	unc1	cod1	den2	unc2	cod2	den3	unc3	cod3	den4	unc4	cod4
Quercus	*durandii*	QUDU	0.600	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*ellipsoidalis*	QUEL	0.560	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*emoryi*	QUEM	0.700	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*engelmannii*	QUEN	0.700	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*falcata* var. *falcata*	QUFA	0.520	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*falcata* var. *pagodaefolia*	QUFA2	0.610	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*gambelii*	QUGA	0.640	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*garryana*	QUGA2	0.640	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*hypoleucoides*	QUHY	0.700	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*ilicifolia*	QUIL	0.560	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*imbricaria*	QUIM	0.560	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*incana*	QUIN	0.560	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*kelloggii*	QUKE	0.510	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*laevis*	QULA	0.520	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*laurifolia*	QULA2	0.560	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*lobata*	QULO	0.640	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*lyrata*	QULY	0.570	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*macrocarpa*	QUMA	0.580	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*marilandica*	QUMA2	0.560	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*michauxii*	QUMI	0.600	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*muehlenbergii*	QUMU	0.600	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*nigra*	QUNI	0.560	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*nuttalli*	QUNU	0.560	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*oblongifolia*	QUOB	0.700	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*palustris*	QUPA	0.580	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*phellos*	QUPH	0.560	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*prinus*	QUPR	0.570	0.773	0.061	B	0.538	0.063	B	0.309	0.085	B	0.405	0.336	C
Quercus	*rubra*	QURU	0.560	0.578	0.032	B	0.333	0.051	B	0.406	0.090	B	0.393	0.336	C
Quercus	*shumardii*	QUSH	0.560	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*species*	QUSP	0.580	0.599	0.024	B	0.508	0.048	B	0.334	0.085	B	0.329	0.336	C
Quercus	*stellata*	QUST	0.600	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*velutina*	QUVE	0.560	0.648	0.056	B	0.399	0.056	B	0.476	0.095	B	0.405	0.336	C

continued

Appendix C.—continued

Genus	Species	Code	den0	den1	unc1	cod1	den2	unc2	cod2	den3	unc3	cod3	den4	unc4	cod4
Quercus	*virginiana*	QUVI	0.800	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Quercus	*wislizeni*	QUWI	0.700	0.648	0.056	B	0.495	0.062	B	0.401	0.092	B	0.405	0.336	C
Robinia	*neomexicana*	RONE	0.660	0.769	0.170	B	0.616	0.154	B	0.341	0.119	B	0.356	0.338	C
Robinia	*pseudoacacia*	ROPS	0.660	0.769	0.031	B	0.616	0.053	B	0.341	0.119	B	0.356	0.338	C
Salix	*species*	SASP	0.360	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Sapium	*sebiferum*	SASE	0.470	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Sassafras	*albidum*	SAAL	0.420	0.458	0.024	B	0.427	0.047	B	0.355	0.084	B	0.356	0.338	C
Sequoia	*sempervirens*	SESE	0.340	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Sequoiadendron	*giganteum*	SEGI	0.340	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Sorbus	*americana*	SOAM	0.420	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Tamarix	*species*	TASP	0.400	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Taxodium	*distichum* var. *nutans*	TADI	0.420	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Taxus	*brevifolia*	TABR	0.600	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Thuja	*occidentalis*	THOC	0.290	0.326	0.016	B	0.298	0.102	B	0.447	0.059	B	0.240	0.336	C
Thuja	*plicata*	THPL	0.310	0.315	0.016	B	0.298	0.102	B	0.352	0.057	B	0.222	0.336	C
Tilia	*americana*	TIAM	0.320	0.430	0.023	B	0.366	0.045	B	0.269	0.084	B	0.356	0.338	C
Tilia	*heterophylla*	TIHE	0.320	0.430	0.097	B	0.366	0.098	B	0.269	0.107	B	0.356	0.338	C
Tilia	*species*	TISP	0.320	0.430	0.097	B	0.366	0.098	B	0.269	0.107	B	0.356	0.338	C
Torreya	*californica*	TOCA	0.340	0.377	0.041	B	0.366	0.079	B	0.365	0.065	B	0.272	0.336	C
Tsuga	*canadensis*	TSCA	0.400	0.394	0.025	B	0.370	0.080	B	0.462	0.063	B	0.299	0.336	C
Tsuga	*heterophylla*	TSHE	0.440	0.390	0.010	A	0.360	0.020	A	0.290	0.020	A	0.170	0.024	A
Tsuga	*mertensiana*	TSME	0.420	0.376	0.025	B	0.370	0.080	B	0.400	0.066	B	0.299	0.336	C
Tsuga	*species*	TSSP	0.380	0.376	0.025	B	0.370	0.080	B	0.400	0.066	B	0.299	0.336	C
Ulmus	*alata*	ULAL	0.570	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Ulmus	*americana*	ULAM	0.460	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Ulmus	*crassifolia*	ULCR	0.570	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Ulmus	*pumila*	ULPU	0.460	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Ulmus	*rubra*	ULRU	0.480	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Ulmus	*serotina*	ULSE	0.570	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Ulmus	*species*	ULSP	0.500	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Ulmus	*thomasii*	ULTH	0.570	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Umbellularia	*californica*	UMCA	0.510	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C
Vaccinium	*arboreum*	VAAR	0.470	0.565	0.126	B	0.464	0.119	B	0.341	0.119	B	0.356	0.338	C

continued

Appendix C.—continued

Standing Dead Absolute Density Predictions Metadata (Appendix C)

Fieldname	Definition	Code/Units	Method
genus	Sample genus		
species	Sample species		
code	Genus-species code		
den0	Green density (decay class “0”)	g/cm^3	
den1	Density of decay class 1 snag	g/cm^3	
unc1	Uncertainty of den1		
cod1	Uncertainty code for den1 (A, B, C)	A	Species sampled
cod1	Uncertainty code for den1 (A, B, C)	B	Genera sampled
cod1	Uncertainty code for den1 (A, B, C)	C	Species and genus not sampled
den2	Density of decay class 2 snag	g/cm^3	
unc2	Uncertainty of den2		
cod2	Uncertainty code for den2 (A, B, C)	A	Species sampled
cod2	Uncertainty code for den2 (A, B, C)	B	Genera sampled
cod2	Uncertainty code for den2 (A, B, C)	C	Species and genus not sampled
den3	Density of decay class 3 snag	g/cm^3	
unc3	Uncertainty of den3		
cod3	Uncertainty code for den3 (A, B, C)	A	Species sampled
cod3	Uncertainty code for den3 (A, B, C)	B	Genera sampled
cod3	Uncertainty code for den3 (A, B, C)	C	Species and genus not sampled
den4	Density of decay class 4 snag	g/cm^3	
unc4	Uncertainty of den4		
cod4	Uncertainty code for den4 (A, B, C)	A	Species sampled
cod4	Uncertainty code for den4 (A, B, C)	B	Genera sampled
cod4	Uncertainty code for den4 (A, B, C)	C	Species and genus not sampled

Appendix D

Standing dead tree relative density and its uncertainty for each decay class by species present in the U.S. FIA inventory

Genus	Species	Code	den0	rel1	unc1	cod1	rel2	unc2	cod2	rel3	unc3	cod3	rel4	unc4	cod4
Abies	*amabilis*	ABAM	0.400	0.936	0.044	B	0.955	0.022	B	0.803	0.107	B	0.574	0.216	C
Abies	*balsamea*	ABBA	0.340	1.040	0.062	B	1.150	0.023	B	1.101	0.064	B	0.710	0.219	C
Abies	*bracteata*	ABBR	0.360	1.018	0.056	B	0.975	0.091	B	0.803	0.107	B	0.574	0.216	C
Abies	*concolor*	ABCO	0.370	0.996	0.021	B	0.873	0.018	B	0.625	0.054	B	0.541	0.213	C
Abies	*fraseri*	ABFR	0.340	1.018	0.056	B	0.975	0.091	B	0.803	0.107	B	0.574	0.216	C
Abies	*grandis*	ABGR	0.350	1.013	0.011	B	0.966	0.021	B	0.855	0.054	B	0.574	0.216	C
Abies	*lasiocarpa*	ABLA	0.310	1.040	0.030	B	1.068	0.073	B	1.000	0.056	B	0.696	0.214	C
Abies	*magnifica*	ABMA	0.360	1.040	0.017	B	1.080	0.051	B	0.626	0.054	B	0.467	0.213	C
Abies	*magnifica* var. *shastensis*	ABMA2	0.360	1.018	0.056	B	0.975	0.091	B	0.803	0.107	B	0.574	0.216	C
Abies	*procera*	ABPR	0.370	1.035	0.013	B	0.836	0.013	B	0.845	0.054	B	0.575	0.213	C
Abies	*species*	ABIE	0.340	1.018	0.056	B	0.975	0.091	B	0.803	0.107	B	0.622	0.217	C
Acacia	*species*	ACSP2	0.600	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Acer	*barbatum*	ACBA	0.540	0.979	0.035	B	0.766	0.194	B	0.565	0.160	B	0.450	0.221	C
Acer	*glabrum*	ACGL	0.440	0.979	0.035	B	0.766	0.194	B	0.565	0.160	B	0.450	0.221	C
Acer	*grandidentatum*	ACGR	0.440	0.979	0.035	B	0.766	0.194	B	0.565	0.160	B	0.450	0.221	C
Acer	*macrophyllum*	ACMA	0.440	0.979	0.035	B	0.766	0.194	B	0.565	0.160	B	0.450	0.221	C
Acer	*negundo*	ACNE	0.440	0.979	0.035	B	0.766	0.194	B	0.565	0.160	B	0.450	0.221	C
Acer	*nigrum*	ACNI	0.520	0.979	0.035	B	0.766	0.194	B	0.565	0.160	B	0.450	0.221	C
Acer	*pensylvanicum*	ACPE	0.440	0.979	0.035	B	0.766	0.194	B	0.565	0.160	B	0.450	0.221	C
Acer	*rubrum*	ACRU	0.490	1.002	0.049	B	0.773	0.056	B	0.618	0.086	B	0.450	0.221	C
Acer	*saccharinum*	ACSA2	0.440	0.979	0.035	B	0.766	0.194	B	0.565	0.160	B	0.450	0.221	C
Acer	*saccharum*	ACSA	0.560	0.956	0.028	B	0.761	0.055	B	0.526	0.077	B	0.450	0.213	C
Acer	*species*	ACER	0.490	0.979	0.035	B	0.766	0.194	B	0.565	0.160	B	0.450	0.221	C
Acer	*spicatum*	ACSP	0.440	0.979	0.035	B	0.766	0.194	B	0.565	0.160	B	0.450	0.221	C
Aesculus	*californica*	AECA	0.380	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Aesculus	*species*	AESP	0.330	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Ailanthus	*altissima*	AIAL	0.370	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Aleurites	*fordii*	ALFO	0.470	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C

continued

Appendix D.—continued

Genus	Species	Code	den0	rel1	unc1	cod1	rel2	unc2	cod2	rel3	unc3	cod3	rel4	unc4	cod4
Alnus	*rubra*	ALRU	0.370	1.030	0.013	B	0.903	0.051	B	0.535	0.074	B	0.393	0.213	C
Alnus	*species*	ALSP	0.370	1.030	0.135	B	0.903	0.228	B	0.535	0.153	B	0.393	0.219	C
Amelanchier	*species*	AMSP	0.660	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Arbutus	*menziesii*	ARME	0.580	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Asimina	*triloba*	ASTR	0.470	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Betula	*alleghaniensis*	BEAL	0.550	1.032	0.135	B	0.713	0.181	B	0.336	0.075	B	0.402	0.213	C
Betula	*lenta*	BELE	0.600	1.040	0.070	B	0.756	0.077	B	0.500	0.084	B	0.439	0.220	C
Betula	*lutea*	BELU	0.600	1.040	0.044	B	0.671	0.048	B	0.400	0.076	B	0.439	0.220	C
Betula	*nigra*	BENI	0.560	1.032	0.135	B	0.713	0.181	B	0.511	0.148	B	0.439	0.220	C
Betula	*occidentalis*	BEOC	0.530	1.032	0.135	B	0.713	0.181	B	0.511	0.148	B	0.439	0.220	C
Betula	*papyrifera*	BEPA	0.480	1.016	0.052	B	0.713	0.181	B	0.777	0.120	B	0.439	0.220	C
Betula	*papyrifera var. commutata*	BEPA2	0.480	1.032	0.135	B	0.713	0.181	B	0.511	0.148	B	0.439	0.220	C
Betula	*populifolia*	BEPO	0.450	1.032	0.135	B	0.713	0.181	B	0.511	0.148	B	0.439	0.220	C
Betula	*species*	BESP	0.480	1.032	0.135	B	0.713	0.181	B	0.511	0.148	B	0.439	0.220	C
Bumelia	*lanuginosa*	BULA	0.470	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Calocedrus	*decurrens*	CADE3	0.370	1.040	0.074	B	0.972	0.035	B	1.011	0.059	B	0.596	0.218	C
Carpinus	*caroliniana*	CACA	0.580	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Carya	*aquatica*	CAAQ	0.610	0.988	0.069	B	0.705	0.064	B	0.404	0.080	B	0.396	0.219	C
Carya	*cordiformis*	CACO	0.600	1.040	0.075	B	0.661	0.056	B	0.440	0.077	B	0.396	0.219	C
Carya	*glabra*	CAGL	0.660	0.988	0.069	B	0.705	0.064	B	0.404	0.080	B	0.396	0.219	C
Carya	*illinoensis*	CAIL	0.600	0.988	0.069	B	0.705	0.064	B	0.404	0.080	B	0.396	0.219	C
Carya	*laciniosa*	CALA	0.620	0.988	0.069	B	0.705	0.064	B	0.404	0.080	B	0.396	0.219	C
Carya	*myristicaeformis*	CAMY	0.560	0.988	0.069	B	0.705	0.064	B	0.404	0.080	B	0.396	0.219	C
Carya	*ovata*	CAOV	0.640	0.895	0.062	B	0.808	0.073	B	0.510	0.081	B	0.396	0.219	C
Carya	*species*	CASP	0.620	1.040	0.033	B	0.727	0.035	B	0.334	0.074	B	0.396	0.213	C
Carya	*texana*	CATE	0.540	0.988	0.069	B	0.705	0.064	B	0.404	0.080	B	0.396	0.219	C
Carya	*tomentosa*	CATO	0.640	0.977	0.056	B	0.627	0.038	B	0.332	0.078	B	0.396	0.219	C
Castanea	*dentata*	CADE	0.400	0.936	0.043	B	0.940	0.046	B	0.668	0.082	B	0.525	0.223	C
Castanea	*ozarkensis*	CAOZ	0.400	0.936	0.123	B	0.940	0.237	B	0.676	0.185	B	0.525	0.223	C

continued

Appendix D.—continued

Genus	Species	Code	den0	rel1	unc1	cod1	rel2	unc2	cod2	rel3	unc3	cod3	rel4	unc4	cod4
Castanea	*pumila*	CAPU	0.400	0.936	0.123	B	0.940	0.237	B	0.676	0.185	B	0.525	0.223	C
Castanopsis	*species*	CAST	0.420	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Catalpa	*species*	CATA	0.380	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Celtis	*laevigata*	CELA	0.470	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Celtis	*occidentalis*	CEOC	0.490	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Celtis	*species*	CESP	0.490	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Cercis	*canadensis*	CECA	0.580	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Cercocarpus	*intricatus*	CEIN	1.000	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Cercocarpus	*ledifolius*	CELE	1.000	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Cercocarpus	*montanus*	CEMO	1.000	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Chamaecyparis	*lawsoniana*	CHLA	0.390	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Chamaecyparis	*nootkatensis*	CHNO	0.420	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Chamaecyparis	*thyoides*	CHTH	0.310	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Cladrastis	*lutea*	CLLU	0.520	0.982	0.129	B	0.844	0.199	B	0.775	0.163	B	0.525	0.223	C
Cornus	*florida*	COFL	0.640	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Cornus	*nuttallii*	CONU	0.580	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Cornus	*species*	COSP	0.640	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Cotinus	*obovaus*	COOB	0.470	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Crataegus	*species*	CRSP	0.620	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Cupressus	*species*	CUSP	0.440	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Diospyros	*virginiana*	DIVI	0.640	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Eucalyptus	*species*	EUSP	0.670	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Fagus	*grandifolia*	FAGR	0.560	1.015	0.056	B	0.663	0.041	B	0.508	0.076	B	0.533	0.213	C
Fraxinus	*americana*	FRAM	0.550	0.899	0.061	B	0.562	0.049	B	0.604	0.079	B	0.525	0.223	C
Fraxinus	*latifolia*	FRLA	0.500	0.899	0.118	B	0.622	0.159	B	0.575	0.162	B	0.525	0.223	C
Fraxinus	*nigra*	FRNI	0.450	0.899	0.118	B	0.622	0.159	B	0.575	0.162	B	0.525	0.223	C
Fraxinus	*pennsylvanica*	FRPE	0.530	0.899	0.118	B	0.622	0.159	B	0.575	0.162	B	0.525	0.223	C
Fraxinus	*profunda*	FRPR	0.540	0.899	0.118	B	0.622	0.159	B	0.575	0.162	B	0.525	0.223	C
Fraxinus	*quadrangulata*	FRQU	0.530	0.899	0.118	B	0.622	0.159	B	0.575	0.162	B	0.525	0.223	C
Fraxinus	*species*	FRSP	0.540	0.899	0.118	B	0.622	0.159	B	0.575	0.162	B	0.525	0.223	C

continued

Appendix D.—continued

Genus	Species	Code	den0	rel1	unc1	cod1	rel2	unc2	cod2	rel3	unc3	cod3	rel4	unc4	cod4
Gleditsia	*aquatica*	GLAQ	0.600	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Gleditsia	*triacanthos*	GLTR	0.600	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Gordonia	*lasianthus*	GOLA	0.370	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Gymnocladus	*dioicus*	GYDI	0.500	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Halesia	*species*	HASP	0.320	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Ilex	*opaca*	ILOP	0.500	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Juglans	*cinerea*	JUCI	0.360	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Juglans	*species*	JUSP	0.510	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Julglans	*nigra*	JUNI	0.510	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Juniperus	*monosperma*	JUMO	0.450	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Juniperus	*occidentalis*	JUOC	0.440	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Juniperus	*species*	JUSP2	0.440	0.982	0.129	B	0.844	0.199	B	0.775	0.163	B	0.525	0.223	C
Larix	*laricina*	LALA	0.490	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Larix	*lyallii*	LALY	0.480	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Larix	*occidentalis*	LAOC	0.480	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Larix	*species*	LASP	0.440	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Liquidambar	*styraciflua*	LIST	0.460	1.017	0.013	B	0.778	0.039	B	0.526	0.075	B	0.525	0.223	C
Liriodendron	*tulipifera*	LITU	0.410	0.910	0.030	A	0.850	0.020	A	0.554	0.075	B	0.501	0.214	C
Lithocarpus	*densiflorus*	LIDE	0.580	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Maclura	*pomifera*	MAPO	0.760	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Magnolia	*acuminata*	MAAC	0.450	0.884	0.026	B	0.862	0.074	B	0.530	0.080	B	0.525	0.223	C
Magnolia	*species*	MASP	0.450	0.884	0.116	B	0.862	0.218	B	0.530	0.152	B	0.525	0.223	C
Malus	*species*	MASP2	0.610	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Melia	*azedarach*	MEAZ	0.470	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Morus	*alba*	MOAL	0.590	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Morus	*rubra*	MORU	0.590	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Morus	*species*	MOSP	0.590	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Nyssa	*aquatica*	NYAQ	0.460	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Nyssa	*ogeche*	NYOG	0.460	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Nyssa	*sylvatica*	NYSY	0.460	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C

continued

Appendix D.—continued

Genus	Species	Code	den0	rel1	unc1	cod1	rel2	unc2	cod2	rel3	unc3	cod3	rel4	unc4	cod4
Olneya	*tesota*	OLTE	1.000	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Ostrya	*virginiana*	OSVI	0.630	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Oxydendrum	*arboreum*	OXAR	0.500	1.040	0.104	B	0.877	0.043	B	0.714	0.084	B	0.525	0.223	C
Paulownia	*tomentosa*	PATO	0.380	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Persea	*borbonia*	PEBO	0.510	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Picea	*abies*	PIAB	0.370	1.010	0.083	A	1.010	0.040	A	0.991	0.159	B	0.605	0.218	C
Picea	*breweriana*	PIBR	0.330	1.038	0.074	B	0.987	0.270	B	0.991	0.159	B	0.605	0.218	C
Picea	*engelmannii*	PIEN	0.330	0.953	0.068	B	0.899	0.021	B	0.991	0.159	B	0.504	0.213	C
Picea	*glauca*	PIGL2	0.370	1.038	0.074	B	0.987	0.270	B	0.991	0.159	B	0.605	0.218	C
Picea	*lutzii*	PILU	0.360	1.060	0.020	A	1.060	0.020	A	1.110	0.040	A	0.564	0.213	C
Picea	*mariana*	PIMA	0.380	1.038	0.074	B	0.987	0.270	B	0.991	0.159	B	0.605	0.218	C
Picea	*pungens*	PIPU	0.380	1.038	0.074	B	0.987	0.270	B	0.991	0.159	B	0.605	0.218	C
Picea	*rubens*	PIRU	0.380	1.040	0.058	B	0.987	0.270	B	1.107	0.107	B	0.605	0.218	C
Picea	*sitchensis*	PISI	0.370	1.040	0.013	B	0.998	0.022	B	0.984	0.055	B	0.676	0.213	C
Picea	*species*	PICE	0.380	1.038	0.074	B	0.987	0.270	B	0.991	0.159	B	0.605	0.218	C
Pinus	*albicaulis*	PIAL	0.370	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*aristata*	PIAR	0.370	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*arizonica*	PIAR2	0.370	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*attenuata*	PIAT	0.370	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*balfouriana*	PIBA	0.370	0.916	0.061	A	0.876	0.095	A	1.018	0.155	A	0.598	0.215	C
Pinus	*banksiana*	PIBA2	0.420	0.953	0.040	A	0.920	0.030	A	0.780	0.091	A	0.598	0.215	C
Pinus	*clausa*	PICL	0.460	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*contorta*	PICO	0.400	0.980	0.010	A	1.040	0.030	A	1.020	0.010	A	0.727	0.213	C
Pinus	*coulteri*	PICO2	0.370	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*discolor*	PIDI	0.500	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*echinata*	PIEC	0.470	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*edulis*	PIED	0.500	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*elliotti*	PIEL	0.540	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*engelmannii*	PIEN2	0.370	0.953	0.057	B	0.950	0.075	B	0.991	0.089	B	0.598	0.215	C
Pinus	*flexilis*	PIFL	0.370	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C

continued

Appendix D.—continued

Genus	Species	Code	den0	rel1	unc1	cod1	rel2	unc2	cod2	rel3	unc3	cod3	rel4	unc4	cod4
Pinus	*glabra*	PIGL	0.410	1.038	0.062	B	0.987	0.078	B	0.991	0.095	B	0.605	0.215	C
Pinus	*jeffreyi*	PIJE	0.370	0.904	0.025	B	0.960	0.037	B	0.883	0.062	B	0.645	0.214	C
Pinus	*lambertiana*	PILA	0.340	1.040	0.038	B	0.906	0.014	B	0.735	0.054	B	0.517	0.213	C
Pinus	*leiophylla*	PILE	0.370	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*monophylla*	PIMO	0.500	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*monticola*	PIMO3	0.350	1.022	0.012	B	0.996	0.015	B	1.170	0.055	B	0.598	0.215	C
Pinus	*muricata*	PIMU	0.370	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*nigra*	PINI	0.410	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*palustris*	PIPA	0.540	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*ponderosa*	PIPO	0.380	0.925	0.011	B	1.007	0.020	B	1.154	0.061	B	0.481	0.213	C
Pinus	*pungens*	PIPU2	0.490	1.038	0.062	B	0.987	0.078	B	0.991	0.095	B	0.605	0.215	C
Pinus	*radiata*	PIRA	0.370	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*resinosa*	PIRE	0.410	0.862	0.052	B	0.950	0.075	B	0.876	0.088	B	0.520	0.214	C
Pinus	*rigida*	PIRI	0.470	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*sabiniana*	PISA	0.370	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*serotina*	PISE	0.510	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*strobiformis*	PIST2	0.350	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*strobus*	PIST	0.340	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Pinus	*sylvestris*	PISY	0.380	0.990	0.020	A	0.980	0.020	A	0.830	0.080	A	0.598	0.215	C
Pinus	*taeda*	PITA	0.470	0.862	0.014	B	0.784	0.012	B	0.732	0.053	B	0.601	0.213	C
Pinus	*virginiana*	PIVI	0.450	0.953	0.057	B	0.950	0.075	B	0.927	0.091	B	0.598	0.215	C
Planera	*aquatica*	PLAQ	0.530	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Platanus	*occidentalis*	PLOC	0.460	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Populus	*alba*	POAL	0.370	1.006	0.132	B	0.793	0.201	B	0.868	0.229	B	0.613	0.227	C
Populus	*angustifolia*	POAN	0.340	1.006	0.132	B	0.793	0.201	B	0.868	0.229	B	0.613	0.227	C
Populus	*balsamifera*	POBA	0.310	1.006	0.132	B	0.793	0.201	B	0.868	0.229	B	0.613	0.227	C
Populus	*deltoides*	PODE	0.370	1.006	0.132	B	0.793	0.201	B	0.868	0.229	B	0.613	0.227	C
Populus	*fremontii*	POFR	0.340	1.006	0.132	B	0.793	0.201	B	0.868	0.229	B	0.613	0.227	C
Populus	*grandidentata*	POGR	0.360	0.970	0.063	B	0.793	0.201	B	0.878	0.092	B	0.613	0.227	C
Populus	*heterophylla*	POHE	0.370	1.006	0.132	B	0.793	0.201	B	0.868	0.229	B	0.613	0.227	C

continued

Appendix D.—continued

Genus	Species	Code	den0	rel1	unc1	cod1	rel2	unc2	cod2	rel3	unc3	cod3	rel4	unc4	cod4
Populus	*sargentii*	POSA	0.370	1.006	0.132	B	0.793	0.201	B	0.868	0.229	B	0.613	0.227	C
Populus	*species*	POSP	0.370	1.040	0.136	B	0.793	0.201	B	0.860	0.227	B	0.613	0.227	C
Populus	*tremuloides*	POTR	0.390	0.970	0.040	A	0.750	0.050	A	0.540	0.070	A	0.613	0.227	C
Prosopis	*species*	PRSP	0.580	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Prunus	*americana*	PRAM	0.470	1.040	0.136	B	1.045	0.263	B	0.708	0.192	B	0.525	0.223	C
Prunus	*nigra*	PRNI	0.470	1.040	0.136	B	1.045	0.263	B	0.708	0.192	B	0.525	0.223	C
Prunus	*pensylvanica*	PRPE	0.360	1.040	0.031	B	1.011	0.041	B	0.636	0.076	B	0.525	0.223	C
Prunus	*serotina*	PRSE	0.470	1.040	0.073	B	1.080	0.059	B	0.780	0.103	B	0.525	0.223	C
Prunus	*species*	PRSP2	0.470	1.040	0.136	B	1.045	0.263	B	0.708	0.192	B	0.525	0.223	C
Prunus	*virginiana*	PRVI	0.360	1.040	0.136	B	1.045	0.263	B	0.708	0.192	B	0.525	0.223	C
Pseudotsuga	*menziesii*	PSME	0.450	0.892	0.015	B	0.831	0.017	B	0.591	0.054	B	0.433	0.213	C
Quercus	*agrifolia*	QUAG	0.700	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*alba*	QUAL	0.600	1.012	0.032	B	0.806	0.035	B	0.591	0.078	B	0.398	0.214	C
Quercus	*arizonica, grisea*	QUAR	0.700	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*bicolor*	QUBI	0.640	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*chrysolepis*	QUCH	0.700	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*coccinea*	QUCO	0.600	0.990	0.052	B	0.904	0.047	B	0.781	0.078	B	0.591	0.216	C
Quercus	*douglasii*	QUDO	0.510	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*durandii*	QUDU	0.600	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*ellipsoidalis*	QUEL	0.560	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*emoryi*	QUEM	0.700	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*engelmannii*	QUEN	0.700	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*falcata var. falcata*	QUFA	0.520	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*falcata* var. *pagodaefolia*	QUFA2	0.610	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*gambelii*	QUGA	0.640	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*garryana*	QUGA2	0.640	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*hypoleucoides*	QUHY	0.700	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*ilicifolia*	QUIL	0.560	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*imbricaria*	QUIM	0.560	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C

continued

Appendix D.—continued

Genus	Species	Code	den0	rel1	unc1	cod1	rel2	unc2	cod2	rel3	unc3	cod3	rel4	unc4	cod4
Quercus	*incana*	QUIN	0.560	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*kelloggii*	QUKE	0.510	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*laevis*	QULA	0.520	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*laurifolia*	QULA2	0.560	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*lobata*	QULO	0.640	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*lyrata*	QULY	0.570	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*macrocarpa*	QUMA	0.580	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*marilandica*	QUMA2	0.560	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*michauxii*	QUMI	0.600	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*muehlenbergii*	QUMU	0.600	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*nigra*	QUNI	0.560	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*nuttalli*	QUNU	0.560	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*oblongifolia*	QUOB	0.700	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*palustris*	QUPA	0.580	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*phellos*	QUPH	0.560	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*prinus*	QUPR	0.570	1.040	0.079	B	0.927	0.086	B	0.547	0.077	B	0.591	0.216	C
Quercus	*rubra*	QURU	0.560	1.031	0.044	B	0.859	0.074	B	0.731	0.093	B	0.591	0.216	C
Quercus	*shumardii*	QUSH	0.560	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*species*	QUSP	0.580	1.013	0.021	B	0.861	0.045	B	0.688	0.079	B	0.686	0.213	C
Quercus	*stellata*	QUST	0.600	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*velutina*	QUVE	0.560	1.020	0.051	B	0.700	0.072	B	0.858	0.118	B	0.591	0.216	C
Quercus	*virginiana*	QUVI	0.800	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Quercus	*wislizeni*	QUWI	0.700	1.020	0.051	B	0.841	0.084	B	0.705	0.106	B	0.591	0.216	C
Robinia	*neomexicana*	RONE	0.660	1.040	0.136	B	0.916	0.231	B	0.618	0.171	B	0.525	0.223	C
Robinia	*pseudoacacia*	ROPS	0.660	1.040	0.033	B	0.916	0.055	B	0.618	0.171	B	0.525	0.223	C
Salix	*species*	SASP	0.360	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Sapium	*sebiferum*	SASE	0.470	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Sassafras	*albidum*	SAAL	0.420	1.040	0.030	B	0.998	0.051	B	0.853	0.077	B	0.525	0.223	C
Sequoia	*sempervirens*	SESE	0.340	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Sequoiadendron	*giganteum*	SEGI	0.340	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C

continued

Appendix D.—continued

Genus	Species	Code	den0	rel1	unc1	cod1	rel2	unc2	cod2	rel3	unc3	cod3	rel4	unc4	cod4
Sorbus	*americana*	SOAM	0.420	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Tamarix	*species*	TASP	0.400	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Taxodium	*distichum var. nutans*	TADI	0.420	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Taxus	*brevifolia*	TABR	0.600	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Thuja	*occidentalis*	THOC	0.290	1.040	0.039	B	0.960	0.163	B	1.330	0.075	B	0.655	0.213	C
Thuja	*plicata*	THPL	0.310	1.040	0.074	B	0.960	0.326	B	1.064	0.058	B	0.656	0.213	C
Tilia	*americana*	TIAM	0.320	1.040	0.026	B	1.080	0.046	B	0.848	0.076	B	0.525	0.223	C
Tilia	*heterophylla*	TIHE	0.320	1.040	0.136	B	1.080	0.272	B	0.848	0.225	B	0.525	0.223	C
Tilia	*species*	TISP	0.320	1.040	0.136	B	1.080	0.272	B	0.848	0.225	B	0.525	0.223	C
Torreya	*californica*	TOCA	0.340	0.994	0.071	B	0.951	0.260	B	0.902	0.146	B	0.605	0.218	C
Tsuga	*canadensis*	TSCA	0.400	1.035	0.060	B	0.882	0.241	B	1.081	0.087	B	0.604	0.218	C
Tsuga	*heterophylla*	TSHE	0.440	0.900	0.030	A	0.830	0.040	A	0.661	0.050	A	0.380	0.050	A
Tsuga	*mertensiana*	TSME	0.420	0.953	0.052	B	0.882	0.241	B	0.906	0.079	B	0.604	0.218	C
Tsuga	*species*	TSSP	0.380	0.953	0.052	B	0.882	0.241	B	0.906	0.079	B	0.604	0.218	C
Ulmus	*alata*	ULAL	0.570	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Ulmus	*americana*	ULAM	0.460	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Ulmus	*crassifolia*	ULCR	0.570	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Ulmus	*pumila*	ULPU	0.460	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Ulmus	*rubra*	ULRU	0.480	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Ulmus	*serotina*	ULSE	0.570	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Ulmus	*species*	ULSP	0.500	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Ulmus	*thomasii*	ULTH	0.570	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Umbellularia	*californica*	UMCA	0.510	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C
Vaccinium	*arboreum*	VAAR	0.470	0.982	0.129	B	0.793	0.201	B	0.618	0.171	B	0.525	0.223	C

continued

Appendix D.—continued

Standing Dead Tree Relative Density Predictions Metadata (Appendix D)

Fieldname	Definition	Code/Units	Method
genus	genus		
species	species		
code	genus-species code		
den0	green density	g/cm^3	
rel1	relative density decay class 1	dimensionless	
unc1	uncertainty of rel1	dimensionless	
cod1	uncertaintly code for rel1	A	Species sampled
		B	Genera sampled
		C	Species and genus not sampled
rel2	relative density decay class 2	dimensionless	
unc2	uncertainty of rel2	dimensionless	
cod2	uncertaintly code for rel2	A	Species sampled
		B	Genera sampled
		C	Species and genus not sampled
rel3	relative density decay class 3	dimensionless	
unc3	uncertainty of rel3	dimensionless	
cod3	uncertaintly code for rel3	A	Species sampled
		B	Genera sampled
		C	Species and genus not sampled
rel4	relative density decay class 4	dimensionless	
unc4	uncertainty of rel4	dimensionless	
cod4	uncertaintly code for rel4	A	Species sampled
		B	Genera sampled
		C	Species and genus not sampled

Harmon, Mark E.; Woodall, Christopher W.; Fasth, Becky; Sexton, Jay; Yatkov, Misha. 2011. **Differences between standing and downed dead tree wood density reduction factors: A comparison across decay classes and tree species.** Res. Pap. NRS-15. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 40 p.

Woody detritus or dead wood is an important part of forest ecosystems and has become a routine facet of forest monitoring and inventory. Biomass and carbon estimates of dead wood depend on knowledge of species- and decay class-specific density or density reduction factors. While some progress has been made in determining these parameters for dead and downed trees (DD), there are very few estimates of these key parameters for standing dead trees (SD). We evaluated indicators of decay to relate subjective SD and DD decay classifications then compared SD and DD density and density reduction factors by decay class for a total of 19 tree species at nine sites in the United States and Russia. Results indicate that SD density declined with decay class for all examined species. By applying these results, a new set of SD density reduction factors was developed for 260 species inventoried by the U.S. Forest Service's Forest Inventory and Analysis program in forests of the United States.

KEY WORDS: standing dead trees, downed dead trees, carbon, biomass, decay reduction factor

The U.S. Department of Agriculture (USDA) prohibits discrimination in all its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex, marital status, familial status, parental status, religion, sexual orientation, genetic information, political beliefs, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternate means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at (202)720-2600 (voice and TDD). To file a complaint of discrimination, write to USDA, Director, Office of Civil Rights, 1400 Independence Avenue, S.W., Washington, DC 20250-9410, or call (800)795-3272 (voice) or (202)720-6382 (TDD). USDA is an equal opportunity provider and employer.

Printed on Recycled Paper



www.nrs.fs.fed.us

Chapter 4: Northern Spotted Owl Habitat and Populations: Status and Threats

Damon B. Lesmeister, Raymond J. Davis, Peter H. Singleton, and J. David Wiens[1]

Introduction

The northern spotted owl (*Strix occidentalis caurina*) was listed as threatened under the Endangered Species Act in 1990 (USFWS 1990). Providing adequate amounts of suitable forest cover to sustain the subspecies was a major component of the first recovery plan for northern spotted owls (USFWS 1992) and a driver in the basic reserve design and old-forest restoration under the Northwest Forest Plan (NWFP, or Plan) (USDA and USDI 1994). The reserve design included large contiguous blocks of late-successional forest, which was expected to be sufficient to provide habitat for many interacting pairs of northern spotted owls. As such, the selection of reserves generally favored areas with the highest quality old-growth forests, but some areas of younger forest were also included with the expectation that they would eventually develop suitable forest structure characteristics and contribute to spatial patterns that would sustain spotted owl populations.

Northern spotted owls are now one of the most studied birds in the world. Much of the research and interest in spotted owls stem from the economic and ecological implications surrounding management for the subspecies. Courtney et al. (2004) and the U.S. Fish and Wildlife Service (USFWS 2011b) completed comprehensive reviews and syntheses of scientific information regarding the status, ecology, and threats to the northern spotted owl. In the 10-year science synthesis of the NWFP, Raphael (2006) detailed the expectations and observations for northern spotted owl populations and suitable forest types under the Plan. Here we provide a 20-year synthesis of northern spotted owl science and review key information concerning the ecology and expectations for conservation of northern spotted owls under the NWFP. We build upon previous syntheses and address guiding questions by focusing on the scientific understanding accumulated from 2005 to 2016 on the ecology, conservation, and management of northern spotted owls. We also provide an overview of the main scientific debates surrounding conservation and management of northern spotted owls. We discuss the distinction between associated forest cover types and the relative value of habitat in different forest types for the subspecies. Where needed, we review and draw inference from research related to Mexican spotted owls (*S. o. lucida*) and California spotted owls (*S. o. occidentalis*), but keep the focus of this synthesis on published literature specific to northern spotted owls (spotted owl hereafter).

Major threats to spotted owls identified at the time of design and initial implementation of the NWFP and species recovery plan included the effects of past and current timber harvest, loss of old forest to wildfire, and competition with rapidly encroaching barred owls (*Strix varia*) (USDA and USDI 1994, USFWS 1992). Studies of associations between spotted owls and forest cover published since 2005 have reinforced previous work indicating a strong association of nest and roost sites with older forest conditions and a wider range of forest cover types used for foraging and dispersal (Anthony et al. 2006; Carroll and Johnson 2008; Dugger et al. 2005, 2016; Forsman et al. 2011, 2015; Hamer et al. 2007; Irwin et al. 2012, 2013; McDonald et al. 2006; Olson et al. 2005; Sovern et al. 2015). In the southern portions of the range, abiotic environmental factors begin to play larger roles in territorial owl use (Glenn et al. 2017), and at the very southern end of the range (Marin County, California), spotted owls occur at higher densities and tend to nest in a wider variety of forest cover types and ages (Stralberg et al. 2009). The difference in localized spotted owl densities and generalist vegetation associations appear to be driven by the diversity of forest conditions and high prey density prevalent in that landscape.

[1] **Damon B. Lesmeister** is a research wildlife biologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331; **Raymond J. Davis** is the northern spotted owl and old growth monitoring lead, U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, 3200 SW Jefferson Way, Corvallis, OR 97331; **Peter H. Singleton** is a research wildlife biologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 1133 N Western Avenue, Wenatchee, WA 98801; and **J. David Wiens** is a research wildlife biologist, U.S. Department of the Interior, Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331.

Every study that has assessed rangewide population trends of spotted owls found steady declines since standardized monitoring efforts started in 1985 (Anthony et al. 2006, Dugger et al. 2016, Forsman et al. 2011, Franklin et al. 1996). Loss of suitable forest and competitive interactions with barred owls are the primary threats that have contributed to those declines. In the following sections, we review recent information on the status and trends of spotted owl populations and suitable forest, effects of interactions with barred owls, prey ecology, disturbance impacts, climate change, and other threats. We also review population trends and range expansion of barred owls, their habitat and prey, and identify other sensitive wildlife and ecological processes that may ultimately be affected by the invasion of barred owls. We conclude by outlining considerations for management and research needs for spotted owls and forest types most critical to their persistence.

Guiding Questions

We used the following questions received from forest managers to guide our synthesis and focus on relevant spotted owl literature. Following each question, we provide the section that most effectively addresses the question, or if a question could not be adequately addressed because of a lack of published literature on the subject.

1. What is the current understanding about spotted owl population status? Will continuing to implement the NWFP reverse the downward trend in spotted owl populations?
    - Information can be found in the "Population Status and Trends" and "Conclusions and Management Considerations" sections.
2. Is the NWFP maintaining or restoring forest conditions necessary to support viable populations of spotted owls?
    - Despite old-forest loss to wildfire and timber harvest, implementation of the NWFP has been successful for putting federal lands on a trajectory for restoring forest capable of supporting spotted owls on federal lands. Information can be found in the "Habitat Status and Trends," "Disturbance," and "Conclusions and Management Considerations" sections.
3. What are the effects of various timber management practices and wildfire on forests used by spotted owls?
    - Information can be found in the "Habitat Status and Trends," "Disturbance," and "Research Needs" sections.
4. How is space use by spotted owls affected by timber management? Are there ways to modify management activities (i.e., silvicultural treatments) to benefit spotted owls? How do managed stands compare to untreated forests in terms of use by spotted owls?
    - Information can be found in the "Habitat Status and Trends," "Disturbance," "Research Needs," and "Conclusions and Management Considerations" sections.
5. Do spotted owls use forests following wildfire? If so, how? Do the impacts of treatments that reduce risk of wildfire outweigh the risks of suitable forest loss resulting from wildfire?
    - The short- and long-term response by spotted owls to wildfire remains largely unknown, and scientific debate remains. We were unable to fully address this question, but do provide a synthesis of available literature in the "Habitat Status and Trends," "Disturbance," "Research Needs," and "Scientific Uncertainty" sections.
6. How effective are protections for buffered areas around nest sites in retaining spotted owls across treated landscapes? Are site buffers equally effective as landscape-scale forest management in ensuring species persistence, dispersal, and habitat connectivity?
    - We were unable to address this question fully owing to the lack of published literature, but some information about the effectiveness of buffered management areas can be found in the "Habitat Status and Trends," and "Forest protection effectiveness" sections.

7. Which provides a higher level of spotted owl persistence: the current spotted owl critical habitat or the NWFP late-successional reserve network?
    - Information can be found in the "Habitat Status and Trends," and "Forest protection effectiveness" sections.
8. Does treating late-successional stands improve spotted owl persistence when wildfire, insects, disease, and climate change threaten the ability of these forests to provide habitat for spotted owls?
    - Information can be found throughout the chapter in the "Habitat Status and Trends," "Barred Owls," "Disturbance," "Climate Change," "Other Threats," "Research Needs," "Scientific Uncertainty," and "Conclusions and Management Considerations" sections.
9. What are the effects of barred owls on spotted owls? What is the relationship of wildfires to barred owl encroachment? Can a barred owl management program be effectively implemented at a scale that will have meaningful conservation value for spotted owls?
    - Information about the effects of barred owls is found in "Barred Owls." We were unable to adequately address questions about the relationship between barred owls and wildfire, and barred owl management, because of a paucity of literature. In addition, some of this research was ongoing at the time this synthesis was being prepared. We provide further details in "Research Needs, Uncertainties, Information Gaps, and Limitations."
10. What are the management considerations and research needs for spotted owls?
    - Based on our synthesis of available literature within the context of the guiding management questions we received, we specifically address high-priority information needs in "Research Needs, Uncertainties, Information Gaps, and Limitations." We conclude the chapter with "Conclusions and Management Considerations."

Key Findings

Population Status and Trends

Understanding vital rates (e.g., birth, death) and the factors affecting those parameters over time and space can provide crucial information for management and conservation. Since the listing of the spotted owl, demographic rates have been monitored in up to 14 demographic study areas distributed across the spotted owl's geographic range. Franklin et al. (1996) developed a general framework to estimate demographic parameters and population trends of spotted owls that has been used in subsequent spotted owl population analyses. In the past 10 years, three meta-analyses (Anthony et al. 2006, Dugger et al. 2016, Forsman et al. 2011) documented a continued decline in spotted owl populations throughout their range. Those meta-analyses built upon the Franklin et al. (1996) methods to analyze survival, reproduction, and territory occupancy data that has been collected consistently for nearly three decades.

The number of study areas in which spotted owls have been monitored has changed through time owing to changes in funding and institutional support. Anthony et al. (2006) used data from 14 study areas (1985 to 2003), Forsman et al. (2011) used data from 11 study areas (1985 to 2008), and Dugger et al. (2016) used data from 11 study areas (1985 to 2013) to evaluate survival, fecundity, recruitment, and rate of population change of spotted owls throughout the subspecies' geographic range (fig. 4-1). Dugger et al. (2016) also investigated territory occupancy dynamics (gains and losses of occupied territories; i.e., local colonization and extinction rates). All three meta-analyses investigated relationships between population demography of spotted owls and the distribution of suitable forest cover types, local and regional variation in climatic conditions, and presence of barred owls. Study areas included in these meta-analyses comprised about 9 percent of the spotted owl's range, were distributed throughout the geographic range, and were selected to encompass the broad range of forest conditions used by the subspecies.

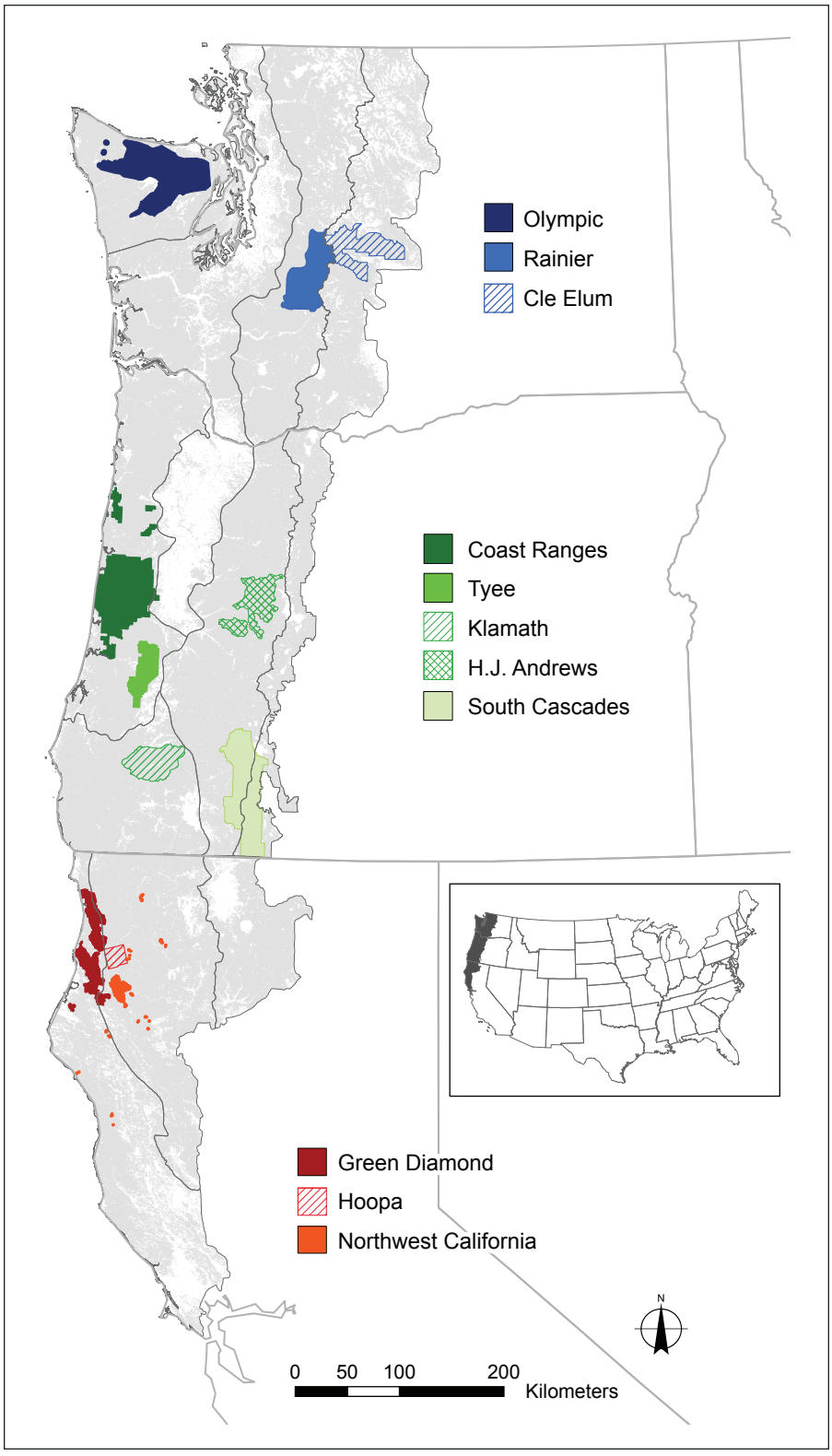


Figure 4-1—Locations of 11 study areas used in the analysis of vital rates and population trends of northern spotted owls, 1985 to 2013 (Dugger et al. 2016).

When the NWFP was developed, populations of spotted owls were estimated to be declining at about 4.5 percent (confidence interval [CI] 1.1 to 7.9) per year (Burnham et al. 1996, USDA and USDI 1994). The population was expected to continue declining for up to 50 years until younger second-growth forest in reserves matured to a point at which it would provide suitable structural conditions for nesting and roosting (Lint 2005, USDA and USDI 1994). During the first 10 years of the NWFP, the overall rate of population decline in Washington was much greater than in Oregon and California (Anthony et al. 2006, Lint 2005). Three study areas in southern Oregon had stable populations during the first decade. Anthony et al. (2006) estimated an annual decline of 3.7 percent (CI = 1.9 to 5.5) across the range, but that analysis included lands outside of the NWFP monitoring area. The eight federal study areas within the boundaries of the NWFP area (i.e., lands under federal management) used for effectiveness monitoring of the NWFP had a decline of 2.4 percent (CI = 1.0 to 3.8) compared to a 5.8 percent (CI = 2.6 to 9.0) decline for study areas composed primarily of nonfederal lands, suggesting that implementation of the NWFP had a positive effect on the demography of spotted owls (Anthony et al. 2006, Raphael 2006). Forsman et al. (2011) estimated an annual decline of 2.9 percent (CI = 1.7 to 4.0) throughout the northern spotted owl's range, and Davis et al. (2011) estimated an annual decline of 2.8 percent (CI = 1.5 to 4.2) within the eight federal study areas. The most recent meta-analysis indicated that spotted owl populations were continuing to decline throughout the range of the subspecies, and that annual rates of decline were accelerating in many areas (Dugger et al. 2016). The population was declining by about 3.8 percent (CI = 0.1 to 7.5) per year and declines ranged from 1.2 percent to 8.4 percent per year depending on the study area (fig. 4-2) (Dugger et al. 2016). For monitored populations, population change was more sensitive to adult survival than to recruitment (Glenn et al. 2010). Other studies have also documented declines in populations throughout the range of the spotted owl (Farber and Kroll 2012, Funk et al. 2010, Kroll et al. 2010).

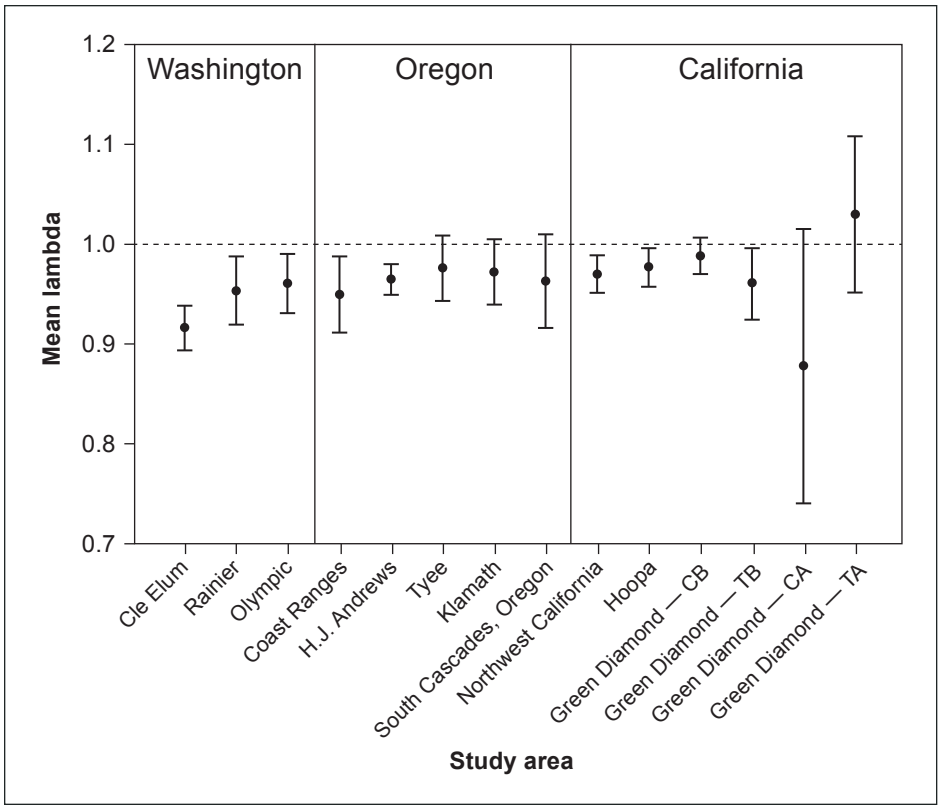


Figure 4-2—Estimated mean rates of population change (mean lambda) and 95 percent confidence limits for spotted owls from 1985 to 2013 at 11 sites: Cle Elum, Rainier, and Olympic, Washington; Coast Range, H.J. Andrews, and Tyee, Klamath, and South Cascades, Oregon; and northwest California, Hoopa, and Green Diamond, California (from Dugger et al. 2016). Estimates for Green Diamond are presented separately for control and treatment areas before (1990 to 2008) and after (2009 to 2013) barred owls were removed on the treatment area (CB = control before removal; TB = treatment before removal; CA = control after removal; TA = treatment after removal) (Diller et al. 2016, Dugger et al. 2016).

Habitat Status and Trends

Background and definitions—

Habitat for a species is an area that encompasses the necessary combination of resources and environmental conditions that promotes occupancy, survival, and reproduction of that species (Morrison et al. 2006). Typical wildlife habitat components include food, water, shelter (including nesting or denning sites), security from predators and competitors, and proper spatial arrangement of those features (Morrison et al. 2006). Although this concept of habitat may seem simple, the ways in which these individual components and animal needs interact in space and time result in very complex relationships (Mathewson and Morrison 2015).

Spotted owl habitat has often been characterized as older forest with large trees and moderate to closed canopy (Courtney et al. 2004, Forsman et al. 1984). Spotted owl site occupancy has repeatedly been shown to be influenced by the presence of these forest conditions (e.g., Dugger et al. 2016), likely because they often provide important habitat components that are suitable for nesting (e.g., cavities or platforms) (Sovern et al. 2011), abundant prey populations (Carey et al. 1992, Forsman et al. 2004, Wilson and Forsman 2013), and security from predators, including other raptors (Forsman et al. 1984, Sovern et al. 2014). An advantage of characterizing spotted owl habitat based on forest structure is that these forest types can be mapped for the entire subspecies' range using remotely sensed data (Davis et al. 2016). Other habitat components like prey abundance, predation risk, and presence of competitors are much more difficult, if not impossible, to map independently. For example, the recent colonization of the range of northern spotted owls by barred owls has confounded efforts to quantify the amount of habitat available for spotted owls because barred owls use similar forest types and can displace spotted owls from those areas (see "Barred Owl" section below).

In addition to availability, the arrangement of habitat components at a variety of scales is also important for understanding spotted owl habitat. Typically, spotted owl habitat is discussed in terms of forest cover types (stand-level forest structure and composition) most suitable for nesting, roosting, foraging, or dispersal (Davis et al. 2016, Lint 2005, Thomas et al. 1990). However, the spatial and temporal dynamics of suitable forest cover types, and how environmental conditions including climate and topography interact with vegetation patterns, are also important for producing and sustaining habitat for spotted owls (USFWS 2012a, 2012b). For example, Glenn et al. (2017) constructed habitat models using forest cover types and abiotic environmental conditions, and estimated the density of spotted owl territories on a landscape before and after barred owl invasion.

In this chapter, we define spotted owl habitat as those areas with the full suite of resources (e.g., abundant prey, available nest structures) and environmental conditions (e.g., appropriate climate, suitable forest structure, and infrequent presence of barred owls) suitable for occupancy, reproduction, and survival of the subspecies. As such, habitat is more analogous to a species' realized niche rather than the fundamental niche because habitat is more constrained than the availability of a vegetation type and a subset of environmental conditions. All published models of spotted owl habitat fall short of this definition because the distribution of spotted owls in relation to abundant prey is not known, and the distribution of an important competitor—barred owls—is not fully known. Throughout this chapter we distinguish between spotted owl habitat and components of that habitat (e.g., forest cover types used for nesting and roosting) regardless of the terms used in published literature.

Differing concepts regarding habitat definitions have long caused confusion and uncertainty in the interpretation of scientific literature (Bamford and Calver 2014, Hall et al. 1997, Morrison et al. 2006). The differences in how spotted owl habitat is defined and modeled has also caused confusion. The NWFP monitoring program estimates trends in forest types used by spotted owls (Davis and Lint 2005). The Fish and Wildlife Service (USFWS 2012a) modeled suitable forest and considered the amount and spatial arrangement of forests associated with specific life history requirements (e.g., forest types used for foraging in relation to forests used for nesting and roosting), as well as abiotic factors (e.g., slope, climate). The resulting models were used for delineation and designation of what was considered critical habitat (USFWS 2011b). The models of potential spotted owl habitat developed by the NWFP monitoring

program and the Fish and Wildlife Service have important differences that result in different amounts of what is considered suitable forest for spotted owls. Estimates of the amount of suitable forest for spotted owls are highly scrutinized because of the conflict caused by the importance of that forest type for the reproduction and survival of spotted owls and because merchantable large timber is important economically for many of the rural areas where old forest occurs. The different estimates of suitable forest cover for spotted owls resulted in litigation filed in relationship to critical habitat designation. Carpenters Industrial Council et al. vs. Ashe and Salazar (District of Columbia District Court case number 1:2012cv00111 filed January 24, 2012) claimed that the USFWS (2012a) estimate of approximately 18 million ac (7.3 million ha) of suitable forest conditions (they used the term habitat) for spotted owls was an overestimate of 5.9 million ac (2.4 million ha) because previous documents produced by the agency had used estimates of approximately 12.1 million ac (4.9 million ha) as found in (Davis et al. 2011). The 2.4 million ha difference can be explained by an examination of how habitat was defined and modeled in the different efforts. For example, estimates from Davis et al. (2011) were based on a stand-level designation of forest cover suitable for nesting and roosting (fig. 4-3A), whereas USFWS (2011b) and USFWS (2012a) delineated critical habitat based on a model that included suitable forest stands (Davis et al. 2011) and other landscape components essential for spotted owls at the core-area scale (200 ha) (fig. 4-3B).

The NWFP defined suitable forest for spotted owls as an area with the species of trees, structure associated most commonly with late-successional forest, sufficient area, and adequate food source to meet some or all of the subspecies' life needs, including nesting, roosting, and foraging (USDA and USDI 1994). This definition relied heavily on the work in the Interagency Scientific Committee report (Thomas et al. 1990), which acknowledged the difficulty in defining habitat and chose to characterize the concept based on relative value or suitability of forest stands for spotted owls. Forest cover can be viewed as supporting different spotted owl life functions (e.g., nesting, roosting, foraging) and a suitability gradient in terms of its influence on individual fitness (Thomas et al. 1990). Partitioning of forest cover

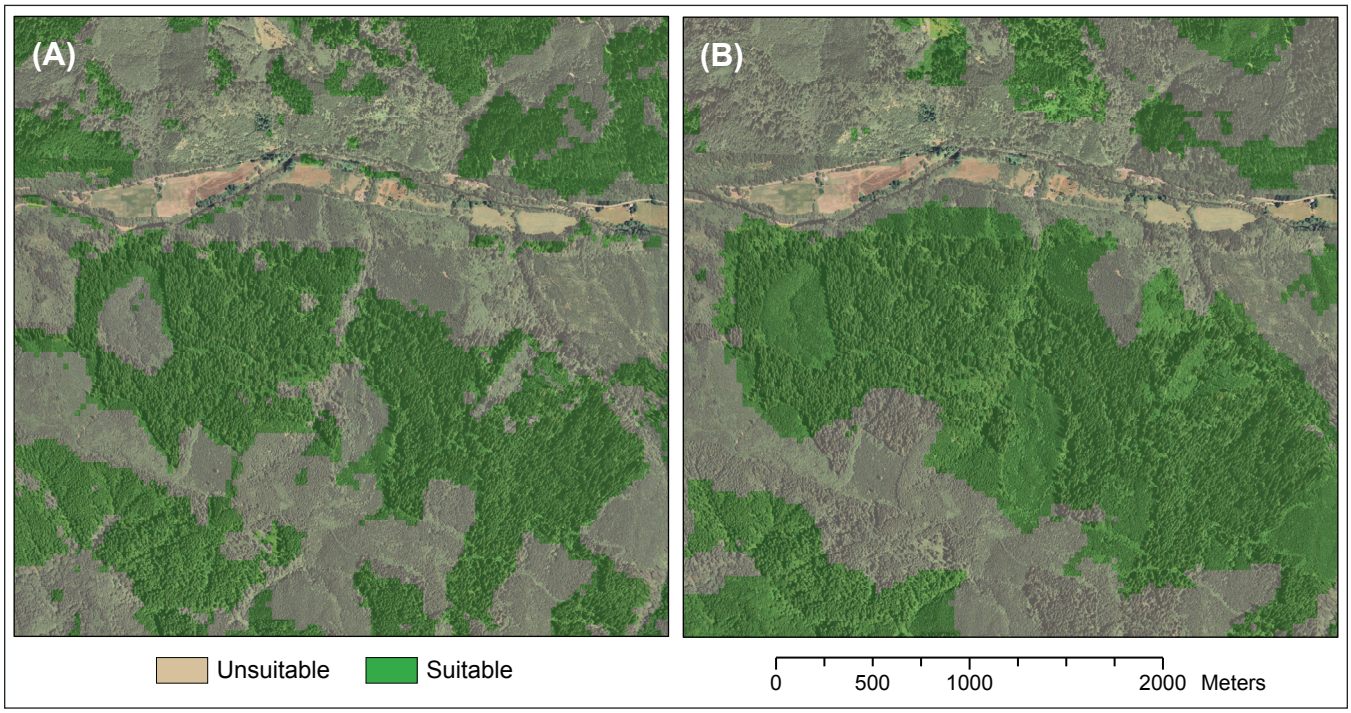


Figure 4-3—Examples of the suitable forest cover at (A) the stand scale developed by the Northwest Forest Plan monitoring program (Davis et al. 2011), and (B) the 200-ha (~250-foot radius) core-area scale used for modeling and delineating critical habitat (USFWS 2012a).

into discrete categories based on established measures of suitability for particular life functions facilitates a common frame of communication and standardization. A monitoring framework to measure relative suitability of forest cover types used by spotted owls was developed as part of a rangewide monitoring program for the subspecies (Davis et al. 2011, 2016; Lint 2005). Monitoring divided a continuous gradient of cover-type suitability into four discrete classes (table 4-1), based on use-versus-availability analyses using documented territorial pair locations. The unsuitable class was used for nesting and roosting by spotted owls less than expected by chance based on availability, the marginal class was used in proportion to its availability, the suitable class was used more often than expected by chance, and the highly suitable class was used much higher than one would expect from chance based on its availability. For monitoring purposes that dates to the life of the NWFP, the suitable and highly suitable classes were combined into a single class to identify forests that were most strongly associated with nesting and roosting locations. Thomas et al. (1990) characterized highly suitable forest cover as forests that include a multilayered, multispecies canopy dominated by large (>30 inch diameter at breast height [d.b.h.]) conifer trees; an understory of shade-tolerant conifers or hardwoods; moderate to high (60 to 80 percent) canopy cover (they used the term closure, but by definition they had described cover) (Jennings et al. 1999); substantial decadence in the form of large, live coniferous trees with deformities (e.g., cavities, broken tops, and dwarf mistletoe infections); numerous large snags; large accumulations of logs; and other woody debris. The unsuitable or marginal classes do not imply unimportance to spotted owls because the classification was restricted to describe only suitability for nesting and roosting activities by spotted owls. The marginal class is likely important for supporting dispersal, foraging, and nonbreeding (i.e., floater) individuals that can replace adult mortality and dispersal at nesting territories. Likewise, unsuitable and marginal classes may be important forest types for many prey species used by spotted owls. Forests that are suitable for nesting and roosting have similar characteristics throughout the range of spotted owls, but the path of development to those conditions typically differ based on the fire regime within the area (chapter 3; table 4-2, fig. 4-4).

Thomas et al. (1990) defined forest suitable for dispersal as having ≥11 inch (28 cm) d.b.h. trees and ≥40 percent canopy cover occurring on ≥50 percent of a 36 mi^2 township; this definition became known as the 50/11/40 rule. Analyses of movement data of spotted owls suggest that most (90 percent) dispersal occurred through landscapes meeting these criteria and are generally considered

Table 4-1—General descriptions of forest cover type classes used to estimate the amount of suitable forest available for nesting and roosting by spotted owls.

Cover type class	General description
Unsuitable	Younger forests or older forests with higher basal area of pine or high-elevation tree species or more open canopies. Usually smaller than average tree diameters, and lacking the presence of residual large trees and multiple canopy layers.
Marginal	Usually mid-seral forests, but can also be older forests lacking large-diameter trees, having simpler stand structure, or primarily composed of pine or high-elevation tree species.
Suitable	Forest stands older than 125 years of age, except in the California redwoods, where younger stands are used. Average tree diameters are usually above 20 inches (50 cm) d.b.h., with the presence of at least a few large trees exceeding 30 inches (75 cm) d.b.h. Canopy cover is usually greater than 60 percent, and the stand has multiple canopy layers.
Highly suitable	Typically forests 150 and 200 years of age or older. Average tree diameters often in excess of 30 inches (75 cm) d.b.h. except in drier portions of the range, where tree ages and sizes are typically smaller (e.g., 120 years and 24 inches). Canopy cover is usually in excess of 70 percent, and the stand has multiple canopy layers with high diversity of tree sizes.

d.b.h. = diameter at breast height.
Source: Davis et al. 2016.

Table 4-2—General descriptions of how forest cover types suitable for nesting and roosting by spotted owls typically develop within four general fire regimes within the Northwest Forest Plan (NWFP) area

Fire regime	Typical development of suitable nesting/roosting forest
Infrequent—high severity (Coast Range, fig. 4-4)	Large contiguous patches that form following infrequent, yet very large, high-severity wildfires. Once established, these large patches persist for long periods until the next large high-severity wildfire. Immediately following a large wildfire, large areas of the landscape are unsuitable for nesting and roosting for decades until closed canopies redevelop in areas that had remnant tree structures that could serve as nest trees. During this period, fine-scale gaps created by root-rot pockets, windstorms, landslides, and other small-scale processes produce complex stand structure. Complex structure sometimes does not develop over large areas for several decades following a wildfire. Produces the largest diameter and tallest nest trees; nests are usually in cavities or broken tops.
Moderately frequent—mixed severity (West Cascades, fig. 4-4)	Abundant to moderately abundant on the landscape, but very well connected across the landscape owing to the lack of extremely large high-severity wildfire patches. High-severity wildfire created smaller patches of complex early-seral forest cover type within an otherwise older forest matrix. Through time, these wildfire-created patches produced complex forest structure at the stand scale and a diverse mosaic of seral stages at the landscape scale.
Frequent—mixed severity (Klamath Mountains, fig. 4-4)	Moderately abundant on the landscape but more confined to topographic positions that functioned as wildfire refugia (e.g., lower slopes, north aspects, etc.). These areas allowed for the development and persistence of large trees required for nesting structures. In the Klamath Mountains and California Coast Range physiographic provinces, evergreen hardwoods (e.g., tanoak) are an important component that increase the suitability of use in these stands. In addition to forest stand structure and species composition, climate, and topography are important predictors of use by spotted owls.
Very frequent—low severity (East Cascades, fig. 4-4)	Not naturally abundant within the NWFP area; primarily restricted to the east side of the Cascade Mountains and eastern parts of northern California. Occurred historically in areas where the topography or soil conditions created a productive environment suitable for the development of large Douglas-fir and grand fir. Once established, these closed-canopy, structurally complex forest cover conditions can be relatively resistant to most fires, but burn with high severity under extreme weather conditions (chapter 3).

capable of supporting dispersal (Davis et al. 2011, 2016; Forsman et al. 2002; Lint 2005). However, the Thomas et al. (1990) 50/11/40 hypothesis was not based on juvenile resource selection data and remains largely untested. Only two studies (Miller et al. 1997, Sovern et al. 2015) have empirically studied forest-type selection during juvenile dispersal. Both studies found that juveniles strongly select for old forest with closed canopy (>70 percent canopy cover) and large-diameter trees (>20 inch d.b.h.), which are similar forest conditions selected by adult spotted owls for nesting and roosting (Miller et al. 1997, Sovern et al. 2015). Given the importance of forest cover classified as suitable for nesting and roosting to juvenile dispersal, the canopy cover recommendations of Thomas et al. (1990) are unlikely to be sufficient to facilitate juvenile movements on the landscape. Sovern et al. (2015) suggested that stands managed for dispersing spotted owls should be at least 80 percent canopy cover and have large average tree diameter.

Both the nesting/roosting and dispersal maps of suitable cover types produced by the NWFP monitoring program were designed to match the conceptual descriptions of forest vegetation components defined by Thomas et al. (1990) and used at the time of the NWFP development. Mapping of forests used by spotted owls is continuing to

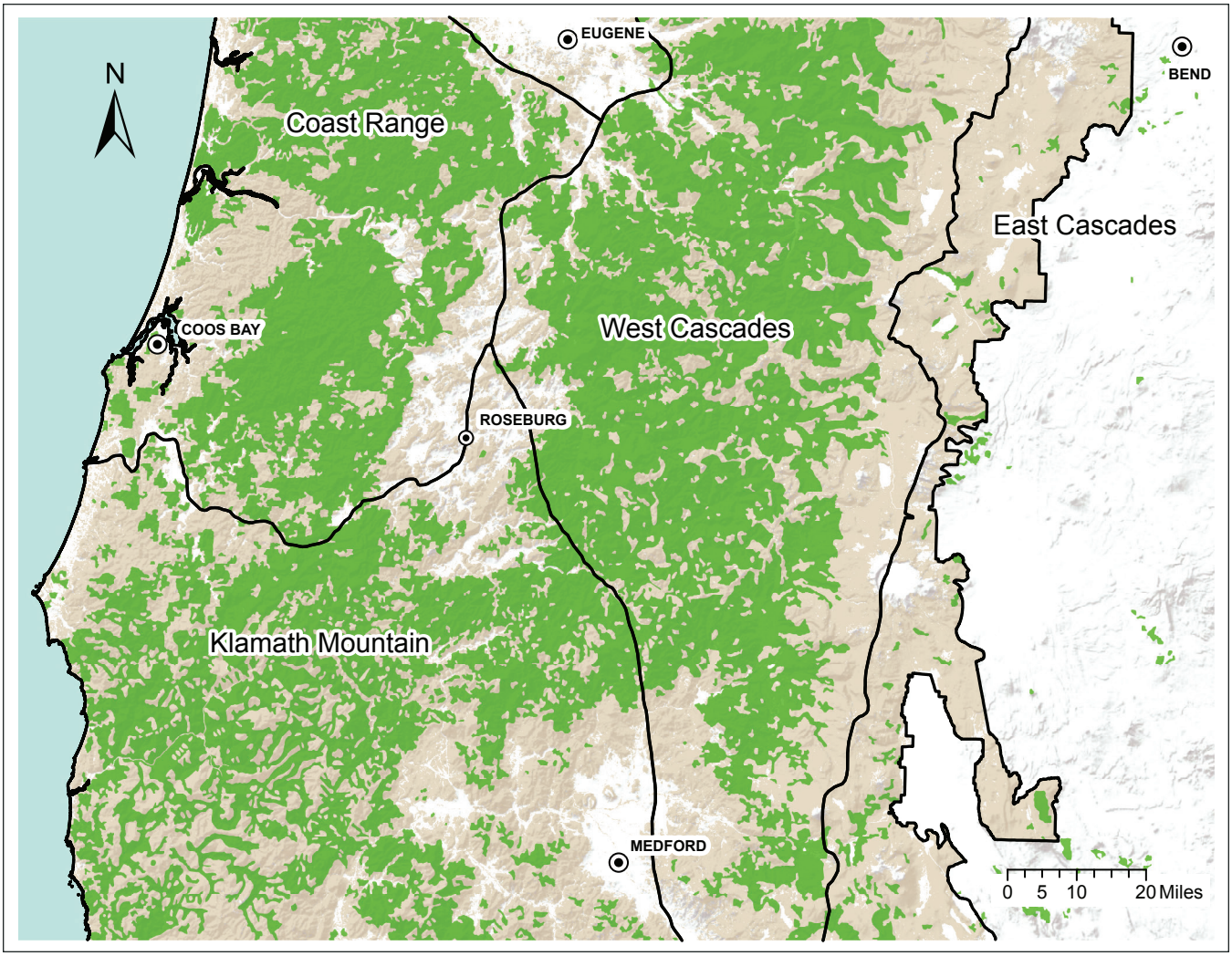


Figure 4-4—Differing historical patterns of old-growth Douglas-fir and mixed-conifer forest (green shaded areas) in west-central Oregon (Andrews and Cowlin 1940) within four areas with different fire regimes (Coast Range, infrequent—high severity; West Cascades, moderately frequent—mixed severity; Klamath Mountains, frequent—mixed severity; East Cascades, very frequent—low severity).

evolve (Ackers et al. 2015). For example, recent maps of suitable forest types (e.g., Glenn et al. 2017; USFWS 2011b, 2012a) differed from the original monitoring maps in that they factored in the spatial arrangement of discrete forest cover types (e.g., nesting, roosting, foraging) as well as abiotic factors (e.g., slope, topographic position, etc.) to produce maps describing a more comprehensive view of suitable forest (i.e., potential habitat). However, even the most recent efforts are not complete models of spotted owl habitat because they lack the impact of prey and barred owls on restricting distribution by limiting access to otherwise suitable forest for spotted owls. An important need is a better understanding and mapping of the differences between the potential and realized habitat for spotted owls. This is discussed in the "Research Needs, Uncertainties, Information Gaps, and Limitations" section below.

Patterns of change—

***Federal vs. nonfederal lands*—**Davis et al. (2016) estimated that there were about 12.6 million ac (5.1 million ha) of suitable nesting and roosting cover type distributed across the spotted owl's geographic range at the time of NWFP development (1993), the majority (73 percent) of which occurred on federal lands. By 2012, suitable nesting/roosting forest

cover decreased to 12.1 million ac (4.9 million ha) (74 percent occurring on federal lands), resulting in an overall net change of -3.4 percent. Net decreases were -1.5 percent on federal lands (primarily caused by wildfire) and -8.3 percent on nonfederal lands (primarily caused by timber harvest). During those two decades, forest cover suitable for dispersal decreased from 26.2 to 25.7 million ac (10.6 to 10.4 million ha) (-2.3 percent net change) on all lands. On federal lands, forest cover suitable for dispersal increased by 2.2 percent, and it decreased by 8.6 percent on nonfederal lands (Davis et al. 2016). Gains occurred because of forest succession, whereas losses were primarily a result of wildfire, disease, and timber harvest (Kennedy et al. 2012).

Timber harvest accounted for the majority (63 percent) of the losses across all lands. The vast majority of losses on nonfederal lands was caused by timber harvest (94 percent), whereas timber harvests accounted for 18 percent of total losses on federal lands (Davis et al. 2016). In Washington alone from 1996 to 2004, most (85 percent) of the timber harvest that resulted in lost forest cover suitable for nesting and roosting of spotted owls occurred on private lands (Kennedy et al. 2012, Pierce et al. 2005). Following timber harvest, wildfire was the next largest cause of loss (31 percent of total losses), which was 73 percent of the losses on federal land and only 3 percent of the losses on nonfederal land.

***Moist vs. dry forests*—**Primary causes of loss differed by ecoregion and forest type. The loss of nesting and roosting forest cover from wildfire occurred primarily in drier, fire-prone portions of the spotted owl's geographic range (i.e., northern California, southern Oregon, and eastern Cascade Range). Losses owing to insects and disease (and other natural disturbances) was the next most significant disturbance and mainly occurred in the eastern Cascades of Washington and Oregon (Davis et al. 2016, Kennedy et al. 2012).

Recruitment of forest cover suitable for nesting and roosting by spotted owls was estimated at 257,591 ac (104 288 ha) from 1993 to 2012 (Davis et al. 2016). Most of the gain occurred on nonfederal lands within the redwood (*Sequoia sempervirens*) zone of coastal California (fig. 4-5). On federal lands, the largest net gain (40,385 ac [16 350 ha]) occurred in the eastern Cascades of Oregon, where fire suppression allowed forest succession of Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*) to develop in areas that historically had frequent low-severity fires and were formerly dominated by open ponderosa pine-dominated forests (*Pinus ponderosa*) (Davis et al. 2016).

Effects of forest change—
Loss of suitable forest cover for nesting and roosting, especially on nonfederal lands, has been an important contributor to declining populations of spotted owls (Dugger et al. 2016). Those spotted owls that had territories with more forest cover associated with nesting and roosting conditions typically had better survival, fecundity, occupancy dynamics, recruitment, and rate of population change (Dugger 2016; Dugger et al. 2005, 2011; Forsman et al. 2011; Seamans and Gutiérrez 2007). For example, Dugger et al. (2005) found that owl territories with the greatest fitness potential were characterized by >50 percent old-forest habitat within a 412-ac (167-ha) circle centered on used nest locations. Relationships among population parameters of spotted owls and older forests vary over different spatial scales (e.g., individual territory vs. study area), and can be independent of, or interact with, the presence of barred owls. Concentrated areas of older forest suitable for nesting and roosting, or increased amounts of heterogeneity (i.e., mixture of conditions used for foraging), have positive effects on the vital rates of spotted owls (Dugger et al. 2016, Forsman et al. 2011, Franklin et al. 2000, Olson et al. 2004).

In some landscapes, fragmentation of older forest can have negative or positive effects on spotted owl occupancy depending on the scale of fragmentation and edge characteristics. Schilling et al. (2013) found that spotted owls had decreased survival and increased home-range size with increased forest fragmentation in southwestern Oregon. In Washington, territory-level extinction rates decreased with increased amount of late-seral edge, and colonization decreased with more late-seral patches within a territory (Sovern et al. 2014). It is also important to consider spatial scale, and level of contrast between edge, when assessing the influence of forest edges on foraging and space use by spotted owls. Comfort et al. (2016) found that spotted owls radio-marked in southern Oregon were negatively associated with hard edges (high contrast in forest structure and height) at a fine scale (telemetry location), but showed a lack

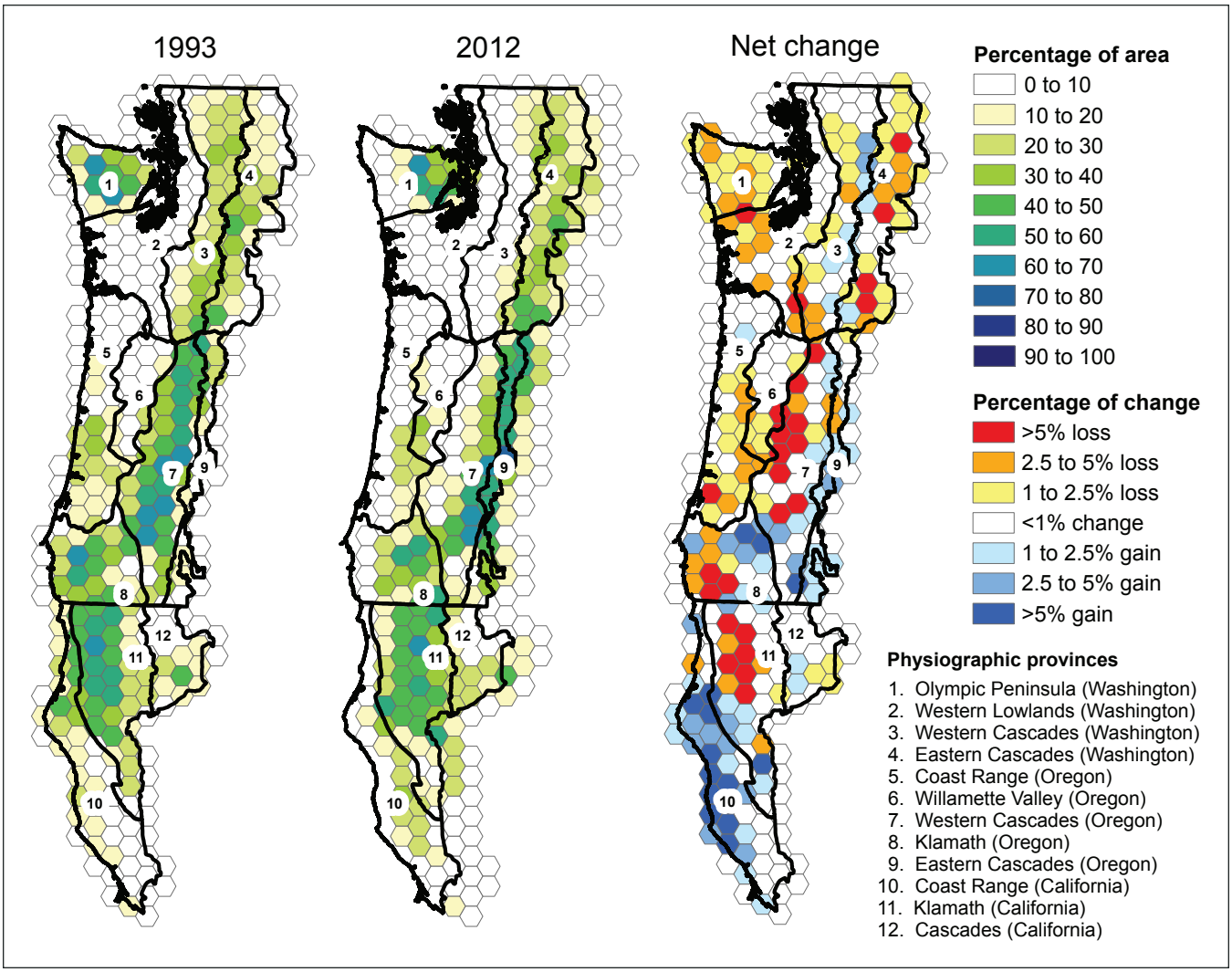


Figure 4-5—Loss and recruitment of forest types suitable for nesting and roosting by spotted owls in 1993 versus 2012, based on change in percentage of cover estimated within 18.6 mi (30 km) (center to center) hexagons across the Northwest Forest Plan area.

of negative response to hard edges at broader scales (territory or home-range scales). At least at the territory scale, heterogeneity can contribute to accessibility to different forest types. Regardless of spatial scale, spotted owls were positively associated with softer, more diffuse edge types created by disturbances such as low- and mixed-severity fire (Comfort et al. 2016). Collectively, these and other studies suggest that spotted owls select for abundant, structurally diverse closed-canopy forest with diffuse late-seral forest edge at the territory scale, and relatively lower fragmentation in nesting areas (Franklin et al. 2000, Olson et al. 2004, Sovern et al. 2014).

Forest protection effectiveness—

The NWFP included a network of large late-successional reserves (LSRs) that were designed to conserve forest for species dependent on older forests (FEMAT 1993). The LSR network was intended to meet the resource needs of many species, but a substantial focus was placed on creating and maintaining forest cover features from a draft recovery plan for the spotted owl (USFWS 1992). LSRs contained enough suitable forest cover to support multiple pairs of spotted owls and were distributed to facilitate movement of spotted owls across their geographic range. Although many of the LSRs contained large areas of older forest, a

significant portion of them were delineated in fragmented landscapes that contained stands of younger forest. Dispersal between LSRs is important for spotted owl conservation, and the NWFP was expected to facilitate that dispersal by designated riparian reserves, retention of green trees in timber harvest units in the matrix, protection of 100 ac (40 ha) areas at known owl sites (managed as LSRs within the matrix), and other administratively withdrawn areas (USDA and USDI 1994). However, these assumptions are largely untested, so it remains unknown if the NWFP is sufficient to facilitate adequate dispersal, which may be a limiting factor of spotted owl populations.

In addition to broad-scale LSRs, forest protections for spotted owls include circles of varying radii centered on used nest locations, within which various amounts of suitable nesting, roosting, and foraging forest cover types are protected. For example, the Fish and Wildlife Service developed guidelines for consultation under section 7 of the Endangered Species Act that included a 2.9-km-radius circle (6,424 ac [2600 ha]) around spotted owl nest locations for evaluating ''incidental take'' for projects affecting suitable habitats (USDA and USDI 1994). The rationale for this circle size was developed based on preliminary analysis of the median home-range size of radio-marked spotted owls. States also developed rules for state and private forestry practices to protect spotted owl nest sites. For example, the 2006 Washington State Forest Practices Board Rules called for protection of 40 percent cover of suitable nesting and roosting forest within a 6,422 ac (2600 ha) circle around nest sites (WAC 222-10-041). Forsman et al. (2015) suggested that level of protection would not be sufficient because spotted owl home ranges contained more suitable forest cover than would be protected under the Washington forest practices rules. Furthermore, new methods for delineating owl territories (e.g., Thiessen polygons) used by Dugger et al. (2016) provide better representations of the territory.

At the time LSRs were delineated, it was estimated that they contained on average 43 percent older forest (USDA and USDI 1994). The expectation was that all LSRs would eventually fill in and achieve the 60-percent-or-greater area threshold needed to support multiple breeding pairs and collectively would facilitate spotted owl population recovery. The success of meeting that threshold depends on the frequency, severity, and spatial extent of disturbance (e.g., wildfire, timber harvests), as well as the rate of forest succession, and interactions among these processes on forest recruitment (chapter 3). As of the most recent monitoring report (Davis et al. 2016), the rangewide estimate for suitable nesting/roosting forest cover in LSRs was an average of 42.4 percent in 1993. As of 2012, this average decreased to 42.0 percent. Larger LSRs (≥10,000 ac) averaged 45.0 percent, decreasing to 44.5 percent by 2012. These losses were due mainly to wildfire and exceeded the regional-scale expected rate of loss (2.5 percent per decade) (FEMAT 1993). Most of the losses of nesting and roosting forest cover have been in the more fire-prone portions of the spotted owl's range (Davis et al. 2011, 2016). For example, within LSRs and other reserves (e.g., administratively withdrawn, wilderness areas, etc.) in the Klamath Mountains physiographic province, losses were as high as 18.9 percent between 1993 and 2012 (fig. 4-5), and largely the result of the 2002 Biscuit Fire, which burned 494,000 ac (>200 000 ha).

Forest cover trends on federal lands during the next two to three decades are expected to benefit spotted owls because significant recruitment of suitable nesting/roosting forest cover is expected to offset many pre-NWFP losses (chapter 3) (Davis et al. 2016). However, this expectation is based on current rates of harvest and wildfire occurrence on federal lands, which may change depending on future forest plan revisions and the predicted increased spatial extent, frequency, and severity of wildfires due to climate change (chapter 2) (Jones et al. 2016, Westerling et al. 2006). In addition, competitive pressure from established barred owls (see below) has raised uncertainties about whether recruitment of suitable forest cover will be enough to conserve spotted owls over the long term. If spotted owls are to persist in LSRs under competitive pressure from barred owls, it will likely be only in localized areas that support few barred owls. However, it remains doubtful if there are any areas where spotted owls hold a competitive advantage over barred owls (Pearson and Livezey 2007, Singleton 2013, Wiens et al. 2014).

The potential effects of climate change add to the uncertainty of how competitive dynamics with barred owls and availability of suitable habitat will affect spotted owls in the future. Carroll et al. (2010) used a climatic niche modeling approach to evaluate the regional system of LSRs for resiliency to climate change for providing necessary resources of species associated with old forest. They developed distribution models integrating climate data with vegetation variables for a large suite of species, including the spotted owl. The LSRs functioned better than expected by chance for capturing all of the species, but community composition and interspecific interactions were also important to consider in evaluating effectiveness of the reserves. A network of fixed reserves with a high level of climatic and topographic heterogeneity (i.e., designed for resilience) has an increased likelihood of retaining the biological diversity of old-forest ecosystems under climate change. Under this scenario, even those species with limited dispersal capability are able to colonize future habitat. Carroll et al. (2010) projected a northward and higher elevation movement of suitable forest for spotted owls; therefore, the current fixed system of LSRs may not have enough climatic and topographic heterogeneity to be adequate for spotted owls into the future. Other reserves designated before the NWFP, such as parks and wilderness areas, may become increasingly important for the subspecies' persistence. LSRs successfully protected areas with greater biological importance for spotted owls when the NWFP was developed, but in the face of climate change, it may be necessary to have another evaluation and planning phase that results in a reserve system designed for more robust resilience (Carroll et al. 2010) (see chapter 3 for more discussion of alternative reserve designs), especially in the dry forest zone where management for ecosystem and spotted owls may not be compatible at stand and small landscape scales (chapter 12). Even with relatively little modification in response to climate change, suitable forest conditions on the east side and southern portions of the range are at risk of losses. Dense, multilayered forests in the dry forest zone are vulnerable to a host of mortality forces, especially wildfire (see chapters 3 and 12).

Barred Owls

Barred owl range expansion and population trends— Competition with established populations of barred owls has emerged as a much more prominent and complex threat to the long-term persistence of the spotted owl than was anticipated during the development of the NWFP. Once confined to forests of eastern North America, the barred owl is a medium-size, ecologically similar species whose newly extended geographic range now completely overlaps that of the northern spotted owl (Gutiérrez et al. 2007, Livezey 2009). Newly colonizing barred owls in the Pacific Northwest have been classified as native invaders—species that, under the influence of events such as climate change or human modifications to the landscape, have become invasive by expanding their populations into new areas (Carey et al. 2012, Valéry et al. 2009, Wiens et al. 2014). The range expansion of barred owls in western North America is well documented (Dark et al. 1998, Dunbar et al. 1991, Kelly et al. 2003, Livezey 2009, Taylor and Forsman 1976). Initial colonization of different regions by barred owls was variable, but barred owls now appear to co-occupy and outnumber spotted owls throughout the entire range of the threatened subspecies (Dugger et al. 2016, Pearson and Livezey 2003, Singleton et al. 2010, Wiens et al. 2011, Yackulic et al. 2012). Barred owls have also invaded the range of the California spotted owl in the Sierra Nevada (Seamans et al. 2004). The cause of this range expansion is unknown, but landscape changes facilitated by European settlement or historical changes in climate are factors that may have enabled barred owls to expand their range from eastern to western North America (Livezey 2009, Monahan and Hijmans 2007).

With few exceptions, barred owls have not been systematically surveyed in the Pacific Northwest, and the majority of information on their distribution and population trends is limited to incidental observations during surveys of spotted owls (Dugger et al. 1991, 2016; Gutiérrez et al. 2007; Wiens et al. 2011). Despite this shortcoming, incidental field data show a rapid increase in barred owls as they expanded their populations westward and southward into the range of the spotted owl (fig. 4-6) (Dugger et al. 2016). Studies focused on barred owls found much higher densities than estimates based on incidental field observations

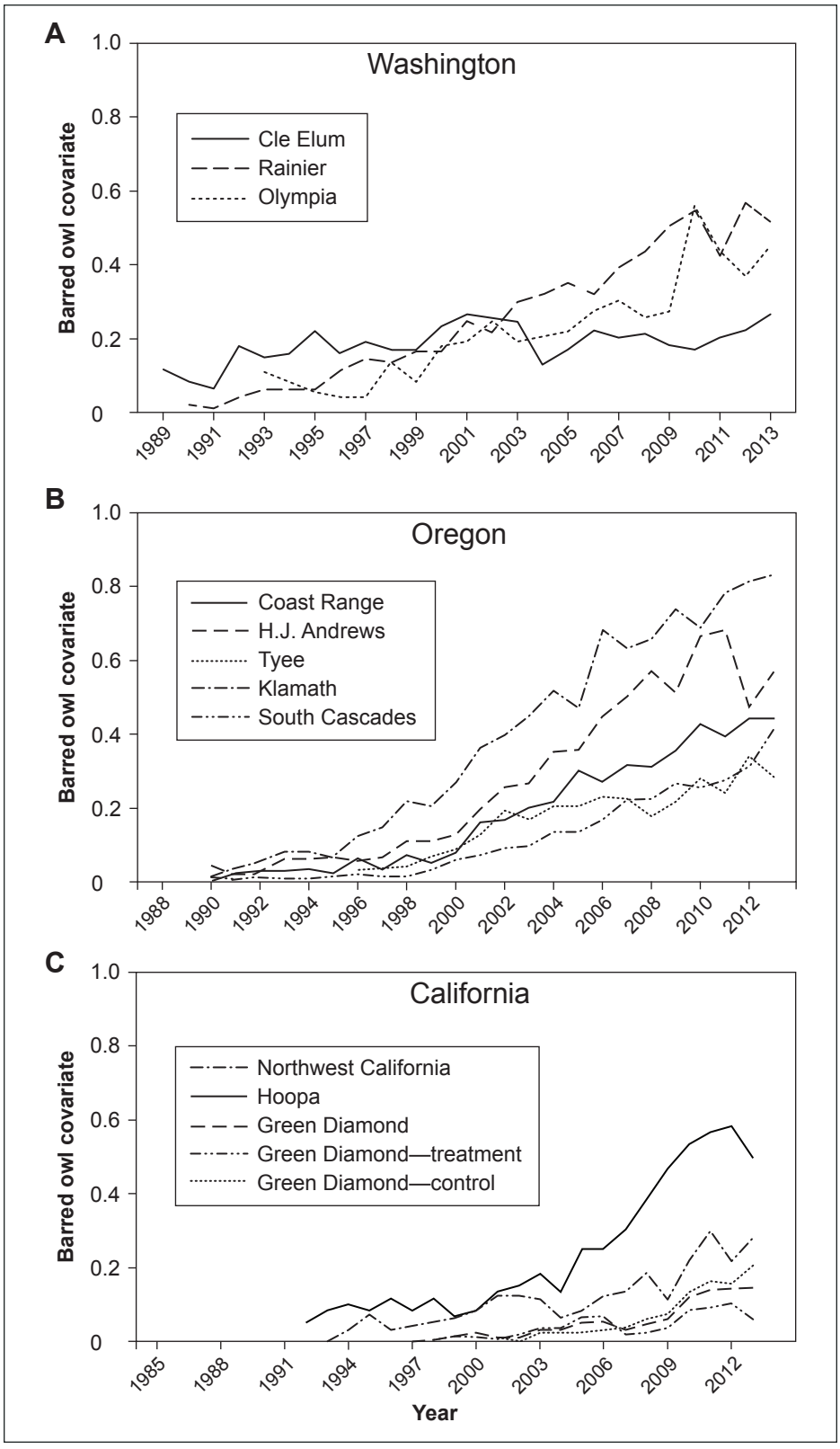


Figure 4-6—Annual increase in the proportion of spotted owl territories with detections of barred owls at (A) three sites in Washington, (B) five sites in Oregon, and (C) three sites in California from 1985 to 2013 (Dugger et al. 2016). Estimates for Green Diamond are presented separately for control and treatment areas and after (2009 to 2013) barred owls were removed from the treatment area from 2009 to 2013.

(Hamer et al. 2007; Singleton et al. 2010; Wiens et al. 2011, 2014; Yackulic et al. 2012, 2014). For example, Wiens et al. (2011) conducted surveys of barred owls during 2009 in the Oregon Coast Range and identified approximately 11 territorial pairs of barred owls per 100 km^2 (39 mi^2; 3 to 8 times higher density than spotted owls) with 89 percent of the landscape occupied, which peaked on publicly owned lands with greater amounts of mature and old coniferous forest. More recent (2015–2016) surveys of barred owls indicate an even greater probability of landscape occupancy in the Oregon Coast Range (~0.94) (Wiens et al. 2017). The degree to which the colonizing population of barred owls has reached carrying capacity within the geographic range of the spotted owl is currently unknown, but studies are underway that can help address this uncertainty (e.g., Wiens et al. 2017). Barred owl populations may continue to increase depending on the capacity of available habitat and food resources, which varies regionally with forest composition and latitudinal changes in prey communities and climate.

Barred owl effects on spotted owls— Compared to spotted owls, barred owls are slightly larger (Gutiérrez et al. 2007), have more diverse diets (Hamer et al. 2001, Wiens et al. 2014), and use a broader range of forest conditions for nesting (Herter and Hicks 2000, Livezey 2007, Pearson and Livezey 2003) and foraging (Hamer et al. 2007, Singleton 2015, Singleton et al. 2010, Weisel 2015, Wiens et al. 2014). Barred owls also have higher annual survival (fig. 4-7), higher reproductive output, and, in most areas, use much smaller home ranges than spotted owls (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014). The exception is in northern California,

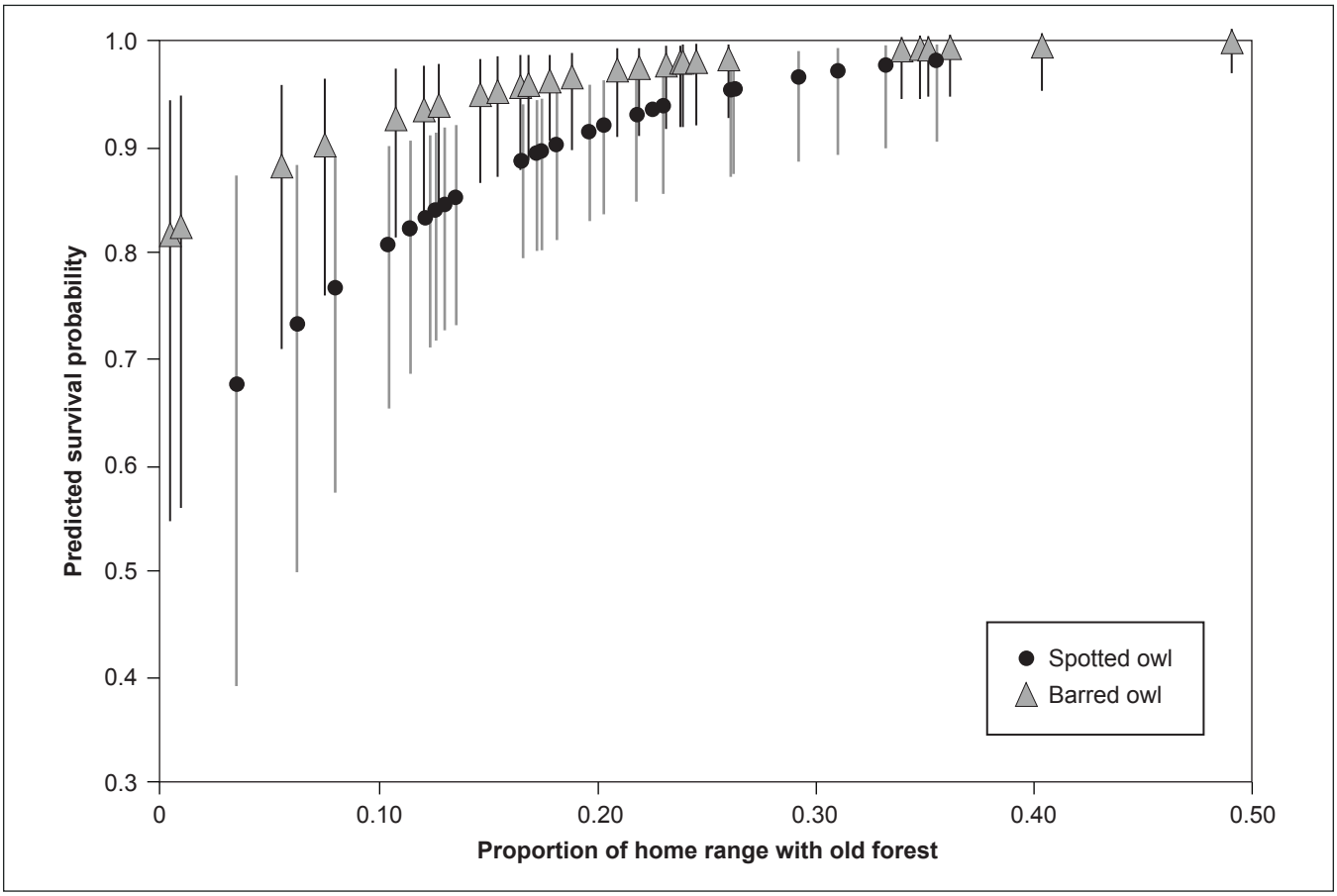


Figure 4-7—Survival (with 95-percent confidence limits) of individual adult barred owls and spotted owls increased with increasing amount of old forest (≥120 years) conifer forest within their home ranges in the Oregon Coast Range (Wiens et al. 2014).

where the two species used relatively small home ranges of similar size (Weisel 2015). Barred owls also defend their territories more aggressively than spotted owls (Van Lanen et al. 2011), which can result in increased mortality of spotted owls from agonistic interactions and direct killing of spotted owls by barred owls (Leskiwand Gutiérrez 1998, Wiens et al. 2014).

The dramatic increase in populations of barred owls since implementation of the NWFP has significant implications for management of forests inhabited by spotted owls. Several lines of evidence indicate that increases in the abundance of barred owls has had a strong and negative impact on spotted owls. Increasing abundance of barred owls has been documented to have the following effects on spotted owl populations:

1. Occupancy of historical spotted owl territories is lower (fig. 4-8) (Bailey et al. 2009, Dugger 2016, Dugger et al. 2011, Kelly et al. 2003, Kroll et al. 2010, Olson et al. 2005, Sovern et al. 2014; Yackulic et al. 2014).
2. Apparent survival is lower (Anthony et al. 2006, Diller et al. 2016, Dugger et al. 2016, Forsman et al. 2011, Glenn et al. 2011a).
3. Reproduction is lower (Dugger et al. 2016, Forsman et al. 2011, Olson et al. 2004).
4. Population size declines more rapidly (Anthony et al. 2006, Dugger et al. 2016, Forsman et al. 2011).
5. Hybridization between the species is increased (Barrowclough et al. 2005, Dark et al. 1998, Gutiérrez et al. 2007, Haig et al. 2004, Hamer et al. 1994, Kelly and Forsman 2004).
6. Detection rates during surveys are lower (Bailey et al. 2009, Crozier et al. 2006, Dugger et al. 2011, Dugger et al. 2016, Kroll et al. 2010, Olson et al. 2005, Sovern et al. 2014, Yackulic et al. 2014).

Moreover, studies of competitive interactions and resource partitioning showed that barred owls can directly alter the movements, resource use, and reproduction of spotted owls (Wiens et al. 2014). Barred owls also display demographic superiority over spotted owls; annual rate of

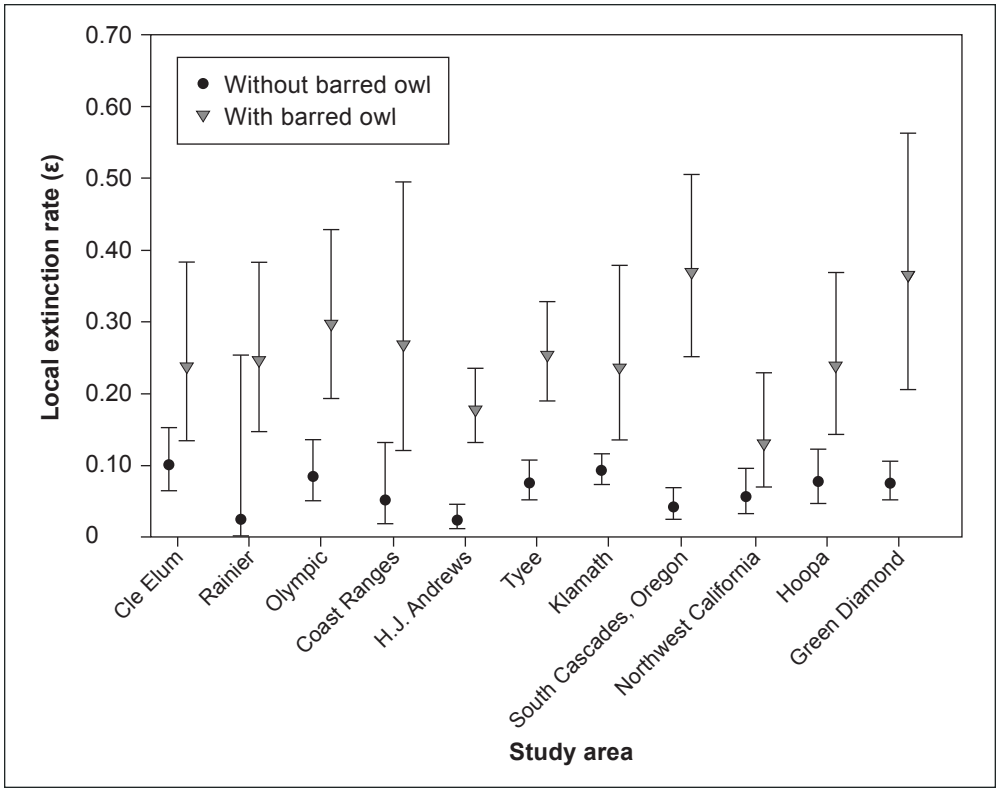


Figure 4-8—Mean annual local extinction rates (with 95 percent confidence limits) for northern spotted owls on 11 study areas in Washington, Oregon, and California relative to with (gray triangles) and without (black circles) the presence of barred owls (Dugger et al. 2016).

survival was greater for barred owls (0.92 ± 0.04) than for spotted owls (0.81 ± 0.05), and mean reproductive output of barred owl pairs was 4.4 times greater than that observed for spotted owls over 3 years in western Oregon (Wiens et al. 2014). More recently, studies in California have demonstrated a positive association between removal of barred owls and population trends of spotted owls (fig. 4-2) (Diller et al. 2016, Dugger et al. 2016). Collectively, these studies provide strong evidence that interspecific competition with an increasing number of barred owls, combined with continued loss of potentially suitable forest cover, is contributing to population declines of spotted owls despite widespread conservation of old forest under the NWFP.

Barred owl densities are now thought to be high enough across the range of the spotted owl that, despite the continued management and conservation of suitable forest cover on federal lands, the long-term persistence of spotted owls is in question without additional management intervention (Buchanan et al. 2007, Diller et al. 2016, Dugger et al. 2016, USFWS 2013). In a few cases, populations of spotted owls have responded positively to the removal of barred owls during pilot removal experiments; supporting the hypothesis that along with forest conservation and management, removal of barred owls might slow or reverse local declines in spotted owl populations in some areas (Diller et al. 2016, Dugger et al. 2016). However, the effectiveness and moreover the feasibility of large-scale barred owl removal for conservation of spotted owls remain to be demonstrated, and barred owl removal activities would likely need to be continued for the foreseeable future to maintain low barred owl densities in control areas.

Barred owl habitat and prey—

Barred owls occupy a broader range of forest types and consume a wider variety of prey than northern spotted owls (Livezey 2007), and use a variety of different forest types in the Pacific Northwest, including fragmented mixed-deciduous forest in rural and urban landscapes (Rullman and Marzluff 2014). Hamer et al. (2007) reported that, in the northern Cascade Range of Washington, barred owls tended to use old forest more than expected, but used most cover types in proportion to availability. Compared to spotted owls, barred owls occupied areas at lower elevations (Hamer et al. 2007). In the eastern Cascades of Washington, Singleton et al. (2010) reported that barred owls typically established their home ranges in areas that had canopy cover more than 72 percent, medium to large trees (tree crown diameter >21 ft [>6.5 m]), low topographic position (<25 percent), and gentle slopes (<11 degrees). Within those home ranges, barred owls used structurally diverse mixed grand fir forest more intensively than open ponderosa pine or Douglas-fir (Singleton 2015). In the Oregon Coast Range, foraging barred owls most often used patches of old (>120 years) conifer forest in addition to riparian-hardwood forests in relatively flat areas (Wiens et al. 2014). In the redwood region of coastal California, barred owls most often used sites with greater understory vegetation height and more hardwood trees, perhaps in response to greater densities of woodrats (*Neotoma* spp.) in these conditions (Weisel 2015). Collectively, these studies showed that barred owls, in areas where they were sympatric with spotted owls, were most commonly associated with relatively gentle slopes in structurally diverse, mature and old-conifer forests or lowland riparian areas containing large hardwood trees. Use of older forest in combination with moist, valley-bottom forest was also consistent with forest associations described for barred owl nesting areas (Buchanan et al. 2004, Herter and Hicks 2000, Pearson and Livezey 2003). Barred owls use the full range of forest types used by spotted owls, and a broader range of forest cover types outside of areas historically occupied by spotted owls. However, systematic studies have yet to quantify the full range of forest conditions that support barred owls in the Pacific Northwest. There are currently no known forest management actions that would benefit spotted owls more than barred owls.

Dietary studies are lacking for barred owls in California, but their diets in Washington and Oregon included a broad variety of small- to medium-size mammals, birds, frogs, salamanders, lizards, snakes, crayfish, snails, fish, and insects (Graham 2012, Hamer et al. 2001, Wiens et al. 2014). Mammalian prey of barred owls primarily included northern flying squirrels (*Glaucomys sabrinus*), woodrats, brush rabbits (*Sylvilagus bachmani*), snowshoe hares (*Lepus americanus*), moles (*Scapanus* spp.), Douglas squirrels (*Tamiasciurus douglasii*), red tree voles (*Arborimus longicaudus*),

red-backed voles (*Myodes californicus*), shrews (*Sorex* spp.), and deer mice (*Peromyscus maniculatus*) (Hamer et al. 2001, Wiens et al. 2014). Although there is substantial geographic variation in diets of barred owls corresponding with differences in prey distributions, northern flying squirrels appear to be a primary contributor to diets in Oregon and Washington (Graham 2012, Hamer et al. 2001, Wiens et al. 2014).

Although there is some evidence that barred owls were more strongly associated with riparian areas than spotted owls, studies clearly indicate a high degree of ecological overlap between the two species, especially in their use of old-growth forests and associated prey species (Hamer et al. 2001, 2007; Singleton et al. 2010; Weisel 2015; Wiens et al. 2014). In the eastern Cascades of Washington, spotted owls used drier midslope areas less likely to be occupied by barred owls, possibly as a mechanism to minimize interactions with barred owls, at least in the near term (Singleton 2013). This pattern reflects displacement of spotted owls by barred owls from highly suitable forest into conditions less favorable to long-term reproduction and survival of spotted owls, a finding consistent with long-term demographic studies of spotted owls throughout the range of the subspecies (Dugger et al. 2016, Forsman et al. 2011, Singleton 2013, Wiens et al. 2014).

In addition to impacts on spotted owls, changes in the abundance and distribution of an apex predator like the barred owl can have cascading effects on prey populations and food web dynamics (Holm et al. 2016, Wiens et al. 2014), as well as populations of other small sympatric owls (Acker 2012, Elliot 2006). Differences in space use, abundance, demography, suitable forest, diets, and behavior collectively suggest that the barred owl is not a direct functional replacement of the spotted owl in old-growth forest ecosystems (Holm et al. 2016, Wiens et al. 2014). As a consequence, additional changes in community structure and ecosystem processes are anticipated as a result of barred owl encroachment into areas managed under the NWFP.

Spotted Owl Prey

Like all predators, spotted owls are dependent on abundant and vulnerable prey. Much is known about the ecology and population demography of spotted owls, but little information exists on how fluctuations in populations of prey species influence behavior, space use, reproduction, or population growth of spotted owls. Spotted owls in some areas during some periods have had a strong 2-year cycle of high reproduction one year followed by a year of low reproduction (Anthony et al. 2006). One hypothesis for the cycle in reproductive output is variation in prey abundance. However, simple prey relationship models do not explain the highly synchronous and temporally dynamic patterns of spotted owl reproductive performance (Rosenberg et al. 2003). Northern flying squirrels, woodrats, red-backed voles, and red tree voles are the primary prey of spotted owls throughout different regions of the spotted owl's geographic range (Barrows 1980; Bevis et al. 1997; Forsman et al. 1984, 2004, 2005; Hamer et al. 2001; Rosenberg et al. 2003; Wiens et al. 2014; Zabel et al. 1995). None of these studies had data that could be used to examine relationships between annual variation in prey abundance and annual variation in survival or fecundity of spotted owls. Although deer mice are not a primary prey species (<2 percent biomass consumed), one study (Rosenberg et al. 2003) found a positive correlation ($r^2 = 0.68$) between abundance of deer mice and reproductive success of spotted owls.

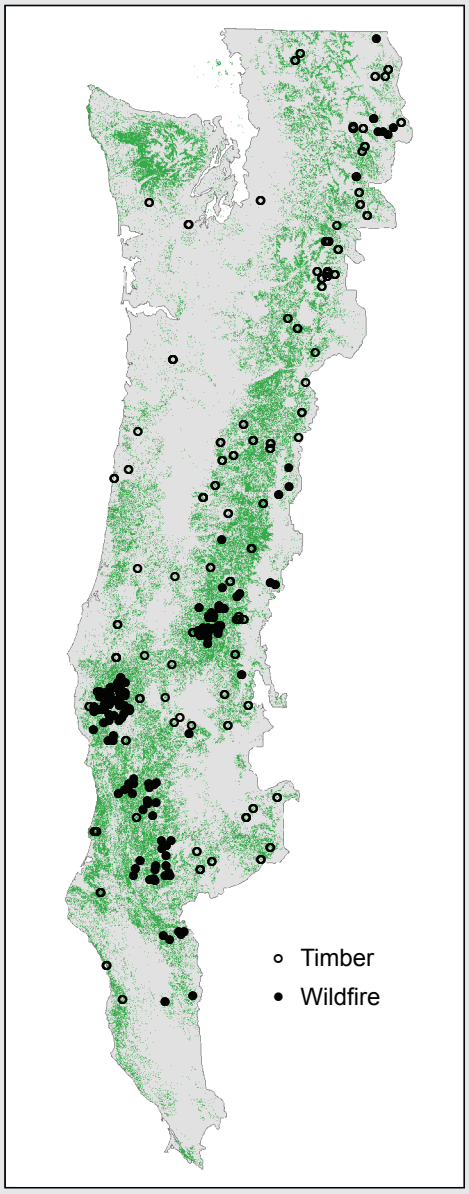
Abundance and distribution of primary prey species can influence space use by spotted owls. For example, spotted owls more frequently use riparian areas within their home ranges (Wiens et al. 2014), perhaps because the cool microclimates associated with stream drainages may be favorable for thermoregulatory purposes during summer months (Barrows 1981), or more importantly, riparian areas are likely to support a rich diversity of prey (primarily small mammals) used by spotted owls (Anthony et al. 2003, Carey et al. 1999, Forsman et al. 2004). Home ranges of spotted owls tend to be smaller in the southern portion of the subspecies range, where woodrats are the primary prey, as compared to the northern portion of the geographic range, where woodrats are uncommon and northern flying squirrels are the primary prey (Forsman et al. 2005, Zabel et al. 1995). In northern California, southwestern Oregon, and the eastern Cascades, woodrats occur in fairly open forests and at much greater densities compared to northern flying squirrels (Carey et al. 1992; Lehmkuhl et al. 2006a, 2006b; Wilson and Forsman 2013; Zabel et al. 1995). Differences

in space use by spotted owls in different portions of their range also relate to regional differences in the availability of prey species. Northern flying squirrels and red tree voles, for example, occur at highest densities in the complex structure of mature Douglas-fir stands with old-growth characteristics, whereas woodrats have greater densities in young stands, along edges, or in brushy areas (Carey et al. 1992, Price et al. 2015, Sakai and Noon 1993, Swingle and Forsman 2009, Walters and Zabel 1995, Zabel et al. 1995). Spotted owls used forest edges to a greater degree when forage consisted primarily of woodrats (Diller et al. 2012), but preferred forest interiors, where they foraged on red tree voles and northern flying squirrels. Timber harvest activities, including thinning of dense plantations, reduce the abundance of northern flying squirrels and red tree voles for several decades, contributing to a reduction in use by spotted owls (Carey 2000, Dunk and Hawley 2009, Gomez and Anthony 1998, Manning et al. 2012, Price et al. 2015, Waters and Zabel 1995, Wilson and Forsman 2013).

Disturbance

In this section, we define disturbances as modifiers of the structural characteristics, species composition, and landscape patterns of forest cover types used by spotted owls. The range of the northern spotted owl encompasses a variety of historical disturbance regimes that are fundamental to the health and diversity of these ecosystems (chapter 3). Important forest disturbances result from wildfire, forest management (e.g., thinning), timber harvests, extreme weather events, or forest insect and disease processes (Davis et al. 2016). Effects that forest disturbances have on spotted owls depends on spatial scale, severity, and season (McKelvey 2015). Biogeographic variation across the large range of spotted owls also results in very different levels of disturbance type, frequency, and severity (see "Wildfire" below). Major disturbance events influence forest cover types that have been used by spotted owls for many decades, and have different effects depending on the magnitude of change and the time since disturbance. For example, in the short term, a disturbance that creates open canopy conditions could reduce value for spotted owl roosting, but have long-term benefits by enhancing understory vegetation diversity and conditions for spotted owl prey. Further, disturbances can stimulate the development of large-tree, complex-structure stand conditions over time (Lehmkuhl et al. 2015). An important secondary effect of forest disturbances for spotted owls are changes in prey abundance or vulnerability. These effects can be positive by creating conditions that increase abundance or vulnerability for some prey species, or negative by removing critical forest structure required by primary prey populations (e.g., northern flying squirrel, red tree vole) (Manning et al. 2012, Wilson and Forsman 2013). Some disturbances have a neutral affect, particularly when limited in severity or spatial extent, and ample suitable forest remains available at core and home-range scales.

Spotted owls were listed as a threatened species under the Endangered Species Act largely because of concerns regarding loss of old forest resulting from commercial timber harvest (Thomas et al. 2006, USFWS 2011b). Subsequent to reductions in harvest of old forest, high-severity wildfire has become the leading cause of suitable forest loss for spotted owls on federal lands, especially in fire-prone landscapes. However, commercial timber harvest still contributes substantially to the loss of suitable forest cover in some areas, especially on nonfederal lands (Davis et al. 2016, Pierce et al. 2005). Recent research on disturbance effects on spotted owls indicates that disturbances such as mixed-severity fires that generate heterogeneity at landscape and stand scales are not necessarily adverse, provided that adequate nesting and roosting structural conditions remain after the disturbance (Clark et al. 2013, Comfort et al. 2016). High-severity disturbances that broadly alter stands and landscapes within nesting territories can remove critical components of forest structure (e.g., high canopy cover and density of large live trees) required for spotted owl survival and reproduction (Dugger et al. 2005, Franklin et al. 2000, Olson et al. 2004). Timber harvesting and wildfire can both reduce the living tree components of a stand and reduce the overall suitability for spotted owls (see sidebars on pages 265 and 266). An important difference between timber harvest and wildfire is the removal of trees and ground disturbance in a timber harvest. For most wildfires, there is limited physical soil disturbance (although fire



The graph to the right is from Davis et al. (2015) and shows the relationship between these classes and monitoring trends in burn severity classes.

Effects of Forest Disturbances on Nesting/Roosting Forest Cover

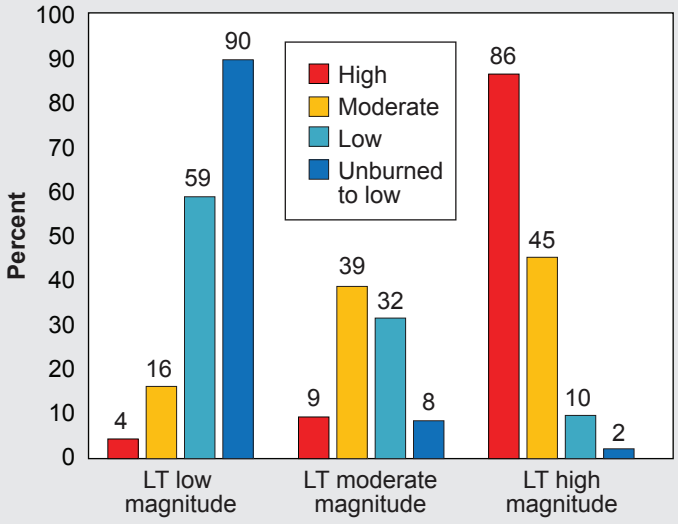
Map data from the most recent northern spotted owl habitat monitoring report (Davis et al. 2016) and Forest Inventory Analysis and Current Vegetation Survey plots were used to assess changes resulting from forest disturbances on stand structure elements used in the Davis et al. (2011, 2016) nesting/roosting cover type modeling and mapping procedure.

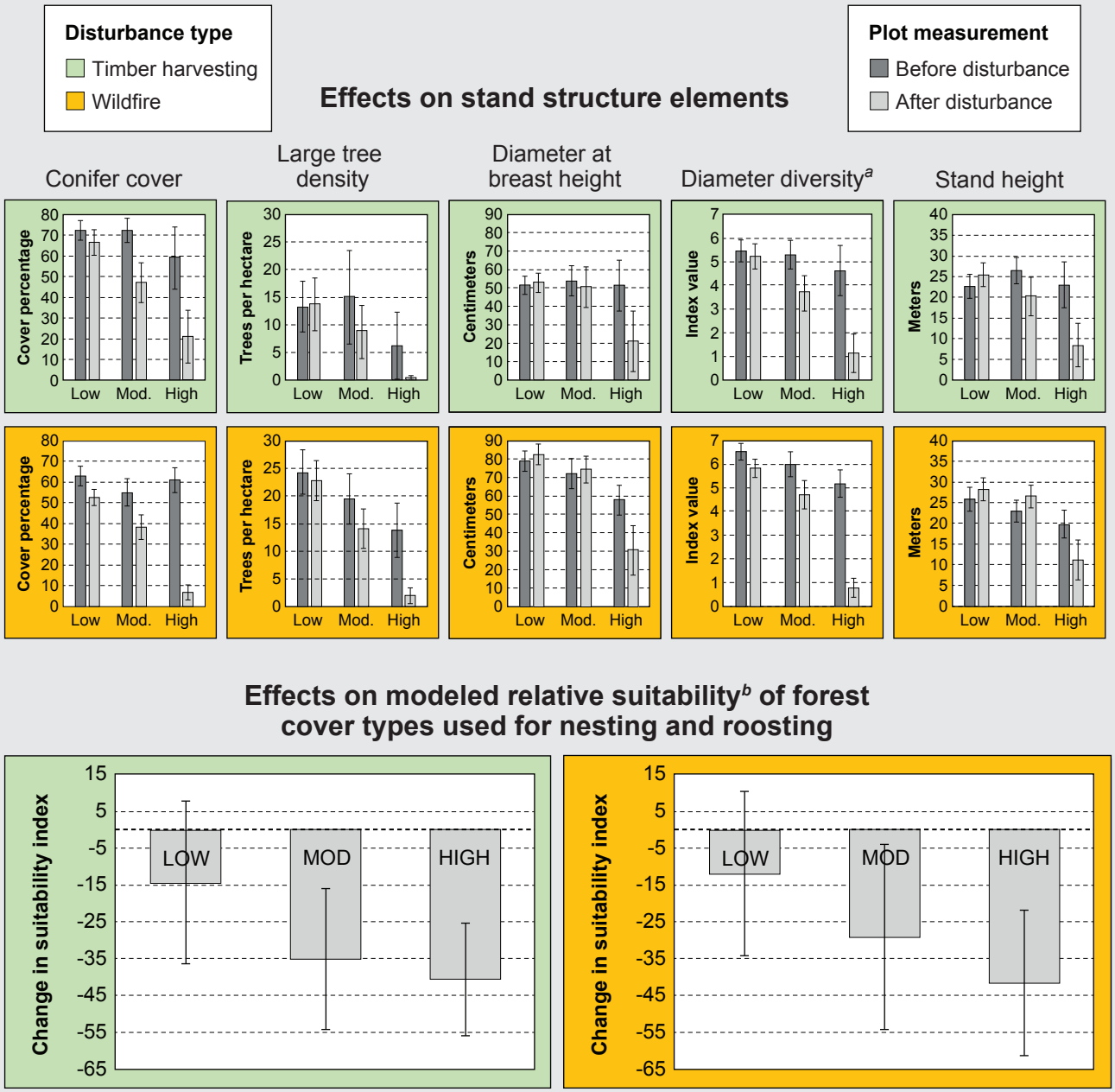
Plots used in this analysis occurred in mapped suitable nesting/roosting cover type in 1993 that experienced a disturbance between 1994 and 2012 from either timber harvesting or wildfire, which occurred between the initial plot measurement and remeasurement dates.

Changes in the mapped nesting/roosting relative suitability index were also analyzed by differencing the 2012 and 1993 relative suitability maps.

LandTrendr (LT) data (Kennedy et al. 2012) of forest disturbance magnitude are satellite-based measurements of loss of vegetation cover. We divided them into three classes:

- Low (<33 percent cover loss)
- Moderate (33 to 66 percent cover loss)
- High (>66 percent cover loss





[a] The diameter diversity index is a measure of the stuctural diversity of a forest stand based on live tree densities in diameter at breast height classes. An index value of 1 represents a single-story stand. Higher index values represent more complex multistoried stand structure.

[b] Modeled relative suitability from Davis et al. (2016). The index for suitable nesting/roosting forest cover type ranges from 31 to 40, depending on the modeling region.

can have substantial impacts on soil chemistry and organic matter composition), and patches of live trees, snags, and logs remain in situ, which contributes to enhanced biodiversity, future quality of complex forest, and forest succession (Swanson et al. 2011).

Wildfire—

Wildfires occur throughout the entire range of the spotted owl. Some physiographic provinces are more environmentally suitable for wildfire occurrence at a decadal scale, while other provinces have wildfire-return intervals of several centuries (see chapter 3) (Agee 1993). Beyond frequency, the severity and spatial extent of wildfires differ across the NWFP area (Davis et al. 2011). The physiographic provinces of the eastern Cascades, southern portions of the western Cascades, and the Klamath Mountains are characterized by frequent low- and mixed-severity fire regimes (Baker 2015, Hessburg et al. 2007, Perry et al. 2011). Owing to more than a century of fire exclusion (e.g., from grazing, fire suppression, and historical forest management practices), many of these fire-prone landscapes have experienced significant increases in stand density and loss of large trees, threatening forest health and biodiversity (Hagmann et al. 2013, 2014; Hessburg et al. 2007; Perry et al. 2011). The historical extent of forest cover types suitable for nesting and roosting by spotted owls in dry and mesic mixed-conifer forests in the eastern Cascades and other fire-frequent forests was likely historically limited but has increased substantially in recent decades (Hagmann et al. 2013, 2014; Hessburg et al. 2007; Merschel et al. 2014). Moreover, in this fire-prone landscape, forest structure conditions that are more resilient to low- and mixed-severity fires (i.e., single-story old forests with large ponderosa pines) are not suitable for nesting and roosting by spotted owls. Areas occupied by spotted owls in the fire-prone landscapes of the eastern Cascade Range are often dense, closed-canopy, medium-size tree forests with a substantial true fir (*Abies* spp.) component and structural diversity enhanced by a variety of insect and disease processes, including dwarf mistletoe (Stine et al. 2014). These are the conditions that have been promoted through fire suppression and removal of fire-resilient large Douglas-fir and ponderosa pine trees. Compared to forest structure conditions that are more resilient to wildfire, areas occupied by spotted owls in these fire-prone landscapes are at higher risk to high-severity wildfire (Dennison et al. 2014, Stine et al. 2014). All forest types in these landscapes are vulnerable to substantial impacts from high-severity wildfire under extreme weather conditions, which are likely to be more common with climate change (Kennedy and Wimberly 2009, Reilly et al. 2017).

West of these fire-prone areas to the Pacific coastline, the forests become progressively moister and less prone to frequent large wildfire. In these moist forests, large wildfires tend to be infrequent to moderately frequent, and fire severity trends from mixed to high severity (see chapter 3). In less fire-prone landscapes, old and complex forest with large trees—compared to other forest types—has higher moisture retention and cooler microclimates compared to other forest types, and may enhance biodiversity under a changing climate (Frey et al. 2016). In these mixed- and low-frequency fire regime landscapes, old forest may be more resistant to wildfire than young forest with closed canopy under normal fire weather conditions (Thompson and Spies 2009).

Throughout the NWFP area, the fundamental association between spotted owls and multilayer forests with large trees and closed canopies is well established (Dugger et al. 2016, Forsman et al. 1984, Franklin et al. 2000, Olson et al. 2005, Wiens et al. 2014). The severity of the wildfire has a strong influence on the degree to which these forest cover types are altered by wildfire (see sidebar on page 265). Low-severity wildfire can have very little effect on the suitability of nesting and roosting cover types, and can even increase it. Moderate-severity wildfire can change stand structure and species composition, resulting in moderate decreases in cover-type suitability. High-severity wildfire can alter forest cover to the point at which the area is no longer be suitable for nesting, roosting, or dispersal. Multiple lines of research have confirmed the effects of wildfire on stand structure and composition, but much less is understood about the short- and long-term response of spotted owls to wildfire.

Most studies focused on wildfire effects evaluated the short-term response of spotted owls to wildfire, but in one of the few studies of the long-term effects of wildfire

on spotted owls Rockweit et al. (2017) used 26 years of demographic data in a landscape with several wildfires and found that moderate and high burn severities negatively affected spotted owl apparent survival. They also found that burned territories functioned as ecological sinks where recruitment was high, but survival was lower than in nearby unburned territories. Several shorter post-wildfire studies have seemingly contradictory results regarding spotted owls and wildfire. For example, in an occupancy analysis, Jones et al. (2016) found high site extirpation rates of California spotted owls following a large, high-severity wildfire, but in a telemetry study, Bond et al. (2016) observed that burned forests were generally used in proportion to their availability. Other studies of California spotted owls and Mexican spotted owls have shown that wildfire does not necessarily decrease short-term occupancy in low- or moderate-severity burned areas (Bond et al. 2009, Ganey et al. 2011, Lee and Bond 2015, Lee et al. 2013, Roberts et al. 2011). Spotted owls can persist, at least for short periods, in landscapes that have experienced recent wildfires, as long as adequate moderate to closed-canopy nesting/roosting forest cover is retained at nesting core and home range scales. Even with high-severity wildfire, the effects can be insignificant or positive (e.g., increase vulnerability of prey) at larger spatial scales, especially if the forest cover changes caused by high-severity fire comprise only a small portion of a spotted owl's territory (Comfort et al. 2016).

Effects of wildfire interact in complex ways with other historic and current disturbances. Clark et al. (2013) found that local spotted owl site extinction probability was higher for sites with more combined area of past timber harvest, high-severity fire, and salvage logging. They also found evidence that colonization and occupancy rates were higher for sites with older forest burned at low severity (Clark et al. 2013). Coupling wildfire and salvage logging results in a high probability that a site becomes unoccupied after the first year postfire, especially if the core area burns at high severity and is subsequently logged (Bond 2016, Ganey et al. 2011, Lee et al. 2013). Beyond the effects on spotted owls, a human disturbance that directly follows a high-severity natural disturbance can have significant negative consequences to a forest ecosystem by disrupting abiotic and biotic processes, reducing or eliminating biological legacies, simplifying post-disturbance structural complexity, altering vegetation recovery, diminishing natural patterns of landscape heterogeneity, facilitating invasion of nonnative species, decreasing native biodiversity, increasing susceptibility to erosion and repeated high-severity disturbances, and eliminating restorative benefits of disturbance events (Lindenmayer- and Noss 2006, Thorn et al. 2017).

Overall, studies suggest that spotted owls are adapted to a forest landscape with a mosaic of successional stages shaped by historical disturbance regimes, accompanied by abundant prey resources, few barred owls, and structurally diverse closed-canopy forest with diffuse late-seral edge at the territory scale, and limited fragmentation occur within nesting areas (Dugger et al. 2011, Forsman et al. 1984, Franklin et al. 2000, Olson et al. 2004, Sovern et al. 2014). Research supports the premise that some spatial heterogeneity in forest conditions can have a positive effect on demography of spotted owls. At the territory scale (~500 to 1500 ha), a mosaic of older forest interspersed with other vegetation types, including early-seral and riparian forests, can promote high survival and reproduction of spotted owls (Comfort et al. 2016, Franklin and Gutiérrez 2002, Franklin et al. 2000). In terms of the effects of wildfire on spotted owls, we emphasize that most available research on impacts to spotted owls has been based to some degree on short-term responses and primarily focused on the other two spotted owl subspecies. The long-term (>5 years) effects of wildfire on spotted owl survival, reproduction, recruitment, and interactions with barred owls are not well documented.

Forest restoration and silvicultural treatments— To meet management objectives of the NWFP, the spotted owl recovery plan, and critical habitat requirements, researchers and federal land managers have focused on ecosystem function (e.g., fire as an ecological process) in developing silvicultural practices that provide ecologically sustainable alternatives to clearcutting and old-growth harvest while still providing for timber production (chapter 3). As a result, alternative thinning methods, including variable-density thinning, have replaced clearcutting as the predominant form of active management on federal

lands, whether for restoration or timber production goals or both (Anderson and Ronnenberg 2013, Lehmkuhl et al. 2015). Ecological objectives for forest management differ by region, forest type, and historic disturbance regime (Franklin and Johnson 2012) (chapter 3).

Moist forest—The focus of silvicultural treatments in moist forests of the western Cascades and Coast Ranges (historically infrequent, high-severity fire regimes) has been an attempt to accelerate development of old-forest conditions in plantations or younger closed-canopy stands (Anderson and Ronnenberg 2013). Typical thinning treatments that create canopy gaps in moist forests west of the Cascade crest can create relatively rapid increases in understory vegetation diversity and productivity (Johnson and Franklin 2013) (chapter 3). The intensity and pattern of retained trees in forest thinning can have dramatic influence on microclimate and ecological response in the short term (Aubry et al. 2009, Heithecker and Halpern 2006). Stand conditions can be either too open or too dense for foraging because spotted owls are adapted to old forest with closed canopies, and the understory must be open enough to fly and access prey (Irwin et al. 2015). In areas where dusky-footed woodrats are primary prey (e.g., southern Oregon, northern California), thinning of young dense stands may increase spotted owl use for foraging, but still not create preferred forest conditions for other life history needs such as nesting and roosting (Irwin et al. 2015). Wilson and Forsman (2013) found that the abundance of mice, terrestrial voles, and shrews increased immediately following thinning, but that northern flying squirrels and red tree voles—important prey species for spotted owls—decreased dramatically in abundance in treated areas for up to 11 years after treatment (Wilson 2010). Thus, spotted owls respond to silvicultural treatments differently where the primary prey are northern flying squirrels, which includes most of the northern and western portions of their range in Oregon, Washington, and British Columbia.

When assessing the potential effects of thinning on prey species, the landscape context should be considered. For example, the effects of thinning within heterogeneous landscapes with well-connected, intact old-forest cover may be less detrimental to northern flying squirrels than if thinning occurs within a highly fragmented forest landscape (Sollmann et al. 2016). Some degree of landscape heterogeneity resulting from forest restoration activities in west-side forests does not adversely impact spotted owls, provided that sufficient large-tree, closed-canopy forest for nesting and roosting is available at core and home range scales (Andrews et al. 2005). For example, in northern California, Franklin et al. (2000) found that territories with the highest fitness (survival and reproduction) were those with a mixture of old forest and about 40 percent of other vegetation types. Diller et al. (2012) reported that forest cover heterogeneity (i.e., juxtaposition of young and older stands) had positive effects on survival and reproduction of spotted owls on commercial timberlands in northern California, where disturbance regimes were historically of mixed severity. Highly productive growing conditions and abundant hardwoods contribute to structural complexity in these managed forests. However, survival of spotted owls decreased in southern Oregon when the amount of nesting/roosting forest cover within the territory center was less than 50 percent (Dugger et al. 2005), and a similar relationship was found in other studies (Franklin et al. 2000, Olson et al. 2004, Wiens et al. 2014).

Dry forest—In the drier forests of the eastern Cascades, southern Oregon, and northern California, wildfire was historically more frequent and burned with mixed- and low-severity effects. In these areas, forest management treatments have focused on accelerating the development of old-forest conditions, but also have focused more on restoring or promoting fire-resilient forest structure, species composition, and landscape pattern (Hessburg et al. 2016, Lehmkuhl et al. 2015, Stine et al. 2014). Landscape managers implementing forest restoration treatments in drier, mixed- and low-severity fire regime forests face substantial challenges in balancing the tradeoffs between known short-term forest cover impacts on spotted owls from restoration and fuel reduction treatments versus potential benefits of reducing losses of forests with larger trees from high-severity, large-scale wildfire (Hessburg et al. 2015, 2016; Lehmkuhl et al. 2015; Stine et al. 2014). Management emphasis on wildfire suppression combined with historical harvest of large trees in these landscapes over the past 100 years has contributed to the recruitment of small-tree, closed-canopy forest

(Hessburg et al. 2016). In these regions, the moderate- to closed-canopy forest with multilayer canopy structure enhanced by dwarf mistletoe infestations are used by spotted owls for nesting and roosting areas, and appear to have increased over the latter part of the 20th century into the 21st century (Davis et al. 2016, Lint 2005). Large tree, multistory canopy typical of forest cover types used for nesting and roosting by spotted owls across their range make them less flammable under most fire conditions, but, like most cover types, these are susceptible to burning intensely in extreme weather. Standard treatments focused on increasing stand-level resilience to wildfire by using prescribed fire and removing ladder fuels (e.g., Cochrane et al. 2012, Safford et al. 2012, Stephens et al. 2009), and reducing canopy connectivity (Agee and Skinner 2005) can reduce the risk of stand-replacement high-severity wildfires, but the practices also remove important forest cover elements for spotted owls and their prey (Lehmkuhl et al. 2006a, 2006b, 2015). Prescribed fire treatments as part of fuel reduction projects can further reduce under- and mid-story canopy complexity, and burn up logs and snags, potentially causing additional negative impacts to suitable forest for spotted owls and their prey (Lehmkuhl et al. 2015). Silvicultural practices that promote spatial and structural complexity have been proposed for retaining suitable foraging conditions for spotted owls while also reducing fuel loads (Churchill et al. 2013, Gaines et al. 2010, Hessburg et al. 2016, Johnson and Franklin 2013, Lehmkuhl et al. 2015). However, the effectiveness of these management practices to restore ecological resilience and reduce risk of loss to high-severity wildfire, while maintaining components of suitable forest for spotted owls, remains to be tested in dry forest landscapes (see chapters 3 and 12 for more discussion of this issue).

Several simulation studies have used coupled wildfire and forest growth models to investigate the relative effects of wildfire and forest restoration treatments on recruitment and retention of forest cover types used by spotted owls in fire-prone landscapes. Some of these studies suggest that certain fuel treatment scenarios (i.e., active management) can reduce wildfire-caused losses of forest cover types used by spotted owls (Ager et al. 2007, Roloff et al. 2012). Other modeling efforts found that active management reduced forest cover used by spotted owls more than simulations with no management, (Roloff et al. 2005, Spies et al. 2017). As with any modeling exercise, outcomes of these studies reflect the assumptions incorporated into the simulations. Assumptions regarding wildfire severity, return intervals, and effects of treatments are particularly influential. One general theme from these simulations is that benefits of fuel treatments to forest types used by spotted owls depend on what probability of occurrence is assumed for future high-severity wildfires. If the likelihood and impacts of high-severity wildfire are assumed to be high, thinning treatments are more likely to have a positive outcome for spotted owls (e.g., Roloff et al. 2012). If the likelihood of high-severity wildfire is assumed to be low, however, then thinning treatments are more likely to produce only declines in the amount of suitable forest cover types used by spotted owls.

Climate Change

Climate change will affect spotted owl populations through changes in weather, forest cover, disturbance processes, prey availability, and other ecological interactions. Population growth of spotted owls appears to be positively associated with wetter than normal conditions during the growing season (May–October), which likely increases prey populations and thus availability (Glenn et al. 2010). Population growth and reproduction were also negatively associated with cold, wet winters (pre-nesting) and the number of hot summer days (July–August) (Diller et al. 2012, Glenn et al. 2011b). Annual survival was more closely related to regional climate conditions (Southern Oscillation Index [SOI] and Pacific Decadal Oscillation [PDO]), whereas recruitment was often associated with local weather. Projected future climate conditions have the potential to negatively affect annual survival, recruitment, and, consequently, population growth rates for spotted owls (Glenn et al. 2010). Climatic factors affecting vegetation and prey abundance likely have a greater effect on reproduction and population growth than direct effects of weather on nestlings or adult spotted owls (Glenn et al. 2011a, 2011b). Climate change models for the first half of the 21st century predict warmer, wetter winters

and hotter, drier summers for the Pacific Northwest (Mote et al. 2003) (chapter 2). These conditions are expected to decrease survival of spotted owls in some areas (Glenn et al. 2011a). Climate change can affect development of forest structure by altering temperature and precipitation regimes, and disturbance frequency and intensity (Dale et al. 2001). Altered understory vegetation can reduce prey availability and thus spotted owl fitness (Carey and Johnson 1995, Franklin et al. 2000). Carroll (2010) found that vegetation rather than climate variables best explained distributions of spotted owls. Potential climate-related forest cover losses resulting from large-scale, high-severity wildfires and increased mortality of old-growth trees (Van Mantgem et al. 2009) may be particularly important for future viability of spotted owl populations (chapter 2).

Franklin et al. (2000) found that forest cover patterns explained a high amount of spatial variation in fitness potential among territories occupied by spotted owls in northern California, but climate explained most of the temporal, year-to-year variation in fitness-related traits. Survival and reproduction, for example, were lower when the early nesting period (February–March) was cold and wet. Fecundity, recruitment, and survival decreased across the range of the spotted owl when winters or early springs were colder and wetter than average (Diller et al. 2012; Dugger et al. 2005, 2016; Forsman et al. 1984, 2011). Spotted owl populations in drier forests may be especially vulnerable to climate change because hot, dry summers can reduce prey abundance or availability, and subsequently reduce spotted owl survival (Glenn et al. 2011a). Regional climate patterns, including the SOI and PDO, have also been correlated with demographic rates of spotted owls (Dugger et al. 2016; Forsman et al. 2011; Glenn et al. 2010, 2011a, 2011b). Survival of spotted owls was greater when the PDO was in a warming phase and lower when the SOI was negative (i.e., El Niño events resulting in higher than average temperatures and below normal precipitation) (Dugger et al. 2016).

Extrapolation of the best combination of vegetation-climate models to predicted future climates suggests northward expansion of high-suitability forest cover for spotted owls (Carroll 2010). Increased winter temperature under future climates might be expected to increase winter survival and nesting success, and allow range expansion of prey species such as woodrats, which currently occur at high densities only in the southern portions of the range (Noon and Blakesley 2006). However, it is uncertain how barred owls will respond to changing prey populations, and model results suggest that an initial expansion in the suitable climatic niche may be followed by a contraction as climate change intensifies (Carroll 2010). An important qualifier is that these models did not account for losses of multilayered forests to wildfire and the potential for competition with barred owls to become even more prevalent as climatic change causes shifts in forest communities that in turn further constrain both owl species to a common set of increasingly limited resources.

Other Threats

Genetic diversity and hybridization—
Loss of genetic diversity within a population can contribute to inbreeding depression and decrease adaptive potential. Increased rates of hybridization with barred owls may further compromise the genetic integrity of the spotted owl population (Funk et al. 2010, Gutiérrez et al. 2007). Genetic studies have reinforced other studies that showed spotted owl population declines. Specifically, genetic evidence indicates a loss of genetic variation and increased potential for inbreeding depression in small populations. This suggests a vulnerability of spotted owls to extinction (Funk et al. 2010). Genetic data from spotted owls have indicated population bottlenecks for the Washington eastern Cascades, northern Oregon Coast Range, and Klamath Mountains (Funk et al. 2010), which corresponded temporally with population declines in most of those regions (Anthony et al. 2006, Dugger et al. 2016, Forsman et al. 2011). There was, however, no definitive evidence that suitable forest cover associated with dispersal was limited, or that gene flow was restricted in those regions (Barrowclough et al. 2005, Davis et al. 2011)

Hybridization with barred owls is another potential threat to spotted owl persistence, especially as the spotted owl becomes increasingly rare and the invading species becomes more abundant (Gutiérrez et al. 2007, Haig et al. 2004). Spotted owls occasionally mate with barred

owls (male spotted owl–female barred owl mating is most common) and produce fertile hybrids (Hamer et al. 1994, Kelly and Forsman 2004). In the southern portion of the spotted owl range, 3 percent of spotted owl genetic samples collected prior to 2004 (barred owls were still relatively rare on the landscape) contained barred owl mitochondrial DNA (Barrowclough et al. 2005). There are typical markings of hybrids that can be helpful in field identification (Hamer et al. 1994), but genotyping potential hybrids across generations has shown that field identifications were often wrong (Funk et al. 2007). Hybridization rates may also have changed substantially in recent years as barred owl populations have increased and spotted owls have decreased.

Hybridization with other spotted owl subspecies does not appear to be a concern for spotted owl conservation. The northern spotted owl and California spotted owl are two well-differentiated subspecies connected by a narrow hybrid zone in a region of low population density for both subspecies in north-central California (Barrowclough et al. 2005, 2011; Funk et al. 2008; Gutiérrez and Barrowclough 2005). Spotted owls in the contact zone are highly differentiated and may be a distinct population from other northern spotted owl and California spotted owl populations (Miller et al. 2017).

Diseases and pathogens—
Disease exposure could be a secondary consequence of climate change, blood parasites, and effects of barred owl interactions. Lewicki et al. (2015) found that spotted owls had a higher *Haemoproteus* spp. parasite diversity and probability of infection than sympatric barred owls. Further, avian malaria (*Plasmodium* spp.) is common in barred owls, and only recently was documented in spotted owls; therefore, barred owls likely have an additional competitive advantage because spotted owls are potentially immune-compromised owing to recent exposure to avian malaria (Ishak et al. 2008). Spotted owls are susceptible to West Nile virus and experience high rates of mortality when exposed (Courtney et al. 2004); however, it is unknown what, if any, population-level impacts the disease has caused. Wiens et al. (2014) reported that the leading cause of death in a sample of radio-marked barred owls was bacterial infection associated with endoparasitism.

Environmental contaminants—
Environmental contaminants, especially anticoagulant rodenticides, have recently emerged as a potential threat to spotted owls and their prey. In particular, anticoagulant rodenticides used in illegal marijuana cultivation and urban settings can have significant indirect impacts by the poisoning of nontarget forest predators, including owls (Albert et al. 2010, Gabriel et al. 2012, Riley et al. 2007, Stone et al. 1999). To our knowledge, no studies have addressed potential effects of anticoagulant rodenticides on spotted owls.

Research Needs, Uncertainties, Information Gaps, and Limitations

Research Needs

Effects of barred owls—
It has become increasingly clear that barred owls are a primary driver of spotted owl population declines, but many questions remain about the full impact of barred owls directly on spotted owls, and indirectly through alterations of forest communities. Research is needed to build on the work of Wiens et al. (2014) and others to identify potential processes by which spotted owls and barred owls use resources differently. More research is needed to establish the full suite of cause-and-effect relations of barred owl impacts on spotted owls, and how barred owls interact with other threats to spotted owls. Unfortunately, these types of studies are becoming increasingly difficult because spotted owl numbers are declining so rapidly on most study areas. In a pilot study, Diller et al. (2016) found that spotted owls responded positively to experimental removal of barred owls, but additional removal studies in other physiographic provinces, where owl populations and suitable forests are different, are needed. To determine the feasibility and effectiveness of barred owl removals as a tool for spotted owl recovery, the Fish and Wildlife Service and U.S. Geological Survey initiated a barred owl removal experiment on four study areas in Washington, Oregon, and northern California (USFWS 2013). Continued monitoring of spotted owl populations in those areas will be required to fully assess the short- and perhaps, in particular, long-term response of spotted owls to the removal of an important competitor. More genetic studies are needed to address the frequency

and impact of hybridization between spotted owls and barred owls, and how hybridization rates may have changed with changes in abundance of the two species.

It remains uncertain how climate change will affect interactions between spotted owls and barred owls, or even where barred owl populations are in terms of the invasion process. For example, little research has been conducted to investigate if populations of barred owls are continuing to increase or if carrying capacity has been met in some regions. Fundamental information on barred owl distribution and population trends is needed to address this important issue. Further, little is known about barred owl distribution and populations beyond forest cover types occupied by spotted owls. Ecologists are being challenged to predict how spotted owls will change in abundance and distribution under current climate, availability of suitable forest, and competitive interactions with barred owls. It is well documented that climate change influences species' abundances and distributions, and can have indirect effects on interspecific interactions (Angert et al. 2013). An important area of needed research related to barred owl-spotted owl interactions and climate change will be to better understand how the combined effects of barred owl competition and future changes in the amount and distribution of forests used by spotted owls might contribute to spotted owl population persistence and range shifts under a changing climate.

In addition to impacts on spotted owls, changes in the abundance and distribution of a generalist apex predator like the barred owl can have cascading effects on prey populations and food-web dynamics (Gutiérrez et al. 2007, Holm et al. 2016, Wiens et al. 2014). Barred owls have reached densities in the Pacific Northwest that are far greater than historical populations of northern spotted owls (Wiens et al. 2011, 2014). Moreover, as generalist predators, barred owls capture a greater proportion of diurnal, terrestrial, and aquatic prey than northern spotted owls (Forsman et al. 2004, Hamer et al. 2001, Wiens et al. 2014). These life-history traits indicate that barred owls are not direct functional replacements of northern spotted owls in forested ecosystems of the Pacific Northwest (Holm et al. 2016), and that a wide range of prey species may be affected if they replace northern spotted owls. Further research is needed to determine the potential effects of barred owls on other sensitive wildlife beyond spotted owls.

Finally, critical needs for managers are detailed assessments of those locations where spotted owls persist and a better understanding of the effects of forest management activities on interactions between spotted owls and barred owls, and the species individually. Many spotted owl sites with apparently suitable forest structure for nesting and roosting have been abandoned as a result of displacement by barred owls. Those sites that spotted owls have persisted in the face of barred owls may be a result of the behavioral characteristics of the territorial spotted owl, or perhaps those sites have unique forest characteristics that enhance coexistence between the two species. Thinning treatments could potentially affect competitive interactions either by displacing barred owls into areas occupied by spotted owls, or potentially increasing foraging opportunities for barred owls over spotted owls. These and many other responses are plausible, but it remains unknown how either species responds to many forest management techniques. Recent advances in lightweight geographic positioning system telemetry devices and high-resolution forest structure mapping technologies can provide new opportunities for advancing our understanding of these issues.

Prey populations and population performance— Previous studies have characterized the diet of spotted owls in different portions of the subspecies' range (Barrows 1980; Bevis et al. 1997; Cutler and Hays 1991; Forsman et al. 1984, 2001, 2004), investigated the relationship between forest cover selection, home-range size, and prey availability (Carey et al. 1992; Forsman et al. 1984, 2005; Irwin et al. 2000; Zabel et al. 1995), and evaluated diet overlap with barred owls (Hamer et al. 2001, Wiens et al. 2014). The importance of understanding relationships between spotted owl populations and their prey has repeatedly been acknowledged (Clark et al. 2011, Courtney et al. 2004, Forsman et al. 2004, Glenn et al. 2010, Olson et al. 2004, Rosenberg et al. 2003, Thomas et al. 1990, Wilson and Forsman 2013, Zabel et al. 1995). However, to our knowledge, no efforts have been undertaken to quantify the relationship between interannual fluctuations in prey abundance and

long-term demography of spotted owls. Research is needed to understand how spotted owl reproduction, stress levels, and survival are influenced by prey species composition and abundance, and how prey populations are influenced by disturbance or fluctuations in weather and climate. Population fluctuations in small mammals have been linked with variation in precipitation (Avery et al. 2005, Crespin et al. 2002). However, identifying the mechanisms by which climate influences population processes of spotted owls and their prey remains a challenge (Glenn et al. 2011a).

A better understanding of the effects of thinning treatments and the impacts that anticoagulant rodenticides have on spotted owl prey populations will be critical for managers. Research and an effect analysis is needed to address thinning impacts on spotted owl prey, both within treated stands and at broader landscape scales. This information would contribute to thinning prescription development throughout the range of the spotted owl. The use of anticoagulant rodenticides in natural systems is increasing, especially in areas where illegal marijuana cultivation is prevalent. Studies are also needed to better understand the individual- and population-level impact of rodenticides on spotted owls, and development of management options to reduce the ecological impacts.

Landscape restoration, silvicultural treatments, prescribed fire, and wildfire in moist and dry forests— Research is needed in both dry and moist forest landscapes to evaluate the short- and long-term effects of silvicultural treatments and wildfire on spotted owl occupancy, forest dynamics, and prey, but research questions differ between forest types. For example, the optimization of forest restoration and conservation of spotted owls will require more knowledge about the conditions under which restoration activities can benefit spotted owls in the long term without significant detrimental impact in the short term. Restoration activities and objectives are different between moist and dry forest landscapes. Current conditions in dry forests are generally not sustainable, and some measure of treatment is needed to increase fire resiliency of forest stands in at least some locations (USFWS 2012b). In these fire-prone landscapes, a common objective is to modify and reduce fuels to alter wildfire behavior and to manage for ecological integrity based on the natural range of variability (USDA 2012). Additional information is needed to evaluate the consequences of fuels reduction and restoration treatments relative to the long-term benefits of forest restoration, particularly as large, high-severity fires are expected to become more frequent because of climate change. This is especially true in the frequent low-severity fire regime of the eastern Cascades, where environmental conditions favor open pine-dominated forests. Studies are needed to identify resilient sites for spotted owls in the face of changing forests (e.g., species composition changes) caused by climate change, active forest management, and increased wildfire occurrence.

In moist forest landscapes, research is needed to determine how or if spotted owls use forest stands where thinning has been conducted to accelerate the development of late-successional forest characteristics. If spotted owls avoid these areas in the short term, work is needed to understand the time before they begin using the areas again. To fully understand restoration effects, long-term before/after control-impact studies are needed to elucidate spotted owl and prey responses to forest restoration treatment effects in different ecotypes.

Research to address restoration and silvicultural treatment on spotted owl space use and forest structure development will also need to account for the potential confounding impact that barred owls are likely to have on spotted owl response to restoration efforts. Beyond a better understanding of spotted owl response to silvicultural treatments, managers need information regarding how sympatric populations of barred owls respond to treatments. Additionally, research is needed to understand the effectiveness of ecosystem-scale conservation versus conservation that targets one particular stage of succession (e.g., late-successional forest characteristics for spotted owls). Finally, much more information is needed to evaluate the short- to long-term effects that wildfire has on spotted owls in all landscapes, with a focus on the relative susceptibility of old forest and young forest to high-severity wildfire under a range of weather conditions. Finally, it is important to note that these research topics become increasingly difficult to address as spotted owl populations decline and fewer individual owls are available to study in some landscapes.

Physiological consequences of stress—
An animal's ability to cope with stressors is an important determinant of its physiological conditions, and therefore, health and survival. Environmental perturbations and an individual's response can affect the body's production of hormones, such as glucocorticoids, with negative physiological consequences (Carrete et al. 2013, Strong et al. 2015). For many species, the level of stress hormone corticosterone can be an effective predictor of survival probabilities, reproduction, dispersal, and can have population-level impacts (Carrete et al. 2013, Romero and Wikelski 2001, Romero et al. 2000). Quantification of corticosterone in feathers, which is stable over time, represents an integrated measure of stress levels (Bortolotti et al. 2009, Sheriff et al. 2011). Stress hormones are accumulated in feathers during growth, so can provide a measure of stress levels during that time, and can be a strong predictor for future survival of individuals (Koren et al. 2012). Variation in feather corticosterone can also be quantified among individuals of a population, as well as through time to track stress over space and time to address questions about the health and ecology of a population (Bortolotti et al. 2009).

Hayward et al. (2011) found that spotted owls had a glucocorticoid response to acute noise disturbance and that spotted owls with nests near noisy roads fledged fewer young than those near quiet roads. Corticosterone analyses are needed to determine the physiological response to acute and prolonged exposure to environmental stressors (e.g., barred owls, prey abundance, weather, and human-caused disturbance) and response activity for both juvenile and adult spotted owls. Our understanding of spotted owl ecology will be improved with studies to evaluate the associations between stress levels and survival, reproduction, and dispersal of spotted owls. From a management perspective, it is important to understand the stress response of spotted owls related to management activities like prescribed fire, road construction, various logging systems, and the timing of these activities. Additional research will be important to understand key stressors for spotted owls and inform seasonal restrictions on human activities that can increase stress levels.

Dispersal and suitable forest connectivity—
Dispersal behavior for both juveniles and adults may increase survival and reproductive success, but also increase risks to establishing a home range in an unfamiliar landscape. Juvenile spotted owls disperse within their first year and the condition of matrix forest types between natal and breeding sites can facilitate or hamper survival and movement processes (Forsman et al. 2002). Available information for spotted owls suggests that stands used for roosting during natal dispersal movements have very similar structure as those stands used for nesting and roosting activities of adults (>70 percent canopy cover and large trees >50 cm d.b.h.), but this finding is based on only two studies with no data throughout most of the geographic range (Miller et al. 1997, Sovern et al. 2015). Further research is needed to understand the contemporary dynamics of juvenile dispersal because many assumptions are made about what constitutes forest cover suitable to facilitate dispersal by spotted owls. A better understanding of the forest structure and configuration characteristics of forest conditions that facilitate juvenile dispersal is needed to ensure demographic connectivity among isolated patches of remaining old forests. Further, it remains unknown how barred owls influence juvenile spotted owl survival or dispersal. It is possible that some of these questions could be addressed with a thorough analysis of existing dispersal data from demographic study areas.

Historically, adult spotted owls exhibited strong nesting-site and mate fidelity, with fewer than 8 percent of individuals dispersing to a different territory between years (Forsman et al. 1984, 2002). In recent years, however, field observations suggest that interterritory movements by resident spotted owls are increasing, and that such movements appear to coincide with the colonization of barred owls (Dugger et al. 2011, Olson et al. 2005). Research that addresses how forest alteration and the presence of barred owls interact with social conditions on territories to affect movement decisions and survival of individual spotted owls will improve our ability to implement forest management practices that benefit spotted owls. In addition to helping land managers identify the range of conditions within

individual owl territories that promote high site fidelity and survival, such data can also provide a powerful framework for testing broad ecological theories about the causes and consequences of breeding dispersal in a long-lived predatory bird with declining populations.

Testing alternative monitoring protocols— When the NWFP was developed, mark-recapture and random census (i.e., occupancy framework; the proportion of sites occupied by spotted owls) population monitoring methods were both considered. The decision was made to use the mark-recapture method, which was already in use. Precise estimates from mark-recapture studies require large samples of marked spotted owls; therefore, Lint et al. (1999) recommended the use of an independent estimate of population trend for comparison with the results from spotted owl demographic studies. Monitoring in an occupancy framework (i.e., MacKenzie et al. 2006) could provide an independent, empirical assessment of population trends to compare with estimates of the annual rate of population change. Because of uncertainty about the precision of the occupancy-based approach, Lint et al. (1999) recommended that statistical power and cost effectiveness of the method be explored.

The low number of spotted owls in some study areas suggests that passive acoustic monitoring may be an effective solution for future monitoring of spotted owl populations. Traditional call-back surveys at night (playing spotted owl calls and listening for a spotted owl response) are labor intensive, more risky compared to daytime work, and only generate reliable data for spotted owls. Further, detection probabilities for spotted owls—using call-back surveys—are negatively influenced by the presence of barred owls, and barred owls often do not respond to spotted owl calls (Bailey et al. 2009). Call-back surveys could also have unintended consequences by exposing spotted owls to predation or harassment by barred owls or great-horned owls. Primary advantages of passive acoustic monitoring are as follows: (1) surveys do not require an elicited response from target species; (2) surveys are able to detect and do not bias against many other species (e.g., barred owl, marbled murrelet, western screech-owl, northern pygmy-owl, northern saw-whet owl, and many others); (3) increased crew safety because all work would be conducted during daylight hours; (4) biological training and expertise needed for crew members will be much less than is needed for call-back surveys and demographic studies; and (5) sound recordings provide a permanent record of the detection. A limitation of this approach is the time required to process recordings and data storage. Automated call detection technology has been developed, but improvements are needed, especially for call recognizers for rare birds in areas with excessive background environmental noise (e.g., rain, streams). Research is needed to test alternative methods that take advantage of technological advancements in noninvasive detection equipment to monitor trends in rare populations. The transition to alternative methods to monitor spotted owl populations will be most effective if new methods have spatial and temporal overlap with traditional methods so that robust comparisons can be made between historical and contemporary data.

Population simulation modeling— The program HexSim (Schumaker 2015) provides a simulation framework for systematically investigating factors that influence population function, including forest conservation scenarios and emergent competitors. The implementation of HexSim by the USFWS (2011b) did not include spatially explicit representation of spotted owl interactions with barred owls. Modeling exercises that incorporate a more sophisticated representation of population interactions with barred owls are needed to simulate and predict responses of spotted owls to experimental removal of barred owls. Two-species models implemented in HexSim could also be used to simulate potential efficacy of long-term management programs for barred owls and spotted owls relative to critical habitat designations. Current modeling efforts are female-only models. A two-sex HexSim implementation for the spotted owl population is needed to get at small population processes (e.g., Alee effects and stochasticity in sex ratios) that can drive extinction.

Scientific Uncertainty

Survival estimates—

Adult survival is typically the most important factor influencing population performance in long-lived raptors, and survival estimates for spotted owls have been the focus of extensive research and monitoring. As in other meta-analyses of spotted owl demographic data (e.g., Burnham et al. 1996, Dugger et al. 2016, Forsman et al. 2011), Anthony et al. (2006) used capture-recapture methods to estimate apparent survival rates of spotted owls. Apparent survival is the product of probabilities that an animal survives and remains in the population. If a marked animal permanently emigrates, then it is, for purposes of the estimate, presumed dead, because emigration and mortality are confounded. Further, fates are not known for all individuals because recapture probabilities are less than one even when animals remain in the population. Therefore, models based on capture-recapture data account for imperfect encounter rates in estimates of survival (i.e., apparent survival). Apparent survival rates on individual study areas ranged from 0.75 (± 0.03) to 0.89 (± 0.01) for adults, 0.63 (± 0.07) to 0.89 (± 0.01) for 2-year-olds, and 0.42 (± 0.11) to 0.86 (± 0.02) for 1-year-olds. They found negative effects of reproduction and barred owls in survival rates on several study areas (Anthony et al. 2006).

Elsewhere, Loehle et al. (2005) used telemetry to study annual survival of spotted owls and obtained a known-fate estimate of 0.93 (± 0.07), which was considerably higher than the apparent survival estimates reported by Anthony et al. (2006). Known-fate models estimate survival rate when fates (i.e., alive or dead) of individuals can be determined with certainty. Loehle et al. (2005) used their results to cast doubt on apparent survival estimates from mark-recapture studies of spotted owls. They suggested that survival estimates from mark-recapture studies were too low because some marked individuals left the study areas and were assumed to be dead. Anthony et al. (2006) estimated a declining spotted owl population; Loehle et al. (2005) suggested that the true population change for spotted owls was likely stable and not declining. In response, Franklin et al. (2006) argued that Loehle et al. (2005) had inappropriately compared their study with the work of Anthony et al. (2006) in a number of ways, including (1) the manner in which missing radio-marked individuals were removed from analyses may have overestimated survival; (2) telemetry-based estimates of survival were not valid for estimating bias; and (3) results from the telemetry-based study should not be compared to the capture-recapture study because study areas differed dramatically in size and distribution. Both apparent survival estimates from mark-recapture data and known-fate estimates from telemetry studies are valid estimates of annual survival. However, in this circumstance it was inappropriate to compare telemetry-based survival estimates with results from capture-recapture studies, which was acknowledged by both sides of the disagreement (Franklin et al. 2006, Loehle and Irwin 2006).

Wildfire risk—

The 2008 recovery plan (now withdrawn) for spotted owls (USFWS 2008) suggested a change in the LSR network as the foundation of conservation strategies established in the NWFP. Because of concern about wildfire, the plan recommended a switch from a reserve to a no-reserve strategy in up to 52 percent of the spotted owl's range. For dry forests, the plan recommended thinning stands at regular intervals to reduce fuel loading, and thus wildfire risk. Hanson et al. (2009) suggested that the estimates of wildfire risk used by the USFWS (2008) were overestimated and that there was not a strong basis for major changes to the NWFP conservation strategy for the spotted owl. Spies et al. (2010) defended the estimates of wildfire risk and suggested that Hanson et al. (2009) had underestimated wildfire risk and were biased against active management. Hanson et al. (2010) then responded by calling for less focus on fuel treatments in the recovery plan for the spotted owl. Because of uncertainty about future wildfire occurrence, spatial extent, and severity, we cannot know with complete confidence whether wildfire risk has been over- or underestimated in these efforts. Both the 2008 critical habitat designation and the 2008 recovery plan were challenged in court, and the inspector general of the Department of the Interior issued a report concluding that the decisionmaking process for the

recovery plan was potentially jeopardized by improper political influence (Devaney 2008, USFWS 2011a). The court ordered the Fish and Wildlife Service to withdraw the 2008 recovery plan and issue a revised recovery plan and critical habitat designation.

Spies et al. (2017) projected that the extent of forest cover suitable for spotted owls in the eastern Oregon Cascades is expected to increase in coming decades under recent historical frequencies and severities of wildfire (and current levels of wildfire suppression). Treating the landscape to reduce potential loss of suitable forest cover for spotted owls with high-severity wildfire still resulted in increases in that forest cover type, but not as much as would occur without management. The results suggest that managing for resilience to fire and climate change could occur without necessarily reducing forest cover from its current levels (younger forest is growing into older closed-canopy forests to replace dense forests lost thinning or wildfire). However, these outcomes are likely to be different under climate change or if an alternative landscape-scale treatment design is used (Spies et al. 2017).

Despite the potential negative effects on spotted owl habitat, the overwhelming consensus in the scientific literature is that active management in dry forests is appropriate to reduce wildfire risk and improve ecosystem function. Therefore, the 2011 revised recovery plan (USFWS 2011b) and 2012 critical habitat designation (USFWS 2012a) for spotted owls contained proposals for active management in dry forests. In some regions, project planning has moved forward, and federal land managers are consulting with the Fish and Wildlife Service on a case-by-case basis. The debate about active management related to wildfire risk for forests used by spotted owls remains unresolved and reflects different goals (e.g., ecosystem versus single species) and assumptions about wildfire risk with a changing climate. These differences of opinion highlight legitimate concerns about where to place the burden of proof regarding ecosystem versus species management, but the fundamentals of this controversy lie in the diversity of philosophical views about ecological goals and the role that active management should play on public lands (see chapter 12).

Restoration framework—
Franklin and Johnson (2012) outlined a series of recommendations for an "ecological forestry" framework and a forest restoration strategy within the Plan area that reflect many of the elements of the revised spotted owl recovery plan (USFWS 2011b). They called for reserving older forest stands, thinning plantations to accelerate development of structural complexity, and implementing variable-retention harvests in younger forests to help provide diverse early-seral ecosystems on moist forest sites. On dry forest sites, their strategy called for silvicultural treatments that retain and release older trees, reduce stand densities, shift composition toward fire- and drought-tolerant tree species, and incorporate spatial heterogeneity at multiple spatial scales (Franklin and Johnson 2012). The framework included an extensive set of large patches of dense forests on approximately 30 percent of the forested landscape to retain some suitable forest for spotted owls while reducing the potential for landscape-level high-severity wildfires.

DellaSala et al. (2013) identified seven areas in which the ecological forestry framework may fall short of the stated goals of the NWFP, and offered 14 recommendations to improve the framework and its implementation. They also criticized decisions to incorporate some of the elements of ecological forestry in the revised recovery plan and revised critical habitat designation. Henson et al. (2013) agreed with many of the recommendations made by DellaSala et al. (2013), but differed on two key perspectives. Henson et al. (2013) regarded the potential impacts of wildfire to spotted owls as higher risk to species persistence, and suggested that in many circumstances, the adverse effects associated with active management may be preferable to adverse effects of passive management. As with wildfire risk, the fundamentals of this debate reside in philosophical disagreements about ecological goals and what role active management should play in managing public lands. Most research in dry or frequent-fire forest landscapes suggests that active management is needed to achieve or accelerate restoration objectives, but more study is needed to advance our understanding of disturbance effects on wildlife dependent on old forest, especially interactions between wildfire and a range of prefire and postfire active management actions.

Modeling to inform critical habitat designation— The Fish and Wildlife Service (USFWS 2012a) produced maps of distribution of potentially suitable habitat for spotted owls that did not include the effects of barred owls on spotted owl distribution, but the effort did incorporate the spatial arrangement of forest structure associated with nesting/roosting and foraging, and abiotic factors such as slope and topographic position, to determine the extent of critical habitat. In an alternate analysis, Loehle et al. (2015) conducted an accuracy assessment of vegetation data used as input to develop the USFWS (2012a) models, used independent locations to validate model prediction, correlated model output with spotted owl reproductive success in two study areas, and developed alternate models. Their independent locations and vegetation evaluations suggested a high rate of classification errors, and productivity did not correlate well with predictions in their study areas (Loehle et al. 2015). Dunk et al. (2015) defended the critical habitat model as scientifically rigorous and as meeting the goals established by the Fish and Wildlife Service. They suggested that Loehle et al. (2015) mischaracterized the literature and the Fish and Wildlife Service species distribution model, failed to demonstrate the locations used by the agency were biased, and failed to show significant flaws in analytical methods.

Bell et al. (2015) argued that Loehle et al. (2015) underestimated the predictive performance of critical habitat maps because the field plots they used potentially biased the accuracy assessment toward older forests, and that they examined accuracy at finer scales than the model was intended to predict. Loehle and Irwin (2015) responded to Bell et al. (2015) and Dunk et al. (2015) by arguing that, although the habitat models average out at large spatial scales, errors at smaller scales may limit their utility for conservation. This debate underscores the importance of acknowledging the appropriate scale at which predictive distribution models can be used for conservation purposes. The debate also serves as another example highlighting the need to recognize and carefully evaluate how habitat is defined. The definition of habitat for spotted owls must now consider that forests that were once suitable for spotted owls are less suitable habitat if occupied by barred owls.

Conclusions and Management Considerations

Spotted owls are a resilient subspecies but are faced with significant challenges. Research and monitoring efforts over the past several decades have documented the population declines and risks to spotted owls despite measures to address their long-term sustainability. The framework, standards, and guidelines of the NWFP have been both critical and necessary for spotted owl conservation, and underlie species recovery plans. However, because of barred owls and continued forest perturbations outside of federal lands, the NWFP alone is not sufficient for spotted owl recovery. Additional measures beyond the Plan will be needed for long-term persistence of spotted owls. Suitable habitat continues to decline because of current and lingering effects of extensive forest disturbance, and the recent invasion of a formidable congeneric competitor has reduced the space available for spotted owl recovery. The need to provide habitat for spotted owls has been a critical component of conservation plans and was a major catalyst for developing the NWFP. It is now clear that barred owl presence reduces habitat suitabiliy for spotted owls, so species recovery will require protections for old forest and management actions focused on reducing the threat from barred owls. After only two decades, it is too early to evaluate if the Plan has been effective at improving the conservation status of spotted owls; however, the framework, standards, and guidelines of the NWFP have aided spotted owl conservation; if logging had continued at pre-NWFP levels, spotted owl populations certainly would have declined more rapidly over the past 20 years. Further, the NWFP has put federal lands on a trajectory for providing enough suitable forest for recovery of spotted owl populations over the next several decades. The effectiveness of LSRs established under the NWFP is linked to the frequency, severity, spatial extent, and type of disturbance, as well as how those disturbances are offset by recruitment of suitable forest, primarily through succession. Disturbance events can reduce the suitability of forests used by spotted owls for several decades by creating open canopy conditions and reducing structural complexity. Although disturbance rates have exceeded suitable forest-cover

recruitment rates during the first 20 years of the NWFP, recruitment will likely outpace losses if current timber harvests and wildfire occurrence remain constant. However, climate models suggest that wildfire occurrence may increase, causing significant reductions in cover for spotted owls, and that suitable forest cover for spotted owls will move northward and occur at higher elevations. Therefore, other reserves designated before development of the NWFP, such as parks and wilderness areas, may become increasingly important for spotted owl conservation.

Several lines of compelling evidence indicate that interspecific competition between spotted owls and barred owls is causing accelerated population declines of spotted owls, despite widespread conservation of old forests under the NWFP. Competitive pressure from barred owls may negate the benefits of recruitment of suitable forest cover, because barred owls exclude spotted owls from sites that otherwise are suitable for spotted owls. It remains uncertain how, or if, spotted owls can coexist with barred owls. Although much research has been done on spotted owls, we identified many uncertainties in available information and have identified future research needs important for management of the subspecies. The long-term effects of barred owls and fine-scale partitioning of resources remain unknown, and studies are needed to identify resilient sites for spotted owls in the face of competitive interactions with barred owls, if they exist. Additionally, it remains unknown how, or if, spotted owls will respond to removals of barred owls from historical spotted owl territories.

Abundance and distribution of primary prey species can influence home range size and forest selection by spotted owls. But it remains unknown how spatially and temporally fluctuating prey populations influence the survival and reproduction of spotted owls. Studies are needed to quantify relationships between interannual fluctuations in prey abundance and long-term demography of spotted owls. The short- and long-term effects of silvicultural treatments and wildfire on spotted owl occupancy, forest dynamics, and prey remain unclear. The optimization of forest restoration and conservation of spotted owls will require more knowledge about the conditions under which restoration activities can benefit spotted owls in the long term without significant detrimental impact in the short term.

Management Considerations

Forest management and barred owls— Wiens et al. (2014) found that adult survival of spotted owls and barred owls was higher in home ranges with greater amounts of conifer forest dominated by trees age 120 years or older. Dietary studies also showed that barred owl diet is broader than spotted owls, but both owl species relied on similar prey associated with older forest types (e.g., northern flying squirrels and red tree voles). These findings have important implications for land managers because they suggest that (1) conservation of old forest under the NWFP not only promotes survival of spotted owls, but also survival of barred owls; and (2) availability of old forests (and associated food resources) is a key limiting factor in the competitive relationship between the two owl species (Wiens et al. 2014). As barred owls continue to increase in number, it has become clear that conservation of the spotted owl and its forest cover types need to be extended from ameliorating the effects of old-forest loss and fragmentation to accounting for the impacts of a widespread invasive competitor as well. Although spotted owls are known to use recently thinned stands (e.g., Irwin et al. 2015), it remains unclear how such silvicultural treatments can affect the fitness of spotted owls in the long term or how barred owls may respond to those management actions. Those silvicultural treatments with high disturbance likely increase long-term extinction rates of spotted owls by reducing forest complexity and thus suitability for spotted owls but not necessarily for barred owls (Dugger et al. 2016, Singleton 2015, Singleton et al. 2010, Sovern et al. 2014, Wiens et al. 2014).

Barred owl densities may now be high enough across the range of the spotted owl that, despite the continued management and conservation of suitable forest cover types under the NWFP, the spotted owl population will continue to decline without intervention to reduce barred owl populations (Dugger et al. 2016). Recommendations to conduct experimental removal of barred owls to benefit spotted owls have been criticized as being too difficult to accomplish owing to the effort and cost required to maintain sufficiently low numbers of invasive barred owls (Livezey 2010, Rosenberg et al. 2012). Nonetheless, experimental removal of barred owls on one study area in California suggests that

removal of barred owls may have positive, short-term effects on population trends of spotted owls (Diller et al. 2016, Dugger et al. 2016). In 2013, the Fish and Wildlife Service decided to expand removal experiments to additional sites in California, Oregon, and Washington to determine if similar results can be obtained in areas with different forest conditions and densities of barred owls (USDI 2013, USFWS 2013). Those experiments will yield information about how spotted owls respond, and will convey the economic and logistic feasibility of removal efforts as potential management actions. Such information will be useful in projecting possible long-term consequences and benefits of an active management program for barred owls in the future.

Current evidence suggests that a combination of habitat protection and active management of barred owls are the two highest priorities for stabilizing declining trends in populations of spotted owls. A recent analysis casts doubt on the likely effectiveness of barred owl removals for spotted owl conservation (Bodine and Capaldi 2017). Experimental culling of barred owls will provide information to validate those models and about how, or if, their populations can be controlled at scales sufficient to promote recovery of spotted owls. However, detailed studies of habitat associations and resource use by barred owls have been conducted in only a few limited areas within the range of the spotted owl. More detailed studies in other areas will better enable an understanding of how specific tree species, stand densities, or physiographic conditions are negatively associated with barred owls but not spotted owls.

Wildfire and active management—
Disturbance processes that increase forest or landscape heterogeneity (e.g., wildfire, management activities) can benefit spotted owls as long as the required forest structural conditions are available for foraging, nesting, and roosting activities. Processes that substantially simplify stand structure or landscapes often have negative impacts on the suitability of forest for spotted owls. Our basic understanding of forest structural conditions used by spotted owls has not substantially changed over the past 20 years, but there has been a growing recognition of the contribution of diverse forest conditions to broader ecosystem function and species diversity in conifer forests of the Pacific Northwest. This is especially true in historically moderate- and high-frequency fire regime landscapes where fire suppression and forest management have greatly reduced fire and altered forest structure and composition at stand and landscape scales (chapter 3). For example, nonconiferous vegetation, including shrubs and broad-leaved trees, makes an important contribution to the diversity of forest landscapes. Therefore, allowing shrubs and hardwood trees to develop and persist in early-seral stands, and curtailing vegetation control, will benefit many wildlife species associated with nonconiferous vegetation (Hagar 2007), including some spotted owl prey species (Diller et al. 2012). Additionally, diversity and configuration of different forest types are important for spotted owls at stand, home range, and landscape scales (Franklin et al. 2000). The function and diversity of an ecosystem is enhanced by the presence of high-quality early-seral patches (i.e., a mix of nonforest and forest) because they have high species and structural diversity (Swanson et al. 2011). These early-seral ecosystems can be created using low-intensity approaches for regeneration, combined with retention of biological legacies to promote the development of structurally diverse closed-canopy forest over time (Franklin and Johnson 2012). Indeed, under normal conditions, natural disturbances frequently result in patches of high-quality early-seral ecosystems, provided that intensive salvage and replanting does not occur after the disturbance (Swanson et al. 2011).

Disturbances have different impacts on spotted owls depending on the scale under consideration. A hypothesis that has emerged from recent research is that disturbance processes (e.g., low- and mixed-severity wildfire, light to moderate thinning) that increase stand or landscape heterogeneity can have long-term benefits for spotted owls, as long as enough suitable forest cover for nesting and roosting remain within the territory. Conversely, disturbances that substantially simplify stands or landscapes often have long-lasting negative impacts on spotted owls and their habitat. Finally, we emphasize the importance of conserving sites currently occupied by spotted owls as well as those that are known to have been historically occupied by the subspecies. Many sites, for example, have been abandoned as a result of disturbance to suitable forest cover or displacement by barred owls, but maintain structure suitable for nesting and roosting. Those remaining spotted owls and sites likely

represent unique behavioral or forest characteristics that may not yet be fully recognized, thus they are an important research need. Conserving the unique forest structural conditions of those few sites that remain, particularly in the northern portion of the geographic range, will likely have a positive benefit for the long-term persistence of spotted owls.

Prognosis for the future—

In the 2011 revised recovery plan for spotted owls, the Fish and Wildlife Service's modeling team used the HexSim modeling program (Schumaker 2008) to simulate population-level responses to various conservation strategies and other threats (USFWS 2011b). They developed models based on demographic data (Forsman et al. 2011), dispersal information (Forsman et al. 2002, Thomas et al. 1990), and home range size (Carey et al. 1990; Forsman et al. 1984, 2005; Glenn et al. 2004; Hamer et al. 2007). Objectives of the modeling effort were to (1) evaluate if future viable populations of spotted owls were likely given conditions at the time (demographic rates, LSR network, amount of suitable forest cover, barred owls); (2) estimate population viability under different conservation networks of suitable forest cover; and (3) quantify the effect of forest cover and barred owl management on recovery goals for spotted owls (USFWS 2011b). The modeling results suggested that availability of suitable forest cover was critical for territory acquisition and sustained occupancy by spotted owls. Population viability models suggest that barred owls reduce spotted owl survival and act to depress populations to about half of potential population size without barred owls (fig. 4-9). Simulations did not include the barred owl impact on spotted owl reproduction, forest selection, site fidelity, or detection probability, and were based upon early rates of population growth. More recent population change estimates (Dugger et al. 2016) indicate a further declining growth

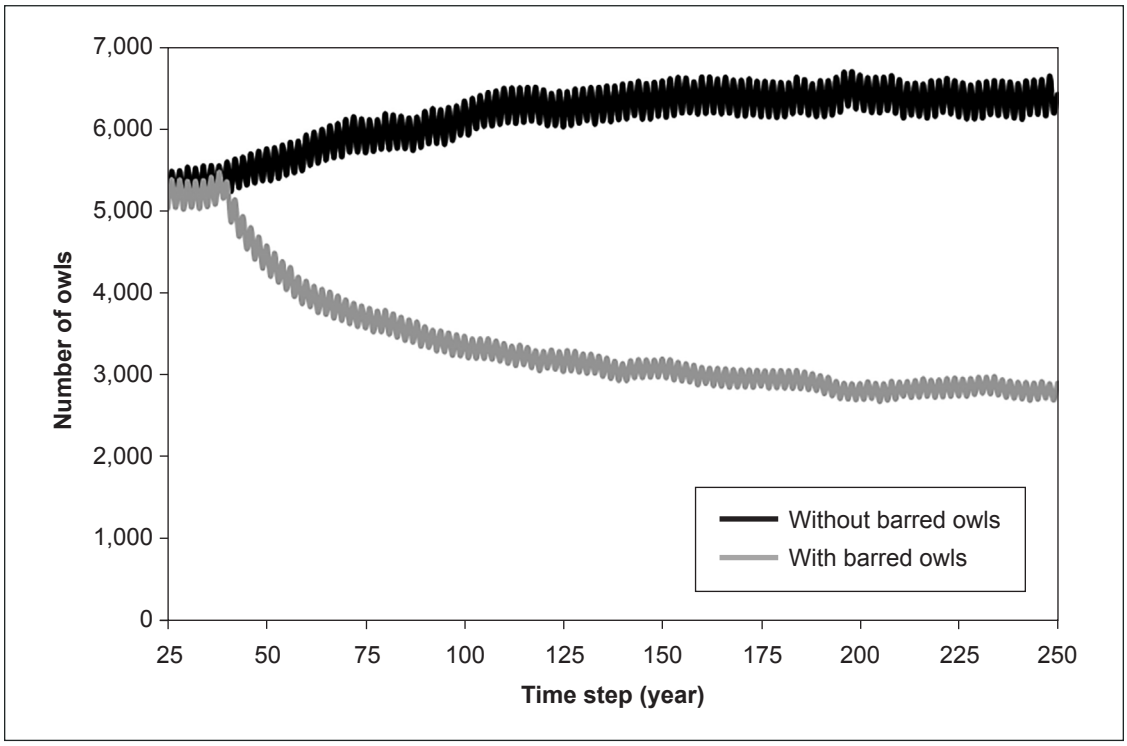


Figure 4-9—HexSim model runs with five replicates each for without barred owl impacts and with barred owl impacts for the spotted owl's geographic range in the United States. The apparent within-year variation that appears in the figure is a function of an "even-odd" year effect on reproduction (USFWS 2011b). The first 30 years of the simulation was a "burn-in" period, which provided for the simulated population to distribute according to available resources and develop an age structure determined by demographic processes. Barred owl effects were not included during the "burn-in" period and were introduced starting at year 30 (USFWS 2011b).

rate, suggesting that USFWS (2011b) projected estimates are more optimistic than what is likely to be observed in spotted owl populations. These studies provide further evidence that the framework, standards, and guidelines of the NWFP are critical components to spotted owl recovery plans, but the impacts of barred owls will likely need to be controlled if spotted owl species recovery is to be successful.

Schumaker et al. (2014) used the HexSim model originally developed by the Fish and Wildlife Service (USFWS 2011b) to simulate and quantify source-sink dynamics and landscape connectivity throughout the range of the spotted owl. Their results indicated that populations are likely to decline in most regions, but that southern Oregon and northern California may serve as source populations. Marcot et al. (2013) also used the HexSim model to evaluate how size and spacing of suitable forest cover types for spotted owls affected simulated population size and persistence. Their results indicated that long-term occupancy rates were significantly higher with suitable forest patches large enough to support 25 spotted owl pairs or more, with less than 9.3 mi (15 km) spacing between patches, and with overall landscapes of at least 35 to 40 percent suitable forest cover types for nesting and roosting. In a sensitivity analysis, Marcot et al. (2015) determined that spotted owl response variables in the HexSim model were most sensitive to the availability of highly suitable forest cover for nesting and roosting. All these studies used static habitat maps that did not incorporate climate change or wildfire impacts on spotted owls. Only the USFWS (2011b) model incorporated effects of barred owls.

Spotted owl populations have continued to decline under the NWFP, but because of slowed timber harvest on federal lands since the late 1980s, forests throughout most of the range of the spotted owl are on a trajectory—through succession—to develop suitable forest characteristics for spotted owls in coming decades. When the NWFP was adopted, spotted owl populations were expected to continue declining for up to 50 years because of lingering impacts of previous losses of suitable forest cover, yet the magnitude and characteristics of barred owl impacts were unknown and unexpected at that time. Per assumptions of the NWFP, we are unable, after only two decades, to use stable or increasing populations (i.e., improved conservation status) of spotted owls as the success criterion for the NWFP. However, if the success criterion is forests capable of supporting interconnected populations of spotted owls in the absence of barred owls, then the implementation of the framework, standards, and guidelines of the NWFP has put federal lands on a trajectory for success, despite recent losses of suitable forest cover to wildfire. In the Pacific Northwest, forest succession from early-seral to climax forest is a slow process, which is in part the reasoning for the NWFP to be a 100-year plan intended to span several human generations (USDA and USDI 1994). Further, conservation and management of spotted owls rests critically on continued implementation of the protections afforded by the NWFP and the Endangered Species Act (Noon and Blakesley 2006). It also rests on improving our understanding of how to minimize impacts of barred owls, and on fine-tuning our ability to retain needed forest structure while also increasing resiliency of forests through strategic management.

U.S. and Metric Equivalents

When you have:	Multiply by:	To get:
Inches	2.54	Centimeters
Meters (m)	3.28	Feet
Hectares (ha)	2.47	Acres

Acknowledgments

We are indebted to the many biologists and funding sources dedicated to studying northern spotted owl populations and factors affecting this threatened subspecies. Heather Roberts (Oregon State University, Department of Forest Ecosystems and Society) assisted with the plot analysis presented in the inset of this chapter. Author salaries were supported by the USDA Forest Service Pacific Northwest Research Station (D. Lesmeister and P. Singleton) and Pacific Northwest Region (R. Davis), and by the USDI Geological Survey, Forest and Rangeland Ecosystem Science Center (J.D. Wiens). We thank E. Forsman, E. Glenn, members of the public, and anonymous reviewers for providing comments and suggested edits that greatly improved this chapter.

Literature Cited

Acker, J. 2012. Recent trends in western screech-owl and barred owl abundances on Bainbridge Island, Washington. Northwestern Naturalist. 93(2): 133–137. doi:10.1898/nwn11-21.1.

Ackers, S.H.; Davis, R.J.; Olsen, K.A.; Dugger, K.M. 2015. The evolution of mapping habitat for northern spotted owls (*Strix occidentalis caurina*): a comparison of photo-interpreted, Landsat-based, and LiDAR-based habitat maps. Remote Sensing of Environment. 156: 361–373. doi:10.1016/j.rse.2014.09.025.

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Washington, DC: Island Press. 505 p.

Agee, J.K.; Skinner, C.N. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management. 211(1–2): 83–96. doi:10.1016/j.foreco.2005.01.034.

Ager, A.A.; Finney, M.A.; Kerns, B.K.; Maffei, H. 2007. Modeling wildfire risk to northern spotted owl (*Strix occidentalis caurina*) habitat in central Oregon, USA. Forest Ecology and Management. 246(1): 45–56.

Albert, C.A.; Wilson, L.K.; Mineau, P.; Trudeau, S.; Elliott, J.E. 2010. Anticoagulant rodenticides in three owl species from western Canada, 1988–2003. Archives of Environmental Contamination and Toxicology. 58(2): 451–459. doi:10.1007/s00244-009-9402-z.

Anderson, P.D.; Ronnenberg, K.L., eds. 2013. Density management in the 21st century: west side story. Gen. Tech. Rep. PNW-GTR-880. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 249 p.

Andrews, H.J.; Cowlin, R.W. 1940. Forest resources of the Douglas-fir region. Misc. Publ. 389. Portland, OR: U.S. Department of Agriculture, Forest Service. 200 p.

Andrews, L.S.; Perkins, J.P.; Thrailkill, J.A.; Poage, N.J.; Tappeiner, J.C. 2005. Silvicultural approaches to develop northern spotted owl nesting sites, central coast ranges, Oregon. Western Journal of Applied Forestry. 20(1): 13–27.

Angert, A.L.; LaDeau, S.L.; Ostfeld, R.S. 2013. Climate change and species interactions: ways forward. Annals of the New York Academy of Sciences. 1297: 1–7. doi: 10.1111/nyas.12286.

Anthony, R.G.; Forsman, E.D.; Franklin, A.B.; Anderson, D.R.; Burnham, K.P.; White, G.C.; Schwarz, C.J.; Nichols, J.D.; Hines, J.E.; Olson, G.S.; Ackers, S.H.; Andrews, L.S.; Biswell, B.L.; Carlson, P.C.; Diller, L.V.; Dugger, K.M.; Fehring, K.E.; Fleming, T.L.; Gerhardt, R.P.; Gremel, S.A.; Gutierrez, R.J.; Happe, P.J.; Herter, D.R.; Higley, J.M.; Horn, R.B.; Irwin, L.L.; Loschl, P.J.; Reid, J.A.; Sovern, S.G. 2006. Status and trends in demography of northern spotted owls, 1985–2003. Wildlife Monographs. 163(1): 1–48.

Anthony, R.G.; O'Connell, M.A.; Pollock, M.M.; Hallett, J.G. 2003. Associations of mammals with riparian ecosystems in Pacific Northwest forests. In: Zabel, C.J.; Anthony, R.G., eds. Mammal community dynamics: management and conservation in the coniferous forests of western North America. Cambridge, United Kingdom: Cambridge University Press: 510–566. Chapter 15.

Aubry, K.B.; Halpern, C.B.; Peterson, C.E. 2009. Variable-retention harvests in the Pacific Northwest: a review of short-term findings from the demo study. Forest Ecology and Management. 258(4): 398–408. doi:10.1016/j.foreco.2009.03.013.

Avery, D.M.; Avery, G.; Palmer, N.G. 2005. Micromammalian distribution and abundance in the Western Cape Province, South Africa, as evidenced by barn owls *Tyto alba* (scopoli). Journal of Natural History. 39(22): 2047–2071. doi:10.1080/00222930500044631.

Bailey, L.L.; Reid, J.A.; Forsman, E.D.; Nichols, J.D. 2009. Modeling co-occurrence of northern spotted and barred owls: accounting for detection probability differences. Biological Conservation. 142(12): 2983–2989. doi:10.1016/j.biocon.2009.07.028.

Baker, W.L. 2015. Historical northern spotted owl habitat and old-growth dry forests maintained by mixed-severity wildfires. Landscape Ecology. 30(4): 655–666. doi:10.1007/s10980-014-0144-6.

Bamford, M.J.; Calver, M.C. 2014. A precise definition of habitat is needed for effective conservation and communication. Australian Zoologist. 37(2): 245–247.

Barrowclough, G.F.; Groth, J.G.; Mertz, L.A.; Gutiérrez, R.J. 2005. Genetic structure, introgression, and a narrow hybrid zone between northern and California spotted owls (*Strix occidentalis*). Molecular Ecology. 14(4): 1109–1120.

Barrowclough, G.F.; Gutierrez, R.J.; Groth, J.G.; Lai, J.E.; Rock, D.F. 2011. The hybrid zone between northern and California spotted owls in the Cascade-Sierran suture zone. Condor. 113(3): 581–589.

Barrows, C. 1980. Feeding ecology of the spotted owl in California. Journal of Raptor Research. 12(3): 73–78.

Barrows, C.W. 1981. Roost selection by spotted owls: an adaptation to heat stress. Condor. 83: 302–309.

Bell, D.M.; Gregory, M.J.; Roberts, H.M.; Davis, R.J.; Ohmann, J.L. 2015. How sampling and scale limit accuracy assessment of vegetation maps: a comment on Loehle et al. (2015). Forest Ecology and Management. 358: 361–364. doi:10.1016/j.foreco.2015.07.017.

Bevis, K.R.; Richards, J.E.; King, G.M.; Hanson, E.E. 1997. Food habits of the northern spotted owl (*Strix occidentalis caurina*) at six nest sites in Washington's east Cascades. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: second international symposium. Gen. Tech. Rep. GTR-NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 68–73.

Bodine, E.N.; Capaldi, A. 2017. Can culling barred owls save a declining northern spotted owl population? Natural Resource Modeling. e12131. doi:10.1111/nrm.12131.

Bond, M.L. 2016. The heat is on: spotted owls and wildfire. Reference Module in Earth Systems and Environmental Sciences: 1–12. doi:10.1016/B978-0-12-409548-9.10014-4.

Bond, M.L.; Bradley, C.; Lee, D.E. 2016. Foraging habitat selection by California spotted owls after fire. Journal of Wildlife Management. doi:10.1002/jwmg.21112.

Bond, M.L.; Lee, D.E.; Siegel, R.B.; Ward, J.P. 2009. Habitat use and selection by California spotted owls in a postfire landscape. Journal of Wildlife Management. 73(7): 1116–1124. doi:10.2193/2008-248.

Bortolotti, G.R.; Marchant, T.; Blas, J.; Cabezas, S. 2009. Tracking stress: localisation, deposition and stability of corticosterone in feathers. Journal of Experimental Biology. 212(Pt 10): 1477–1482. doi:10.1242/jeb.022152.

Buchanan, J.B.; Fleming, T.L.; Irwin, L.L. 2004. A comparison of barred and spotted owl nest-site characteristics in the eastern Cascade Mountains, Washington. Journal of Raptor Research. 38(3): 231–237.

Buchanan, J.B.; Gutiérrez, R.J.; Anthony, R.G.; Cullinan, T.; Diller, L.V.; Forsman, E.D.; Franklin, A.B. 2007. A synopsis of suggested approaches to address potential competitive interactions between barred owls (*Strix varia*) and spotted owls (*S. occidentalis*). Biological Invasions. 9(6): 679–691. doi:10.1007/s10530-006-9068-7.

Burnham, K.P.; Anderson, D.R.; White, G.C. 1996. Meta-analysis of vital rates of the northern spotted owl. In: Forsman, E.D.; DeStefano, S.; Raphael, M.G.; Gutierrez, R.J., eds. Demography of the northern spotted owl. Studies in Avian Biology No. 17. Lawrence, KS: Cooper Ornithological Society: 92–101. Vol. 17.

Carey, A.B. 2000. Effects of new forest management strategies on squirrel populations. Ecological Applications. 10(1): 248–257.

Carey, A.B.; Horton, S.P.; Biswell, B.L. 1992. Northern spotted owls: influence of prey base and landscape character. Ecological Monographs. 62(2): 223–250.

Carey, A.B.; Johnson, M.L. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological Applications. 5(2): 336–352.

Carey, A.B.; Maguire, C.C.; Biswell, B.L.; Wilson, T.M. 1999. Distribution and abundance of neotoma in western Oregon and Washington. Northwest Science. 73(2): 65–80.

Carey, A.B.; Reid, J.A.; Horton, S.P. 1990. Spotted owl home range and habitat use in southern Oregon Coast Ranges. Journal of Wildlife Management. 54(1): 11–17.

Carey, M.P.; Sanderson, B.L.; Barnas, K.A.; Olden, J.D. 2012. Native invaders—challenges for science, management, policy, and society. Frontiers in Ecology and the Environment. 10(7): 373–381. doi:10.1890/110060.

Carrete, M.; Bortolotti, G.R.; Sánchez-Zapata, J.A.; Delgado, A.; Cortés-Avizanda, A.; Grande, J.M.; Donázar, J.A. 2013. Stressful conditions experienced by endangered Egyptian vultures on African wintering areas. Animal Conservation. 16(3): 353–358. doi:10.1111/acv.12001.

Carroll, C. 2010. Role of climatic niche models in focal-species-based conservation planning: assessing potential effects of climate change on northern spotted owl in the Pacific Northwest, USA. Biological Conservation. 143(6): 1432–1437.

Carroll, C.; Dunk, J.R.; Moilanen, A. 2010. Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest, USA. Global Change Biology. 16(3): 891–904.

Carroll, C.; Johnson, D.S. 2008. The importance of being spatial (and reserved): assessing northern spotted owl habitat relationships with hierarchical bayesian models. Conservation Biology. 22(4): 1026–1036.

Churchill, D.J.; Larson, A.J.; Dahlgreen, M.C.; Franklin, J.F.; Hessburg, P.F.; Lutz, J.A. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. Forest Ecology and Management. 291: 442–457. doi:10.1016/j.foreco.2012.11.007.

Clark, D.A.; Anthony, R.G.; Andrews, L.S. 2011. Survival rates of northern spotted owls in post-fire landscapes of southwest Oregon. Journal of Raptor Research. 45(1): 38–47.

Clark, D.A.; Anthony, R.G.; Andrews, L.S. 2013. Relationship between wildfire, salvage logging, and occupancy of nesting territories by northern spotted owls. Journal of Wildlife Management. 77(4): 672–688. doi:10.1002/jwmg.523.

Cochrane, M.A.; Moran, C.J.; Wimberly, M.C.; Baer, A.D.; Finney, M.A.; Beckendorf, K.L.; Eidenshink, J.; Zhu, Z. 2012. Estimation of wildfire size and risk changes due to fuels treatments. International Journal of Wildland Fire. 21(4): 357. doi:10.1071/wf11079.

Comfort, E.J.; Clark, D.A.; Anthony, R.G.; Bailey, J.; Betts, M.G. 2016. Quantifying edges as gradients at multiple scales improves habitat selection models for northern spotted owl. Landscape Ecology. 31: 1227–1240. doi:10.1007/s10980-015-0330-1.

Courtney, S.P.; Blakesley, J.A.; Bigley, R.E.; Cody, M.L.; Dumbacher, J.P.; Fleishcher, R.C.; Franklin, A.B.; Franklin, J.F.; Gutiérrez, R.J.; Marzluff, J.M.; Sztukowski, L. 2004. Scientific evaluation of the status of the northern spotted owl. Portland, OR: Sustainable Ecosystems Institute. 498 p.

Crespin, L.; Verhagen, R.; Stenseth, N.C.; Yoccoz, N.G.; Prevot-Julliard, A.; Lebreton, J. 2002. Survival in fluctuating bank vole populations: seasonal and yearly variations. Oikos. 98: 467–479.

Crozier, M.L.; Seamans, M.E.; Gutierrez, R.J.; Loschl, P.J.; Horn, R.B.; Sovern, S.G.; Forsman, E.D. 2006. Does the presence of barred owls suppress the calling behavior of spotted owls? Condor. 108(4): 760–769.

Cutler, T.L.; Hays, D.W. 1991. Food habits of northern spotted owls in high elevation forests of pelican butte, southwest Oregon. Northwestern Naturalist. 72: 66–69.

Dale, V.H.; Joyce, L.A.; McNulty, S.; Neilson, R.P.; Ayres, M.P.; Flannigan, M.D.; Hanson, P.J.; Irland, L.C.; Lugo, A.E.; Peterson, C.J.; Simberloff, D.; Swanson, F.J.; Stocks, B.J.; Michael Wotton, B. 2001. Climate change and forest disturbances. BioScience. 51(9): 723. doi:10.1641/0006-3568(2001)051[0723:ccafd]2.0.co;2.

Dark, S.J.; Gutierrez, R.J.; Gould, G.I., Jr. 1998. The barred owl (*Strix varia*) invasion in California. Auk. 115(1): 50–56.

Davis, R.J.; Dugger, K.M.; Mohoric, S.; Evers, L.; Aney, W.C. 2011. Northwest forest plan—the first 15 years (1994–2008): status and trends of northern spotted owl populations and habitat. Gen. Tech. Rep. PNW-GTR-850. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 147 p.

Davis, R.J.; Hollen, B.; Hobson, J.; Gower, J.E.; Keenum, D. 2016. Northwest Forest Plan—the first 20 years (1994–2013): status and trends of northern spotted owl habitats. Gen. Tech. Rep. PNW-GTR-929. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 111 p.

Davis, R.J.; Lint, J. 2005. Habitat status and trends. In: Lint, J., ed. Northwest Forest Plan—the first 10 years (1994–2003): status and trends of northern spotted owl populations and habitat. Gen. Tech. Rep. PNW-GTR-648. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 21–82. Chapter 3.

DellaSala, D.A.; Anthony, R.G.; Bond, M.L.; Fernandes, E.S.; Frissell, C.A.; Hanson, C.T.; Spivak, R. 2013. Alternative views of a restoration framework for federal forests in the Pacific Northwest. Journal of Forestry. 111(6): 420–429.

Dennison, P.E.; Brewer, S.C.; Arnold, J.D.; Moritz, M.A. 2014. Large wildfire trends in the Western United States, 1984–2011. Geophysical Research Letters. 41(8): 2928–2933. doi:10.1002/2014gl059576.

Devaney, E.E. 2008. Report of investigation—the endangered species act and the conflict between science and policy. Washington, DC: U.S. Department of the Interior, Office of Inspector General. 141 p.

Diller, L.; Hamm, K.; Lamphear, D.; McDonald, T. 2012. Two decades of research and monitoring of the northern spotted owl on private timberlands in the redwood region: what do we know and what challenges remain? In: Standiford, R.B.; Weller, T.J.; Piirto, D.D.; Stuart, J.D., eds. Proceedings of the coast redwood forests in a changing California: a symposium for scientists and managers. Gen. Tech. Rep. PSW-GTR-238. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 399–408.

Diller, L.V.; Hamm, K.A.; Early, D.A.; Lamphear, D.W.; Dugger, K.M.; Yackulic, C.B.; Schwartz, C.J.; Carlson, P.C.; McDonald, T.L. 2016. Demographic responses of northern spotted owls to barred owl removal. Journal of Wildlife Management. 80(4): 691–707. doi:10.1002/jwmg.1046.

Dugger, K.M.; Anthony, R.G.; Andrews, L.S. 2011. Transient dynamics of invasive competition: barred owls, spotted owls, habitat, and the demons of competition present. Ecological Applications. 21(7): 2459–2468.

Dugger, K.M.; Forsman, E.D.; Franklin, A.B.; Davis, R.J.; White, G.C.; Schwarz, C.J.; Burnham, K.P.; Nichols, J.D.; Hines, J.E.; Yackulic, C.B.; Doherty Jr., P.F.; Bailey, L.L.; Clark, D.A.; Ackers, S.H.; Andrews, L.S.; Augustine, B.; Biswell, B.L.; Blakesley, J.A.; Carlson, P.C.; Clement, M.J.; Diller, L.V.; Glenn, E.M.; Green, A.; Gremel, S.A.; Herter, D.R.; Higley, J.M.; Hobson, J.; Horn, R.B.; Huyvaert, K.P.; McCafferty, C.; McDonald, T.L.; McDonnell, K.; Olson, G.S.; Reid, J.A.; Rockweit, J.; Ruiz, V.; Saenz, J.; Sovern, S.G. 2016. The effects of habitat, climate and barred owls on the long-term population demographics of northern spotted owls. Condor. 118: 57–116. doi:10.1650/CONDOR-15-24.1.

Dugger, K.M.; Wagner, F.; Anthony, R.G.; Olson, G.S. 2005. The relationship between habitat characteristics and demographic performance of northern spotted owls in southern Oregon. Condor. 107(4): 863–878.

Dunbar, D.L.; Booth, B.P.; Forsman, E.D.; Hethering-ton, A.E.; Wilson, D.J. 1991. Status of the spotted owl, *Strix occidentalis*, and barred owl, *Strix varia*, in southwestern British Columbia. Canadian Field-Naturalist. 105(4): 464–468.

Dunk, J.R.; Hawley, J.J.V.G. 2009. Red-tree vole habitat suitability modeling: implications for conservation and management. Forest Ecology and Management. 258(5): 626–634. doi:10.1016/j.foreco.2009.04.041.

Dunk, J.R.; Woodbridge, B.; Glenn, E.M.; Davis, R.J.; Fitzgerald, K.; Henson, P.; LaPlante, D.W.; Marcot, B.G.; Noon, B.R.; Raphael, M.G.; Schumaker, N.H.; White, B. 2015. The scientific basis for modeling northern spotted owl habitat: a response to Loehle, Irwin, Manly, and Merrill. Forest Ecology and Management. 358: 355–360. doi:10.1016/j.foreco.2015.06.035.

Elliot, K. 2006. Declining numbers of western screech-owl in the lower mainland of British Columbia. British Columbia Birds. 14: 2–11.

Farber, S.L.; Kroll, A.J. 2012. Site occupancy dynamics of northern spotted owls in managed interior Douglas-fir forests, California, USA, 1995–2009. Journal of Wildlife Management. 76(6): 1145–1152. doi:10.1002/jwmg.368.

Forest Ecosystem Management Assessment Team [FEMAT]. 1993. Forest ecosystem management: an ecological, economic, and social assessment. Portland, OR: U.S. Department of Agriculture; U.S. Department of the Interior [and others]. [Irregular pagination].

Forsman, E.D.; Anthony, R.G.; Dugger, K.M.; Glenn, E.M.; Franklin, A.B.; White, G.C.; Schwartz, C.J.; Burnham, K.P.; Anderson, D.R.; Nichols, J.D.; Hines, J.E.; Lint, J.B.; Davis, R.J.; Ackers, S.H.; Andrews, L.S.; Biswell, B.L.; Carlson, P.C.; Diller, L.V.; Gremel, S.A.; Herter, D.R.; Higley, J.M.; Horn, R.B.; Reid, J.A.; Rockweit, J.; Schaberl, J.P.; Snetsinger, T.J.; Sovern, S.G. 2011. Population demography of northern spotted owls. Studies in Avian Biology. 40: 1–106.

Forsman, E.D.; Anthony, R.G.; Meslow, E.C.; Zabel, C.J. 2004. Diets and foraging behavior of northern spotted owls in Oregon. Journal of Raptor Research. 38(3): 214–230.

Forsman, E.D.; Anthony, R.G.; Reid, J.A.; Loschl, P.J.; Sovern, S.G.; Taylor, M.; Biswell, B.L.; Ellingson, A.; Meslow, E.C.; Miller, G.S.; Swindle, K.A.; Thrailkill, J.A.; Wagner, F.F.; Seaman, D.E. 2002. Natal and breeding dispersal of northern spotted owls. Wildlife Monographs. 149: 1–35.

Forsman, E.D.; Kaminski, T.J.; Lewis, J.C.; Maurice, K.J.; Sovern, S.G.; Ferland, C.; Glenn, E.M. 2005. Home range and habitat use of northern spotted owls on the Olympic Peninsula, Washington. Journal of Raptor Research. 39(4): 365–377.

Forsman, E.D.; Meslow, E.C.; Wight, H.M. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs. 48(2): 1–64.

Forsman, E.D.; Otto, I.A.; Sovern, S.C.; Taylor, M.; Hays, D.W.; Allen, H.; Roberts, S.L.; Seaman, D.E. 2001. Spatial and temporal variation in diets of spotted owls in Washington. Journal of Raptor Research. 35(2): 141–150.

Forsman, E.D.; Sovern, S.G.; Taylor, M.; Biswell, B.L. 2015. Home range and habitat selection by northern spotted owls on the eastern slope of the Cascade mountains, Washington. Journal of Raptor Research. 49(2): 109–128.

Franklin, A.B.; Anderson, D.R.; Forsman, E.D.; Burnham, K.P.; Wagner, F.W. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. Studies in Avian Biology. 17: 12–20.

Franklin, A.B.; Anderson, D.R.; Gutierrez, R.J.; Burnham, K.P. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs. 70(4): 539–590.

Franklin, A.B.; Gutiérrez, R.J. 2002. Spotted owls, forest fragmentation, and forest heterogeneity. Studies in Avian Biology. 25: 203–220.

Franklin, A.B.; Nichols, J.D.; Anthony, R.G.; Burnham, K.P.; White, G.C.; Forsman, E.D.; Anderson, D.R. 2006. Comment on "are survival rates for northern spotted owls biased?" Canadian Journal of Zoology. 84(9): 1375–1379. doi:10.1139/z06-129.

Franklin, J.F.; Johnson, K.N. 2012. A restoration framework for federal forests in the Pacific Northwest. Journal of Forestry. 110(8): 429–439. doi:10.5849/jof.10-006.

Frey, S.J.K.; Hadley, A.S.; Johnson, S.L.; Schulze, M.; Jones, J.A.; Betts, M.G. 2016. Spatial models reveal the microclimatic buffering capacity of old-growth forests. Science Advances. 2: e1501392.

Funk, W.C.; Forsman, E.D.; Johnson, M.; Mullins, T.D.; Haig, S.M. 2010. Evidence for recent population bottlenecks in northern spotted owls (*Strix occidentalis caurina*). Conservation Genetics. 11(3): 1013–1021.

Funk, W.C.; Forsman, E.D.; Mullins, T.D.; Haig, S.M. 2008. Introgression and dispersal among spotted owl (*Strix occidentalis*) subspecies. Evolutionary Applications. 1(1): 161–171.

Funk, W.C.; Mullins, T.D.; Forsman, E.D.; Haig, S.M. 2007. Microsatellite loci for distinguishing spotted owls (*Strix occidentalis*), barred owls (*Strix varia*), and their hybrids. Molecular Ecology Notes. 7(2): 284–286. doi:10.1111/j.1471-8286.2006.01581.x.

Gabriel, M.W.; Woods, L.W.; Poppenga, R.; Sweitzer, R.A.; Thompson, C.; Matthews, S.M.; Higley, J.M.; Keller, S.M.; Purcell, K.; Barrett, R.H.; Wengert, G.M.; Sacks, B.N.; Clifford, D.L. 2012. Anticoagulant rodenticides on our public and community lands: spatial distribution of exposure and poisoning of a rare forest carnivore. PLoS ONE. 7: e40163. doi:10.1371/journal.pone.0040163.

Gaines, W.L.; Harrod, R.J.; Dickinson, J.; Lyons, A.L.; Halupka, K. 2010. Integration of northern spotted owl habitat and fuels treatments in the eastern Cascades, Washington, USA. Forest Ecology and Management. 260(11): 2045–2052.

Ganey, J.L.; Ward, J.P.J.; Willey, D. 2011. Status and ecology of Mexican spotted owls in the Upper Gila Mountains recovery unit, Arizona and New Mexico. Gen. Tech. Rep. RMRS-GTR-256. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 94 p.

Glenn, E.M.; Anthony, R.G.; Forsman, E.D. 2010. Population trends in northern spotted owls: associations with climate in the Pacific Northwest. Biological Conservation. 143(11): 2543–2552.

Glenn, E.M.; Anthony, R.G.; Forsman, E.D.; Olson, G.S. 2011a. Local weather, regional climate, and annual survival of the northern spotted owl. Condor. 113(1): 150–158. doi:10.1525/cond.2011.100118.

Glenn, E.M.; Anthony, R.G.; Forsman, E.D.; Olson, G.S. 2011b. Reproduction of northern spotted owls: the role of local weather and regional climate. Journal of Wildlife Management. 75(6): 1279–1294. doi:10.1002/jwmg.177.

Glenn, E.M.; Hansen, M.C.; Anthony, R.G. 2004. Spotted owl home-range and habitat use in young forests of western Oregon. Journal of Wildlife Management. 68(1): 33–50.

Glenn, E.M.; Lesmeister, D.B.; Davis, R.J.; Hollen, B.; Poopatanapong, A. 2017. Estimating density of a territorial species in a dynamic landscape. Landscape Ecology. 32: 563–579. doi:10.1007/s10980-016-0467-6.

Gomez, D.; Anthony, R.G. 1998. Small mammal abundance in riparian and upland areas of five seral stages in western Oregon. Northwest Science. 72(4): 293–302.

Graham, S.A. 2012. Diet composition, niche and geographic characteristics, and prey size preference of barred owls (*Strix varia*) in the Pacific Northwest. Boise, ID: Boise State University. 149 p. M.S. thesis.

Gutiérrez, R.J.; Barrowclough, G.F. 2005. Redefining the distributional boundaries of the northern and California spotted owls: implications for conservation. Condor. 107(1): 182–187.

Gutiérrez, R.J.; Cody, M.; Courtney, S.; Franklin, A.B. 2007. The invasion of barred owls and its potential effect on the spotted owl: a conservation conundrum. Biological Invasions. 9(2): 181–196. doi:10.1007/s10530-006-9025-5.

Hagar, J.C. 2007. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: A review. Forest Ecology and Management. 246(1): 108–122. doi:10.1016/j.foreco.2007.03.054.

Hagmann, R.K.; Franklin, J.F.; Johnson, K.N. 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. Forest Ecology and Management. 304: 492–504.

Hagmann, R.K.; Franklin, J.F.; Johnson, K.N. 2014. Historical conditions in mixed-conifer forests on the eastern slopes of the northern Oregon Cascade Range, USA. Forest Ecology and Management. 330: 158–170. doi:10.1016/j.foreco.2014.06.044.

Haig, S.M.; Mullins, T.D.; Forsman, E.D.; Trail, P.W.; Wennerberg, L. 2004. Genetic identification of spotted owls, barred owls, and their hybrids: legal implications of hybrid identity. Conservation Biology. 18(5): 1347–1357.

Hall, L.S.; Krausman, P.R.; Morrison, M.L. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin. 25(1): 173–182.

Hamer, T.E.; Forsman, E.D.; Fuchs, A.D.; Walters, M.L. 1994. Hybridization between barred and spotted owls. Auk. 111(2): 487–492.

Hamer, T.E.; Forsman, E.D.; Glenn, E.M. 2007. Home range attributes and habitat selection of barred owls and spotted owls in an area of sympatry. Condor. 109(4): 750–768.

Hamer, T.E.; Hays, D.L.; Senger, C.M.; Forsman, E.D. 2001. Diets of northern barred owls and northern spotted owls in an area of sympatry. Journal of Raptor Research. 35(3): 221–227.

Hanson, C.T.; Odion, D.C.; Dellasala, D.A.; Baker, W.L. 2009. Overestimation of fire risk in the northern spotted owl recovery plan. Conservation Biology. 23(5): 1314–1319.

Hanson, C.T.; Odion, D.C.; Dellasala, D.A.; Baker, W.L. 2010. More-comprehensive recovery actions for northern spotted owls in dry forests: reply to Spies et al. Conservation Biology. 24(1): 334–337. doi:10.1111/j.1523-1739.2009.01415.x.

Hayward, L.S.; Bowles, A.E.; Ha, J.C.; Wasser, S.K. 2011. Impacts of acute and long-term vehicle exposure on physiology and reproductive success of the northern spotted owl. Ecosphere. 2(6): 1–20.

Heithecker, T.D.; Halpern, C.B. 2006. Variation microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. Forest Ecology and Management. 226(1–3): 60–71.

Henson, P.; Thrailkill, J.; Glenn, B.; Woodbridge, B.; White, B. 2013. Using ecological forestry to reconcile spotted owl conservation and forest management. Journal of Forestry. 111(6): 433–437. doi:10.5849/jof.13-072.

Herter, D.R.; Hicks, L.L. 2000. Barred owl and spotted owl populations and habitat in the central Cascade range of Washington. Journal of Raptor Research. 34(4): 279–286.

Hessburg, P.F.; Churchill, D.J.; Larson, A.J.; Haugo, R.D.; Miller, C.; Spies, T.A.; North, M.P.; Povak, N.A.; Belote, R.T.; Singleton, P.H.; Gaines, W.L.; Keane, R.E.; Aplet, G.H.; Stephens, S.L.; Morgan, P.; Bisson, P.A.; Rieman, B.E.; Salter, R.B.; Reeves, G.H. 2015. Restoring fire-prone inland pacific landscapes: seven core principles. Landscape Ecology. 30(10): 1805–1835. doi:10.1007/s10980-015-0218-0.

Hessburg, P.F.; Salter, R.B.; James, K.M. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: Inferences from landscape patterns of forest structure. Landscape Ecology. 22: 5–24.

Hessburg, P.F.; Spies, T.A.; Perry, D.A.; Skinner, C.N.; Taylor, A.H.; Brown, P.M.; Stephens, S.L.; Larson, A.J.; Churchill, D.J.; Povak, N.A.; Singleton, P.H.; McComb, B.; Zielinski, W.J.; Collins, B.M.; Salter, R.B.; Keane, J.J.; Franklin, J.F.; Riegel, G. 2016. Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and northern California. Forest Ecology and Management. 366: 221–250. doi:10.1016/j.foreco.2016.01.034.

Holm, S.R.; Noon, B.R.; Wiens, J.D.; Ripple, W.J. 2016. Potential trophic cascades triggered by the barred owl range expansion. Wildlife Society Bulletin. 40(4): 615–624. doi:10.1002/wsb.714.

Irwin, L.L.; Rock, D.F.; Miller, G.P. 2000. Stand structures used by northern spotted owls in managed forests. Journal of Raptor Research. 34(3): 175–186.

Irwin, L.L.; Rock, D.F.; Rock, S.C. 2012. Habitat selection by northern spotted owls in mixed-coniferous forests. Journal of Wildlife Management. 76(1): 200–213. doi:10.1002/jwmg.218.

Irwin, L.L.; Rock, D.F.; Rock, S.C. 2013. Do northern spotted owls use harvested areas? Forest Ecology and Management. 310: 1029–1035. doi:10.1016/j.foreco.2013.04.001.

Irwin, L.L.; Rock, D.F.; Rock, S.C.; Loehle, C.; Van Deusen, P. 2015. Forest ecosystem restoration: initial response of spotted owls to partial harvesting. Forest Ecology and Management. 354: 232–242. doi:10.1016/j.foreco.2015.06.009.

Ishak, H.D.; Dumbacher, J.P.; Anderson, N.L.; Keane, J.J.; Valkiunas, G.; Haig, S.M.; Tell, L.A.; Sehgal, R.N. 2008. Blood parasites in owls with conservation implications for the spotted owl (*Strix occidentalis*). PLoS One. 3(5): e2304. doi:10.1371/journal.pone.0002304.

Jennings, S.B.; Brown, N.B.; Sheil, D. 1999. Assessing forest canopies and understory illumination: canopy closure, canopy cover and other measures. Forestry. 72(1): 59–73.

Johnson, K.N.; Franklin, J.F. 2013. Recommendations for future implementation of ecological forestry projects on BLM western Oregon forests. Portland, OR: U.S. Department of the Interior, Bureau of Land Management, Oregon/Washington State Office. 45 p.

Jones, G.M.; Gutiérrez, R.J.; Tempel, D.J.; Whitmore, S.A.; Berigan, W.J.; Peery, M.Z. 2016. Megafires: an emerging threat to old-forest species. Frontiers in Ecology and the Environment. 14(6): 300–306. doi:10.1002/fee.1298.

Kelly, E.G.; Forsman, E.D. 2004. Recent records of hybridization between barred owls (*Strix varia*) and northern spotted owls (*S. Occidentalis caurina*). Auk. 121(3): 806–810.

Kelly, E.G.; Forsman, E.D.; Anthony, R.G. 2003. Are barred owls displacing spotted owls? Condor. 105(1): 45–53.

Kennedy, R.E.; Yang, Z.; Cohen, W.B.; Pfaff, E.; Braaten, J.; Nelson, P. 2012. Spatial and temporal patterns of forest disturbance and regrowth within the area of the northwest forest plan. Remote Sensing of Environment. 122: 117–133. doi:10.1016/j.rse.2011.09.024.

Kennedy, R.S.H.; Wimberly, M.C. 2009. Historical fire and vegetation dynamics in dry forests of the interior Pacific Northwest, USA, and relationships to northern spotted owl (*Strix occidentalis caurina*) habitat conservation. Forest Ecology and Management. 258(5): 554–566.

Koren, L.; Nakagawa, S.; Burke, T.; Soma, K.K.; Wynne-Edwards, K.E.; Geffen, E. 2012. Non-breeding feather concentrations of testosterone, corticosterone and cortisol are associated with subsequent survival in wild house sparrows. Proceedings of the Royal Society—Biological Sciences (Series B). 279(1733): 1560–1566. doi:10.1098/rspb.2011.2062.

Kroll, A.J.; Fleming, T.L.; Irwin, L.L. 2010. Site occupancy dynamics of northern spotted owls in the eastern Cascades, Washington, USA, 1990–2003. Journal of Wildlife Management. 74(6): 1264–1274. doi:10.2193/2009-429.

Lee, D.E.; Bond, M.L. 2015. Occupancy of California spotted owl sites following a large fire in the Sierra Nevada, California. Condor. 117(2): 228–236. doi:10.1650/condor-14-155.1.

Lee, D.E.; Bond, M.L.; Borchert, M.I.; Tanner, R. 2013. Influence of fire and salvage logging on site occupancy of spotted owls in the San Bernardino and San Jacinto Mountains of southern California. Journal of Wildlife Management. 77(7): 1327–1341. doi:10.1002/jwmg.581.

Lehmkuhl, J.F.; Kistler, K.D.; Begley, J.S. 2006a. Bushy-tailed woodrat abundance in dry forests of eastern Washington. Journal of Mammology. 87(2): 371–379.

Lehmkuhl, J.F.; Kistler, K.D.; Begley, J.S.; Boulanger, J. 2006b. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications. 16(2): 584–600.

Lehmkuhl, J.F.; Peterson, D.W.; Gaines, W.L.; Bailey, J.; Youngblood, A., eds. 2015. Silviculture and monitoring guidelines for integrating restoration of dry mixed-conifer forest and spotted owl habitat management in the eastern Cascade Range. Gen. Tech. Rep. PNW-GTR-915. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 168 p.

Leskiw, T.; Gutiérrez, R.J. 1998. Possible predation of a spotted owl by a barred owl. Western Birds. 29: 225–226.

Lewicki, K.E.; Huyvaert, K.P.; Piaggio, A.J.; Diller, L.V.; Franklin, A.B. 2015. Effects of barred owl (*Strix varia*) range expansion on haemoproteus parasite assemblage dynamics and transmission in barred and northern spotted owls (*Strix occidentalis caurina*). Biological Invasions. 17(6): 1713–1727.

Lindenmayer, D.B.; Noss, R.F. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology. 20(4): 949–958. doi:10.1111/j.1523-1739.2006.00497.x.

Lint, J., ed. 2005. Northwest Forest Plan—the first 10 years (1994–2003): status and trends of northern spotted owl populations and habitat. Gen. Tech. Rep. PNW-GTR-648. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 176 p.

Lint, J.; Noon, B.; Anthony, R.; Forsman, E.; Raphael, M.; Collopy, M.; Starkey, E. 1999. Northern spotted owl effectiveness monitoring plan for the Northwest Forest Plan. Gen. Tech. Rep. PNW-GTR-440. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 43 p.

Livezey, K.B. 2007. Barred owl habitat and prey: a review and synthesis of the literature. Journal of Raptor Research. 41(3): 177–201.

Livezey, K.B. 2009. Range expansion of barred owls, part I: chronology and distribution. American Midland Naturalist. 161: 49–56.

Livezey, K.B. 2010. Killing barred owls to help spotted owls I: a global perspective. Northwestern Naturalist. 91: 107–133.

Loehle, C.; Irwin, L. 2006. Reply to the comment by Franklin et al. on "are survival rates for northern spotted owls biased?" Canadian Journal of Zoology. 84(9): 1380–1382.

Loehle, C.; Irwin, L. 2015. Range wide analysis of northern spotted owl habitat relations: reply to comments. Forest Ecology and Management. 358: 365–368. doi:10.1016/j.foreco.2015.09.033.

Loehle, C.; Irwin, L.; Manly, B.F.J.; Merrill, A. 2015. Range-wide analysis of northern spotted owl nesting habitat relations. Forest Ecology and Management. 342: 8–20. doi:10.1016/j.foreco.2015.01.010.

Loehle, C.; Irwin, L.; Rock, D.; Rock, S. 2005. Are survival rates for northern spotted owls biased? Canadian Journal of Zoology. 83: 1386–1390. doi:10.1139/Z05-137.

MacKenzie, D.I.; Nichols, J.D.; Royle, J.A.; Pollock, K.H.; Bailey, L.L.; Hines, J.E. 2006. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. New York: Academic Press. 324 p.

Manning, T.; Hagar, J.C.; McComb, B.C. 2012. Thinning of young Douglas-fir forests decreases density of northern flying squirrels in the Oregon Cascades. Forest Ecology and Management. 264: 115–124. doi:10.1016/j.foreco.2011.09.043.

Marcot, B.G.; Raphael, M.G.; Schumaker, N.H.; Galleher, B. 2013. How big and how close? Habitat patch size and spacing to conserve a threatened species. Natural Resource Modeling. 26(2): 194–214.

Marcot, B.G.; Singleton, P.H.; Schumaker, N.H. 2015. Analysis of sensitivity and uncertainty in an individual-based model of a threatened wildlife species. Natural Resource Modeling. 28(1): 37–58.

Mathewson, H.A.; Morrison, M.L. 2015. The misunderstanding of habitat. In: Morrison, M.L.; Mathewson, H.A., eds. Wildlife habitat conservation: concepts, challenges, and solutions. Baltimore, MD: Johns Hopkins University Press: 3–8. Chapter 1.

McDonald, T.L.; Manly, B.F.J.; Nielson, R.M.; Diller, L.V. 2006. Discrete-choice modeling in wildlife studies exemplified by northern spotted owl nighttime habitat selection. Journal of Wildlife Management. 70(2): 375–383.

McKelvey, K.S. 2015. The effects of disturbance and succession on wildlife habitat and animal communities. In: Morrison, M.L.; Mathewson, H.A., eds. Wildlife habitat conservation: concepts, challenges, and solutions. Baltimore, MD: Johns Hopkins University Press: 143–156. Chapter 11.

Merschel, A.G.; Spies, T.A.; Heyerdahl, E.K. 2014. Mixed-conifer forests of central Oregon: effects of logging and fire exclusion vary with environment. Ecological Applications. 24(7): 1670–1688.

Miller, G.S.; Small, R.J.; Meslow, E.C. 1997. Habitat selection by spotted owls during natal dispersal in western Oregon. Journal of Wildlife Management. 61(1): 140–150.

Miller, M.P.; Mullins, T.D.; Forsman, E.D.; Haig, S.M. 2017. Genetic differentiation and inferred dynamics of a hybrid zone between northern spotted owls (*Strix occidentalis caurina*) and California spotted owls (*S. o. occidentalis*) in northern California. Ecology and Evolution. 00: 1–13. doi:10.1002/ece3.3260.

Monahan, W.B.; Hijmans, R.J. 2007. Distribution dynamics of invasion and hybridization by *Strix* spp. in western North America. Ornithological Monographs. 63: 55–66.

Morrison, M.L.; Marcot, B.G.; Mannan, R.W. 2006. Wildlife-habitat relationships: concepts and applications. 3rd ed. Washington, DC: Island Press. 520 p.

Mote, P.W.; Parson, E.A.; Hamlet, A.F.; Keeton, W.S.; Lettenmaier, D.; Mantua, N.; Miles, E.L.; Peterson, D.W.; Peterson, D.L.; Slaughter, R.; Snover, A.K. 2003. Preparing for climate change: the water, salmon, and forests of the Pacific Northwest. Climate Change. 61: 45–88.

Noon, B.R.; Blakesley, J.A. 2006. Conservation of the northern spotted owl under the Northwest Forest Plan. Conservation Biology. 20(2): 288–296.

Olson, G.; Anthony, R.G.; Forsman, E.D.; Ackers, S.H.; Loschl, P.J.; Reid, J.A.; Dugger, K.M.; Glenn, E.M.; Ripple, W.J. 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. Journal of Wildlife Management. 69(3): 918–932.

Olson, G.S.; Glenn, E.M.; Anthony, R.G.; Forsman, E.D.; Reid, J.A.; Loschl, P.J.; Ripple, W.J. 2004. Modeling demographic performance of northern spotted owls relative to forest habitat in Oregon. Journal of Wildlife Management. 68(4): 1039–1053.

Pearson, R.R.; Livezey, K.B. 2003. Distribution, numbers, and site characteristics of spotted owls and barred owls in the Cascade Mountains of Washington. Journal of Raptor Research. 37(4): 265–276.

Pearson, R.R.; Livezey, K.B. 2007. Spotted owls, barred owls, and late-successional reserves. Journal of Raptor Research. 41(2): 156–161.

Perry, D.A.; Hessburg, P.F.; Skinner, C.N.; Spies, T.A.; Stephens, S.L.; Taylor, A.H.; Franklin, J.F.; McComb, B.; Riegel, G. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and northern California. Forest Ecology and Management. 262(5): 703–717.

Pierce, D.J.; Buchanan, J.B.; Consentino, B.L.; Snyder, S. 2005. An assessment of spotted owl habitat on non-federal lands in Washington between 1996 and 2004. Final report. Olympia, WA: Washington Department of Fish and Wildlife. 187 p.

Price, A.L.; Mowdy, J.S.; Swingle, J.K.; Forsman, E.D. 2015. Distribution and abundance of tree voles in the northern Coast Ranges of Oregon. Northwestern Naturalist. 96(1): 37–49. doi:10.1898/NWN14-04.1.

Raphael, M.G. 2006. Conservation of listed species: the northern spotted owl and marbled murrelet. In: Haynes, R.W.; Borman, B.T.; Lee, D.C.; Martin, J.R., eds. Northwest Forest Plan—the first 10 years (1994–2003): synthesis of monitoring and research results. Gen. Tech. Rep. PNW-GTR-651. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 117–143. Chapter 7.

Reilly, M.J.; Dunn, C.J.; Meigs, G.W.; Spies, T.S.; Kennedy, R.E.; Bailey, J.D.; Briggs, K. 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). Ecosphere. 8(3): e01695.

Riley, S.; Bromley, C.; Poppenga, R.; Uzal, F.; Whited, L.; Sauvajot, R. 2007. Anticoagulant exposure and notoedric mange in bobcats and mountain lions in urban southern California. Journal of Wildlife Management. 71(6): 1874–1884.

Roberts, S.L.; van Wagtendonk, J.W.; Miles, A.K.; Kelt, D.A. 2011. Effects of fire on spotted owl site occupancy in a late-successional forest. Biological Conservation. 144(1): 610–619. doi:10.1016/j.biocon.2010.11.002.

Rockweit, J.T.; Franklin, A.B.; Carlson, P.C. 2017. Differential impacts of wildfire on the population dynamics of an old-forest species. Ecology. 98(6): 1574–1582.

Roloff, G.J.; Mealey, S.P.; Bailey, J.D. 2012. Comparative hazard assessment for protected species in a fire-prone landscape. Forest Ecology and Management. 277: 1–10. doi:10.1016/j.foreco.2012.04.015.

Roloff, G.J.; Mealey, S.P.; Clay, C.; Barry, J.; Yanish, C.; Neuenschwander, L. 2005. A process for modeling short- and long-term risk in the southern Oregon Cascades. Forest Ecology and Management. 211(1–2): 166–190.

Romero, L.M.; Reed, J.M.; Wingfield, J.C. 2000. Effects of weather on corticosterone responses in wild free-living passerine birds. General and Comparative Endocrinology. 118: 113–122.

Romero, L.M.; Wikelski, M. 2001. Corticosterone levels predict survival probabilities of Galapagos marine iguanas during El Niño events. Proceedings of the National Academy of Sciences. 98(13): 7366–7370. doi:10.1073/pnas.131091498.

Rosenberg, D.K.; Swindle, K.A.; Anthony, R.G. 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. Canadian Journal of Zoology. 81(10): 1715–1725.

Rosenberg, D.K.; Vesely, D.G.; Gervais, J.A. 2012. Maximizing endangered species research. Science. 337: 799.

Rullman, S.; Marzluff, J.M. 2014. Raptor presence along an urban-wildland gradient: influences of prey abundance and land cover. Journal of Raptor Research. 48(3): 257–272. doi:10.3356/jrr-13-32.1.

Safford, H.D.; Stevens, J.T.; Merriam, K.; Meyer, M.D.; Latimer, A.M. 2012. Fuel treatment effectiveness in California yellow pine and mixed conifer forests. Forest Ecology and Management. 274: 17–28. doi:10.1016/j.foreco.2012.02.013.

Sakai, H.F.; Noon, B.R. 1993. Dusky-footed woodrat abundance in different-aged forests in northwestern California. Journal of Wildlife Management. 57(2): 373–382.

Schilling, J.W.; Dugger, K.M.; Anthony, R.G. 2013. Survival and home-range size of northern spotted owls in southwestern Oregon. Journal of Raptor Research. 47(1): 1–14.

Schumaker, N.H. 2008. Hexsim (version 1.3.6.9). http://www.hexsim.net. (13 September 2017).

Schumaker, N.H. 2015. Hexsim (version 4.0.9). http://www.hexsim.net. (13 September 2017).

Schumaker, N.H.; Brookes, A.; Dunk, J.R.; Woodbridge, B.; Heinrichs, J.A.; Lawler, J.J.; Carroll, C.; LaPlante, D. 2014. Mapping sources, sinks, and connectivity using a simulation model of northern spotted owls. Landscape Ecology. 29(4): 579–592.

Seamans, M.E.; Corcoran, J.; Rex, A. 2004. Southernmost record of a spotted owl x barred owl hybrid in the Sierra Nevada. Western Birds. 35: 173–174.

Seamans, M.E.; Gutiérrez, R.J. 2007. Habitat selection in a changing environment: the relationship between habitat alteration and spotted owl territory occupancy and breeding dispersal. The Condor. 109: 566–576.

Sheriff, M.J.; Dantzer, B.; Delehanty, B.; Palme, R.; Boonstra, R. 2011. Measuring stress in wildlife: techniques for quantifying glucocorticoids. Oecologia. 166(4): 869–887.

Singleton, P.H. 2013. Barred owls and northern spotted owls in the eastern Cascade Range, Washington. Seattle, WA: University of Washington. 214 p. Ph.D. dissertation.

Singleton, P.H. 2015. Forest structure within barred owl (*Strix varia*) home ranges in the eastern Cascade Range, Washington. Journal of Raptor Research. 49(2): 129–140.

Singleton, P.H.; Lehmkuhl, J.F.; Gaines, W.L.; Graham, S.A. 2010. Barred owl space use and habitat selection in the eastern Cascades, Washington. Journal of Wildlife Management. 74(2): 285–294. doi:10.2193/2008-548.

Sollmann, R.; White, A.M.; Tarbill, G.L.; Manley, P.N.; Knapp, E.E. 2016. Landscape heterogeneity compensates for fuel reduction treatment effects on northern flying squirrel populations. Forest Ecology and Management. 373: 100–107. doi:10.1016/j.foreco.2016.04.041.

Sovern, S.G.; Forsman, E.D.; Dugger, K.M.; Taylor, M. 2015. Roosting habitat use and selection by northern spotted owls during natal dispersal. Journal of Wildlife Management. 79(2): 254–262. doi:10.1002/jwmg.834.

Sovern, S.G.; Forsman, E.D.; Olson, G.S.; Biswell, B.L.; Taylor, M.; Anthony, R.G. 2014. Barred owls and landscape attributes influence territory occupancy of northern spotted owls. Journal of Wildlife Management. 78(8): 1436–1443.

Sovern, S.G.; Taylor, M.; Forsman, E.D. 2011. Nest reuse by northern spotted owls on the east slope of the Cascade Range, Washington. Northwestern Naturalist. 92(2): 101–106. doi:10.1898/10-01.1.

Spies, T.A.; Miller, J.D.; Buchanan, J.B.; Lehmkuhl, J.F.; Franklin, J.F.; Healey, S.P.; Hessburg, P.F.; Safford, H.D.; Cohen, W.B.; Kennedy, R.S.; Knapp, E.E.; Agee, J.K.; Moeur, M. 2010. Underestimating risks to the northern spotted owl in fire-prone forests: response to Hanson et al. Conservation Biology. 24(1): 330–333; discussion 334–337. doi:10.1111/j.1523-1739.2009.01414.x.

Spies, T.A.; White, E.; Ager, A.; Kline, J.D.; Bolte, J.P.; Platt, E.K.; Olsen, K.A.; Pabst, R.J.; Barros, A.M.G.; Bailey, J.D.; Charnley, S.; Koch, J.; Steen-Adams, M.M.; Singleton, P.H.; Sulzman, J.; Schwartz, C.; Csuti, B. 2017. Using an agent-based model to examine forest management outcomes in a fire-prone landscape in Oregon, USA. Ecology and Society. 22(1): 25. doi:https://doi.org/10.5751/ES-08841-220125.

Stephens, S.L.; Moghaddas, J.J.; Edminster, C.; Fieldler, C.E.; Haase, S.; Harrington, M.; Keeley, J.E.; Knapp, E.E.; McIver, J.D.; Metlen, K.; Skinner, C.N.; Youngblood, A. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. Forests. Ecological Applications. 19(2): 305–320.

Stine, P.; Hessburg, P.; Spies, T.; Kramer, M.; Fettig, C.J.; Hansen, A.; Lehmkuhl, J.; O'Hara, K.; Polivka, K.; Singleton, P.; Charnley, S.; Merschel, A.; White, R. 2014. The ecology and management of moist mixed-conifer forests in eastern Oregon and Washington: a synthesis of the relevant biophysical science and implications for future land management. Gen. Tech. Rep. PNW-GTR-897. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 254 p.

Stone, W.B.; Okoniewski, J.C.; Stedelin, J.R. 1999. Poisoning of wildlife with anticoagulant rodenticides in New York. Journal of Wildlife Diseases. 35(2): 187–193.

Stralberg, D.; Fehring, K.E.; Pomara, L.Y.; Nur, N.; Adams, D.B.; Hatch, D.; Geupel, G.R.; Allen, S. 2009. Modeling nest-site occurrence for the northern spotted owl at its southern range limit in central California. Landscape and Urban Planning. 90(1–2): 76–85.

Strong, R.J.; Pereira, M.G.; Shore, R.F.; Henrys, P.A.; Pottinger, T.G. 2015. Feather corticosterone content in predatory birds in relation to body condition and hepatic metal concentration. General and Comparative Endocrinology. 214: 47–55. doi:10.1016/j.ygcen.2015.03.002.

Swanson, M.E.; Franklin, J.F.; Beschta, R.L.; Crisafulli, C.M.; DellaSala, D.A.; Hutto, R.L.; Lindenmayer, D.B.; Swanson, F.J. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment. 9(2): 117–125. doi:10.1890/090157.

Swingle, J.K.; Forsman, E.D. 2009. Home range areas and activity patterns of red tree voles (*Arborimus longicaudus*) in western Oregon. Northwest Science. 83(3): 273–286.

Taylor, A.L.; Forsman, E.D. 1976. Recent range extension of the barred owl in western North America, including the first records for Oregon. Condor. 78(4): 560–561.

Thomas, J.W.; Forsman, E.D.; Lint, J.B.; Meslow, E.C.; Noon, B.B.; Verner, J. 1990. A conservation strategy for the northern spotted owl. Portland, OR: Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl. 427 p.

Thomas, J.W.; Franklin, J.F.; Gordon, J.; Johnson, K.N. 2006. The Northwest Forest Plan: origins, components, implementation experience, and suggestions for change. Conservation Biology. 20(2): 277–287.

Thompson, J.R.; Spies, T.A. 2009. Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. Forest Ecology and Management. 258(7): 1684–1694. doi:10.1016/j.foreco.2009.07.031.

Thorn, S.; Bässler, C.; Brandl, R.; Burton, P.J.; Cahall, R.; Campbell, J.L.; Castro, J.; Choi, C.-Y.; Cobb, T.; Donato, D.C.; Durska, E.; Fontaine, J.B.; Gauthier, S.; Hebert, C.; Hothorn, T.; Hutto, R.L.; Lee, E.-J.; Leverkus, A.B.; Lindenmayer, D.B.; Obrist, M.K.; Rost, J.; Seibold, S.; Seidl, R.; Thom, D.; Waldron, K.; Wermelinger, B.; Winter, M.-B.; Zmihorski, M.; Müller, J. 2017. Impacts of salvage logging on biodiversity—a meta-analysis. Journal of Applied Ecology. doi:10.1111/1365-2664.12945.

U.S. Department of Agriculture [USDA]. 2012. National Forest System land management planning. Federal Register. 77(68): 21162–21276.

U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management [USDA and USDI]. 1994. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. [Place of publication unknown]. Vol. 1–2 + Record of Decision.

U.S. Department of the Interior [USDI]. 2013. Experimental removal of barred owls to benefit threatened northern spotted owls; record of decision for final environmental impact statement. Federal Register. 78(180): 57171–57173.

U.S. Department of the Interior, Fish and Wildlife Service [USFWS]. 1990. Endangered and threatened wildlife and plants: determination of threatened status for the northern spotted owl. Federal Register. 55(123): 26114–26194.

U.S. Department of the Interior, Fish and Wildlife Service [USFWS]. 1992. Recovery plan for the northern spotted owl. Portland, OR: Pacific Region. 322 p.

U.S. Department of the Interior, Fish and Wildlife Service [USFWS]. 2008. Recovery plan for the northern spotted owl (*Strix occidentalis caurina*). Portland, OR: Pacific Region. 142 p.

U.S. Department of the Interior, Fish and Wildlife Service [USFWS]. 2011a. Endangered and threatened wildlife and plants: revised recovery plan for the northern spotted owl (*Strix occidentalis caurina*). Federal Register. 76(127): 38575–38576.

U.S. Department of the Interior, Fish and Wildlife Service [USFWS]. 2011b. Revised recovery plan for the northern spotted owl (*Strix occidentalis caurina*). Portland, OR: Pacific Region. 258 p.

U.S. Department of the Interior, Fish and Wildlife Service [USFWS]. 2012a. Endangered and threatened wildlife and plants: revised critical habitat for the northern spotted owl. Federal Register. 77(233): 71876–72068.

U.S. Department of the Interior, Fish and Wildlife Service [USFWS]. 2012b. Final environmental assessment: revision of critical habitat for the northern spotted owl. Portland, OR: Pacific Region. 329 p.

U.S. Department of the Interior, Fish and Wildlife Service [USFWS]. 2013. Experimental removal of barred owls to benefit threatened northern spotted owls: final environmental impact statement. Portland, OR: Oregon Fish and Wildlife Office. 505 p.

Valéry, L.; Fritz, H.; Lefeuvre, J.C.; Simberloff, D. 2009. Invasive species can also be native. Trends in Ecology & Evololution. 24(11): 585. doi:10.1016/j.tree.2009.07.003.

Van Lanen, N.J.; Franklin, A.B.; Huyvaert, K.P.; Reiser, R.F.; Carlson, P.C. 2011. Who hits and hoots at whom? Potential for interference competition between barred and northern spotted owls. Biological Conservation. 144(9): 2194–2201. doi:10.1016/j.biocon.2011.05.011.

Van Mantgem, P.J.; Stephenson, N.L.; Byrne, J.C.; Daniels, L.D.; Franklin, J.F.; Fulé, P.Z.; Harmon, M.E.; Larson, A.J.; Smith, J.M.; Taylor, A.H.; Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. Science. 323(5913): 521–524.

Walters, J.R.; Zabel, C.J. 1995. Northern flying squirrel densities in fir forests of northeastern California. Journal of Wildlife Management. 59(4): 858–866.

Waters, J.R.; Zabel, C.J. 1995. Northern flying squirrel densities in fir forests of northeastern California. Journal of Wildlife Management. 59(4): 858–866.

Weisel, L.E. 2015. Northern spotted owl and barred owl home range size and habitat selection in coastal northwestern California. Arcata, CA: Humboldt State University. 54 p. M.S. thesis.

Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science. 313(5789): 940–943. doi: 10.1126/science.1128834.

Wiens, J.D.; Anthony, R.G.; Forsman, E.D. 2011. Barred owl occupancy surveys within the range of the northern spotted owl. Journal of Wildlife Management. 75(3): 531–538. doi:10.1002/jwmg.82.

Wiens, J.D.; Anthony, R.G.; Forsman, E.D. 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. Wildlife Monographs. 185(1): 1–50. doi:10.1002/wmon.1009.

Wiens, J.D.; Dugger, K.M.; Lewicki, K.E.; Simon, D.C. 2017. Effects of experimental removal of barred owls on population demography of northern spotted owls in Washington and Oregon—2016 progress report. Open-File Report 2017-1040. Reston, VA: U.S. Department of the Interior, Geological Survey. 23 p. https://doi.org/10.3133/ofr20171040. (13 September 2017).

Wilson, T.M. 2010. Limiting factors for northern flying squirrels (*Glaucomys sabrinus*) in the Pacific Northwest: a spatio-temporal analysis. Cincinnati, OH: Union Institute & University. 207 p. Ph.D. dissertation.

Wilson, T.M.; Forsman, E.D. 2013. Thinning effects on spotted owl prey and other forest-dwelling small mammals. In: Anderson, P.D.; Ronnenberg, K.L., eds. Density management in the 21st century: west side story. Gen. Tech. Rep. PNW-GTR-880. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 79–90.

Yackulic, C.B.; Reid, J.; Davis, R.; Hines, J.E.; Nichols, J.D.; Forsman, E. 2012. Neighborhood and habitat effects on vital rates: expansion of the barred owl in the Oregon Coast Ranges. Ecology. 93(8): 1953–1966.

Yackulic, C.B.; Reid, J.; Nichols, J.D.; Hines, J.E.; Davis, R.; Forsman, E. 2014. The roles of competition and habitat in the dynamics of populations and species distributions. Ecology. 95(2): 265–279.

Zabel, C.J.; Mckelvey, K.; Ward, J.P. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). Canadian Journal of Zoology. 73(3): 433–439.



Marbled murrelet.
Photo by Kim Nelson, Oregon State University.

USDA
United States Department of Agriculture

Environmental Effects of Postfire Logging: An Updated Literature Review and Annotated Bibliography

Deborah G. Nemens, J. Morgan Varner, and Morris C. Johnson



Forest Service
Pacific Northwest Research Station
General Technical Report PNW-GTR-975
May 2019

In accordance with Federal civil rights law and U.S. Department of Agriculture (USDA) civil rights regulations and policies, the USDA, its Agencies, offices, and employees, and institutions participating in or administering USDA programs are prohibited from discriminating based on race, color, national origin, religion, sex, gender identity (including gender expression), sexual orientation, disability, age, marital status, family/parental status, income derived from a public assistance program, political beliefs, or reprisal or retaliation for prior civil rights activity, in any program or activity conducted or funded by USDA (not all bases apply to all programs). Remedies and complaint filing deadlines vary by program or incident.

Persons with disabilities who require alternative means of communication for program information (e.g., Braille, large print, audiotape, American Sign Language, etc.) should contact the responsible Agency or USDA's TARGET Center at (202) 720-2600 (voice and TTY) or contact USDA through the Federal Relay Service at (800) 877-8339. Additionally, program information may be made available in languages other than English.

To file a program discrimination complaint, complete the USDA Program Discrimination Complaint Form, AD-3027, found online at http://www.ascr.usda.gov/complaint_filing_cust.html and at any USDA office or write a letter addressed to USDA and provide in the letter all of the information requested in the form. To request a copy of the complaint form, call (866) 632-9992. Submit your completed form or letter to USDA by: (1) mail: U.S. Department of Agriculture, Office of the Assistant Secretary for Civil Rights, 1400 Independence Avenue, SW, Washington, D.C. 20250-9410; (2) fax: (202) 690-7442; or (3) email: program.intake@usda.gov.

USDA is an equal opportunity provider, employer, and lender.



Pesticide Precautionary Statement

This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate state or federal agencies, or both, before they can be recommended.

CAUTION: Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or other wildlife—if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

Authors

Deborah G. Nemens is a forest ecologist, University of Washington, School of Environmental and Forest Sciences, Box 352100, Seattle, WA 98195; **J. Morgan Varner** is a research biological scientist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, WA 98512; **Morris C. Johnson** is a research ecologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Pacific Wildland Fire Sciences Laboratory, 400 N 34th Street, Suite 201, Seattle, WA 98103.

Cover: King Fire, El Dorado National Forest, California. Photo by Morris Johnson.

Abstract

Nemens, Deborah G.; Varner, J. Morgan; Johnson, Morris C. 2019. Environmental effects of postfire logging: an updated literature review and annotated bibliography. Gen. Tech. Rep. PNW-GTR-975. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 35 p.

The practice of removing fire-killed trees from burned forests (or "postfire salvage logging") has sparked public controversy and scientific debate when conducted on public lands in the United States. This review synthesizes the current scientific literature on the subject, providing an update to a 2000 literature review (PNW GTR-486) and subsequent synthesis (PNW-GTR-776). Forty-three published studies are reviewed, summarizing ecological effects on wildlife, vegetation, fuels, soils, and other environmental variables. Several key themes emerge from the review and specific research topics for future study are suggested. An annotated bibliography is provided at the conclusion of the document.

Keywords: Ecological effects, fire, fuel dynamics, wildlife, salvage, soil erosion, wildfire.

Contents

1 **Introduction**
3 **Ecological Effects of Postfire Logging**
3 Wildlife
4 Birds
4 Mammals
5 Invertebrates
5 **Vegetation**
5 Tree Regeneration
6 Understory
7 Fuels
9 Soils
10 Abiotic Variables
10 **Conclusions**
10 Limitations
12 Reducing Negative Effects of Postfire Logging
14 Directions for Future Research
15 **Acknowledgments**
15 **Appendix: Literature Cited and Annotations**

Introduction

The harvesting of merchantable timber from forests and woodlands following stand-replacing wildfires (commonly referred to as "salvage logging") on federal lands has been the subject of considerable controversy, both in the public sphere and the scientific literature. The Society of American Foresters (Helms 1998) defines salvage logging as "the removal of dead trees or trees damaged or dying because of injurious agents other than competition, to recover economic value that would otherwise be lost." As such, this practice is often driven by economic concerns, as land managers are motivated to recover the value of fire-killed trees and to support local timber economies in rural areas (Gorton and Kays 1996, McIver and Starr 2000). Promoting future forest development and reducing future fire hazard are additional benefits cited from the harvest of fire-killed trees from burned forests. The use of these latter arguments by managers and policymakers has prompted debate in the scientific literature regarding the validity of these claims. In the past several decades, researchers attempting to assess the ecological effects of postfire logging have published dozens of studies evaluating effects of salvage logging on myriad aspects of forest ecosystems. These studies have been synthesized in several documents in an attempt to provide a cohesive source of information useful to managers and decisionmakers. Relevant research on this topic continues, such that it is occasionally necessary to include the most recent studies in new literature reviews. The purpose of this report is to provide an annotated bibliography of the relevant peer-reviewed literature published in the time since a previous review of the scientific literature on postfire logging (McIver and Starr 2000). As such, it is not intended to be a meta-analysis, or a synthetic review of the state of knowledge on the topic of salvage logging.

The review produced by McIver and Starr (2000) was written in response to a debate that was taking place both in the public arena and the scientific literature over the environmental costs and ecological justifications associated with postfire logging on public forest lands. This debate has a long history. Reacting to pressure from constituents in timber-dependent communities, U.S. Senator Slade Gorton (R-Wash.) attached a salvage rider to the Fiscal Year 1995 Rescissions Act.[1] The stated objective of the rider was to promote forest health and restore timber jobs in rural communities of the Pacific Northwest (Gorton and Kays 1996). The rider led to an open debate among scientists and managers in the region (Beschta et

[1] Oklahoma City Disaster Assistance and Rescissions Act: Emergency Supplemental Appropriations for Additional Disaster Assistance, for Anti-Terrorism Initiatives, for Assistance in the Recovery from the Tragedy that Occurred at Oklahoma City, and Rescissions Act, 1995. Pub. L. No. 104-19.

al. 1995, Everett 1995, McIver and Starr 2000). Beschta et al. (1995) posited that salvage logging had strong negative ecological consequences, arguing that the only value of such action is economic, and they offered a set of recommendations for management of postfire forests. Everett (1995) refuted the conclusions of Beschta et al., arguing for more active management of postfire landscapes, including timber harvest.

The 2000 literature review (McIver and Starr 2000) was an attempt to synthesize the current state of scientific understanding in the field, evaluate knowledge gaps, and provide managers with the basis from which to make informed decisions when applying postfire management practices. Using what they described as "scanty" information, they summarized the findings of 21 studies into several categories and predicted "likely" ecological effects based on the results of these studies. One of the better studied topics, the impacts of salvage logging on wildlife, was well documented, with variable effects on different clades depending on their habitat requirements. In particular, largely negative outcomes were documented for cavity-nesting birds. Additionally, the reviewers found that substantial changes in wildlife habitat, resulting from the removal of structural and functional elements in the form of large-diameter snags and their associated insect communities, were likely following harvest. A predicted result of postfire logging was that the removal of these attractants for forest insect pests may reduce the likelihood of infestation of nearby healthy stands. Although longer term studies were lacking at the time, there was evidence that impacts of logging-related disturbance to understory communities included declines in species richness and diversity, an increase in nonnative plant species cover, and a reduction in vegetative biomass. Negative effects on tree regeneration were predicted if salvage operations are not designed to reduce seedling mortality. The reviewers did not find studies that documented increased soil erosion following postfire logging, but posited that road-building and the use of skid trails might increase its incidence in already compromised burned watersheds. Conversely, one study included in the review found that logging slash remaining from salvage activities might reduce postfire erosion. Little research had been done on the impacts of salvage logging on postfire fuel dynamics, a deficit highlighted in the review. In their conclusions, the authors recommended further study of this and several other subjects. Many of these topics continue to be explored in current research, and more broadly applicable knowledge has been made available in the years since the 2000 review was completed.

In many ways, the 1995 debate continues in the present moment. Although more scientific study has been conducted on this topic (as detailed in this review),

both supporters and detractors of the practice can point to evidence in the literature to support their arguments. Since 2000, many of the scientific questions surrounding the practice of postfire logging have been explored at greater depth and in more detail, but these issues are by no means resolved.

Interpretations of the ecological effects of salvage logging are mutable, as observations depend on the scope, spatial and temporal scales, and class of metric studied. Some effects are initially quite dramatic, but dissipate over time. Other effects may vary based on the attributes of the studied ecosystem. Owing to the structural and functional impacts of severe wildfire on forested ecosystems (e.g., widespread tree mortality, depletion of soil organic matter, consumption of woody fuels), effects of postfire logging can be difficult to distinguish from the effects of the fire itself. All these concerns complicate attempts to synthesize the current state of knowledge in this field. This review seeks to present the last 18 years of published data on this topic in a way that is relevant to managers and scientists while acknowledging the limitations in interpreting the research.

In this report, we reviewed 43 scientific studies published since 2000, and confine our geographic scope to Western United States and Canada, in keeping with the focus of the 2000 review. As with the standards set by McIver and Starr (2000), we adhere to the same definitions to classify published scientific work. If treatments were not imposed by the researchers, the study is classified as **observational**, as opposed to a **replicated** study.

Only peer-reviewed studies reviewed for this paper are annotated in the bibliography; other citations mentioned are presented without additional text.

Ecological Effects of Postfire Logging

Wildlife

When the ecological effects of postfire timber harvest are examined, negative impacts to wildlife are frequently cited in arguments against this type of postfire management. Upon thorough review of the published literature on the subject, it is clear that negative consequences of postfire harvest exist for many species. However, it would not be accurate to apply these results universally to all wildlife species. The response of an individual species to the removal of fire-killed trees is often determined by its unique qualities and the habitat features on which it depends. Although many species experience a loss of habitat when dead trees are removed following a stand-replacing fire, others benefit from the resulting alteration of stand structure, reduction in stand density, increases in understory plant diversity, and changes to surface fuel loads.

Birds

The response of avian species to the removal of fire-killed trees is highly dependent on the habitat requirements of the studied species. In their review, McIver and Starr (2000) noted that birds that depend on snags for forage and nesting structures are the most affected by the removal of dead trees following stand-replacing wildfire, while those that favor open habitats appear to benefit from logging. Cavity-nesting birds, such as the black-backed woodpecker (*Picoides arcticus*), are the archetypal fire-dependent wildlife guild, and their response to postfire harvest has been the focus of much research since the 2000 review. Owing to their dependence on standing dead trees, cavity nesters are often strongly associated with severely burned forests. These species have been found to be more abundant following fire in unmanaged stands than in harvested stands (Cahall and Hayes 2009, Hutto and Gallo 2006, Kronland and Restani 2012, Morissette et al. 2002, Rost et al. 2013, Saab et al. 2007). One contradictory study (notably with low replication) found higher abundance and richness of cavity-nesting birds following salvage (Haggard and Gaines 2001). Other birds species, such as the federally threatened northern spotted owl (*Strix occidentalis caurina*), also appear to be negatively affected by salvage logging (Clark et al. 2013), but this effect is blurred by the impacts on owl site occupancy of high-severity fire. Another study of the related California spotted owl (*S. o. occidentalis*) did not find significant declines in owl populations resulting from either fire or postfire logging, but did emphasize the small yet potentially meaningful compounded effect of fire and logging, which marginally increased the probability of site extinction (Lee et al. 2013). Bird species that use more open habitats generally have positive or neutral responses to salvage logging (Cahall and Hayes 2009, Morissette et al. 2002, Rost et al. 2013, Saab at al. 2007). As studies of this topic have largely focused on the impact of postfire snag removal on birds species that are dependent on them, information is lacking on the influence of salvage logging on the avian community as a whole, as well as on the longer term effects of these postfire management activities.

Mammals

McIver and Starr (2000) observed that, as for bird species, mammal populations tend to shift toward those that prefer more open habitat in response to salvage logging. Few studies have examined the impacts of postfire logging on mammals since 2000, and findings have not been conclusive. In one study, populations of deer mice increased in density following salvage logging, likely owing to the temporary increase in downed woody debris that was the result of harvest (Kronland and Restani 2012). Another study that compared abundance of small terrestrial mammals

across three levels of harvest intensity (unlogged, moderate, and high) found no significant difference among treatments (Brown 2009). In this same study, bat densities were observed to be higher in harvested stands; however, this may have been a consequence of the availability of open habitat for feeding, and not an indication of increased population size resulting from logging. In a study of salvage logging's impacts on trophic relationships, Hebblewhite et al. (2009) found that elk avoided areas logged after fire, largely because of increased predation risk from wolves in these open sites. The authors pointed to the increased road construction associated with postfire harvest as major factors in this disruption of ecosystem dynamics, and recommended that it be minimized. Published studies on this topic are scarce, and as a consequence, little specific information is available on the effects of postfire tree harvest on mammal populations.

Invertebrates

Insects are often abundant following stand-replacing wildfires, and are a critical element of postfire landscapes, providing forage for insectivorous birds, advancing the decay of fire-killed trees, and influencing soil nutrient cycling. Postfire timber harvest has been found to be deleterious to populations of wood-boring beetles, negatively affecting both abundance and species richness (Cobb et al. 2010, Thorn et al. 2018). Cobb et al. (2010) noted that this decrease in populations of saproxylic insects can have cascading impacts on soil nutrients. In contrast, species richness, abundance, and biomass of benthic macroinvertebrates increased in salvage-logged watersheds, though only incrementally, above unharvested burned sites when compared with unburned controls (Silins et al. 2014). Studies of invertebrate response to salvage logging are few and narrow in focus; as such, this field would benefit from further investigation, particularly including a greater diversity of species and over greater time scales following harvests.

Vegetation

Tree Regeneration

Post-wildfire tree regeneration is of great concern to land managers, resulting in the common practice of postfire planting of timber species following stand-replacing fire. McIver and Starr (2000) noted that in the majority of the studies they reviewed, salvage logging operations occurred prior to the establishment of seedlings, avoiding the high mortality (75 percent in one study) that can be caused by logging equipment. In the intervening years, the effect of harvest of fire-killed trees on natural regeneration has been examined by several authors, but results are somewhat equivocal between studies. Two studies found that natural regeneration

of tree species was negatively affected by salvage logging operations (Donato et al. 2006, Keyser et al. 2009), which caused injury to establishing seedlings. Another study found no significant effect of postfire harvest (Peterson and Dodson 2016). Interestingly, these results do not appear to depend on the interval between wildfire and harvest, as at least one of each of the former and latter groups of studies was logged at a point where seedling establishment could be expected to have occurred (2 to 3 years postfire). It is important to note that the former group of studies were conducted within 5 years of wildfire occurrence, and the latter studies examined the longer term (15 and 10 years, respectively) impacts of salvage logging on regeneration. Additionally, although natural regeneration is a concern in many postfire environments, salvage logging prescriptions typically call for post-harvest tree planting. Although species selected for replanting may not accurately reflect local assemblages, the practice reduces the reliance on natural regeneration for forest restoration in salvage-logged stands, rendering any negative impacts to preexisting seedlings less consequential.

Understory

Postfire logging effects on understory vegetation are dependent on temporal scale and site-specific factors. Numerous studies have documented a convergence in understory development between logged and unlogged stands over time (Campbell et al. 2016, Keyser et al. 2009, McGinnis et al. 2010, Peterson and Dodson 2016). In one study, repeated measurements of species richness and community composition similarly demonstrated an initial effect of logging that dissipated over several decades and was overtaken by the influence of canopy structure in the long term (Kurulok and Macdonald 2007). This was not the conclusion of another long-term study, which documented significant changes to plant communities in salvaged sites, particularly along forest edges (Hanson and Stuart 2005). Several researchers have found that other factors, such as burn severity and postfire planting, had greater influence on understory vegetative development than salvage logging (Macdonald 2007, Morgan et al. 2015). Kurulok and Macdonald (2007) found greater short-term species richness and higher shrub abundance in salvaged stands, results that are in stark contrast to Knapp and Richie (2016), who found that shrub cover decreased with salvage intensity. These discrepancies are likely due to differences in the regenerative strategies of the prefire vegetation of the studied sites, as well as the timing of salvage operations, as described by Peterson et al. (2009). Most of these studies found no increase in nonnative plant species abundance resulting from salvage logging (Keyser et al. 2009, Knapp and Ritchie 2016, McGinnis et al. 2010, Peterson and Dodson 2016), though one did find a short-term increase that

dissipated over time (Kurulok and Macdonald 2007). Although most research on the topic has concluded that understory vegetation is resilient to postfire logging over intermediate time periods, this subject would benefit from longer term study, as well as the variable effects on plants with different fire-adaptive strategies (e.g., sprouting vs. reseeding species).

Fuels

Owing to the regular use of the "reburn hypothesis" (which posits that removing dead trees from a burned stand will reduce future wildfire risk and severity) as an ecological justification by managers for removing fire-killed timber, postfire fuel dynamics are an important element of study in the realm of salvage logging research. McIver and Starr (2000) emphasized the paucity of evidence for these claims, and since that time, substantial research has been conducted on this subject. Results of recent studies suggest divergent trajectories for coarse and fine fuels in logged and unmanaged postfire stands, as well as significant changes in fuel conditions through time. The dynamics of fine fuel (fuels < 7.6 cm in diameter; 1-, 10-, and 100-hr timelag fuels) loading are critical to understand in this context, as they are the primary driver of fire spread in wildland fires (Rothermel 1972). However, coarse fuels (fuels > 7.6 cm; 1,000-hr timelag fuels) can contribute to fire behavior as well, via increased local intensity, crown ignition potential to residual surviving trees, and as a source of long-range spotting (Brown et al. 2003). Coarse fuels can also substantially increase burn severity by means of long-term smoldering and local soil heating, which can exceed lethal temperatures for long periods, affecting nutrient cycling (Brown et al. 2003, McIver and Ottmar 2018, Reinhardt et al. 1997).

Many researchers have found that, in the short term, postfire logging increases fine fuel loading when compared with unmanaged stands (Donato et al. 2006, 2013; McGinnis et al. 2010; McIver and Ottmar 2007; Peterson et al. 2015). However, longer term measurements often reveal that this effect is short lived, leading to the convergence of logged and unlogged stands within a decade (Campbell et al. 2016, McGinnis et al. 2010, McIver and Ottmar 2018, Peterson et al. 2015). The temporal variation of fine fuel loads in severely burned sites is particularly compelling in studies that remeasured prior field sites, as in the latter three studies. Note that although some authors posit that increased fine fuel loading will increase fire risk, at least in the short term (Donato et al. 2006, 2013; Thompson et al. 2007), others contend that fire hazard is unaffected by these additional fuels, largely because of the characteristics of postfire fuelbeds (Newton et al. 2006, Ritchie et al. 2013). Empirical evidence that could substantiate either position is lacking on this subject, as opportunities to observe this phenomenon are limited.

Dynamics of coarse surface fuel loading, which are dependent on snag retention in postfire environments, often exhibit the opposite trend. As would be expected, logged stands contain fewer standing snags following harvest than untreated stands. The transition of these aerial fuels to surface fuels is highly dependent on the decomposition rates (which vary by species and local climate) and diameter of remaining dead trees (Campbell et al. 2016, Ritchie and Knapp 2014). A number of studies have found high accumulation of surface coarse woody fuels over time in unharvested stands when compared with logged sites (Dunn and Bailey 2015, Keyser et al. 2009, McIver and Ottmar 2018, Peterson et al. 2015, Ritchie and Knapp 2014, Ritchie et al. 2013) as snags begin to fall. Conversely, a single study (McGinnis et al. 2010) found that large woody debris increased following postfire logging in the Sierra Nevada, although the authors noted that this effect was not significant in older (19 to 21 years since harvest) study sites. Ritchie et al. (2013) observed that, regardless of treatment, the majority of standing dead material remaining following harvest was on the ground 10 years following fire and salvage logging in the Lassen National Forest in California, and suggested that the habitat provided for cavity-nesting wildlife was therefore transient.

Owing to the very small proportion of the forested landscape that has undergone postfire salvage harvesting in the Western United States and Canada, reburn of these areas is unlikely to occur within the timespan covered by this review or its predecessors. Thus, it has been difficult for researchers to design a study that tests the reburn hypothesis in the field. Instead, many studies of postfire salvage impacts on forest fuels use fire behavior and fuels consumption models to simulate a reburn event. Several of these studies, which often pair empirical fuel measurements with modeled fire behavior, have found that models do not project elevated fire behavior or increased fire effects in unlogged stands when compared to salvaged sites (McGinnis et al. 2010, McIver and Ottmar 2007). Researchers in this field note, however, that current fire behavior and consumption models do not accurately represent the influence of large logs and other heavy fuels, which could contribute to additional fire severity via longer residence times and subsequent soil heating (McIver and Ottmar 2018, Peterson et al. 2015). Others cite high postfire shrub cover as having a substantial effect on future fire behavior, potentially overwhelming any influence of post-burn tree harvest (Campbell et al. 2016, Donato et al. 2013, McGinnis et al. 2010). In a study of reburn severity that did not evaluate the impact of postfire salvage logging, Coppoletta et al. (2016) found that postfire shrub cover and snag basal area following an initial fire contributed significantly to fire severity in reburns, but the effect of these variables (particularly snag basal area) was dwarfed by weather conditions during reburn events.

The reburn hypothesis did not receive substantiation from the sole study we found that quantified the impact of postfire logging on reburn severity (Thompson et al. 2007). Although the authors were unable to separate the effects of postfire

planting from salvage logging, they found that fire severity increased in harvested areas when compared with unmanaged sites, potentially refuting the validity of the reburn hypothesis. However, it is important to note that determination of burn severity was based solely on remote sensing data (delta Normalized Burn Ratio, dNBR) and was not verified in the field. This method of measuring burn severity raises concerns about the accuracy of the data (Miller and Thode 2007) and adds an additional level of uncertainty to the study's results. Although it is difficult to arrange the necessary treatments in the field, the limitations of current models make it imperative for researchers to continue to pursue opportunities to examine the relationship of postfire logging and reburn severity when they occur on the landscape.

Soils

An important area of study has been the contribution of postfire logging to soils and watersheds, particularly its effect on erosion and sedimentation in streams. Noting the scarcity of published research on this topic, McIver and Starr (2000) posited that road building and subsequent use would have the greatest influence on post-salvage logging erosion. Since then, several studies have found that salvage logging operations can be a major contributor to soil disturbance and compaction (McIver and McNeil 2006; Slesak et al. 2015; Wagenbrenner et al. 2015, 2016), and the majority of these studies document increased erosion in burned watersheds that were subsequently logged (Slesak et al. 2015; Wagenbrenner et al. 2015, 2016). In contrast to these studies, McIver and McNeil (2006) noted that despite increased soil disturbance, erosion from harvested sites was not significantly greater than untreated stands, and that roads were the greatest contributor to movement of soil. Additionally, these researchers found that some of the impact to soils caused by machinery during postfire harvest can be mitigated by adjusting the employed techniques and the timing of operations (McIver and McNeil 2006). Note that the influence of postfire logging on erosion, when present, does appear to be short lived, as the observed effect can diminish over time (Slesak et al. 2015, Wagenbrenner et al. 2016).

Other effects on soils from postfire logging, such as effects on soil nutrients, soil microbial and fungal communities, and cation exchange capacity, can be difficult to distinguish from the often greater influence of the initial wildfire. However, some studies have noted lasting effects of salvage logging on certain soil parameters, most notably reduction in soil organic carbon (Jennings et al. 2012, Kishchuk et al. 2014). Another study documented changes in soil biogeochemistry, but only in certain horizons (Poirier et al. 2014). Bacterial and fungal communities in soils appeared to be resilient to the disturbance caused by postfire logging (Jennings et al. 2012). Similarly, the influence of postfire harvest on water quality and stream biota can be difficult to distinguish from the signal of wildfire; however, certain parameters show detectable differences (Emelko et al. 2011, Silins et al. 2014).

Abiotic Variables

Effects of postfire logging on abiotic variables are just beginning to receive attention. Recent studies have examined microclimatic changes following salvage logging, as well as the impact of the practice on carbon sequestration and storage. One study observed that surface air temperatures did not increase in logged stands, but noted other small microclimatic changes (such as earlier daytime heating and lower nighttime minimum temperatures) attributed to postfire harvest (Fontaine et al. 2010). Researchers documented a marked decrease in the amount of carbon stored in salvaged sites, particularly those that received intensive management (Powers et al. 2013). The authors of this study emphasized the competing interests of managers, who are likely to include carbon sequestration in an already complex analysis of how best to manage forests. Although more research has been conducted in the period since 2000, results are not conclusive, and much remains to be learned about salvage logging impacts on soils and the abiotic environment, both within salvaged sites and at the landscape level.

Conclusions

Limitations

In their 2000 review, McIver and Starr lamented the fact that little research had been conducted on the effects of postfire logging. Since that time, more than 40 additional studies have been conducted on this topic, but some important scientific questions remain unresolved. One topic of particular interest to researchers, managers, and decisionmakers is the scientific validation or rejection of the reburn hypothesis. Although most studies have documented greater long-term fuel loading in unmanaged stands when compared with logged ones, the majority of studies that attempt to evaluate the reburn hypothesis use simulation models to predict fire behavior and effects, as few opportunities for empirical study have presented themselves. The only empirical study of which we are aware (Thompson et al. 2007) refuted the premise: salvage-logged stands burned at higher severities than comparable unlogged stands, though the authors noted that the high live fuel loading resulting from postfire planting in logged stands was the most likely driver of fire severity, and were not able to separate this variable from the effect of logging alone. Research based on field experiments and modeled analyses using physics-based fire behavior models (such as the Wildland-Urban Fire Dynamics Simulator) presents a potential avenue for improved evaluation of the reburn hypothesis in the future.

Shortcomings with experimental study design mentioned by McIver and Starr (2000) have not been fully addressed in the research conducted since the publication of that review. Of particular concern to those authors was the lack of replicated experiments. In the study of postfire logging effects, researchers are rarely allowed

the opportunity to determine the locations of treatments or their distribution on the landscape, with the result that the majority of studies are observational in nature. This is largely a result of the logistics involved in planning these projects: managers tend to locate harvest units based on proximity to existing road networks, distance from sensitive areas, and operable slope location. As a result, replication is often limited, sites are not randomly distributed, and spatial autocorrelation and pseudo-replication are concerns in the analysis of results. Beyond these, the use of unsalvaged sites as proxies for prefire conditions brings up issues with space-for-time or chronosequence approaches that have been highlighted in other ecological research (Johnson and Miyanishi 2008). The implementation of long-term experiments employing repeated measures over time are necessary to avoid these pitfalls and produce widely applicable, meaningful conclusions.

We found that the geographic diversity of the region is not well represented in the literature: 37 percent of the studies reviewed here were conducted in one U.S. state (Oregon), and 23 percent of published studies focused on only two wildfires (Biscuit Fire and Summit Fire, both in Oregon) (fig. 1). This lack of replication to relevant ecosystems may lead to conclusions derived from the study of one area being broadly applied to other regions where ecosystems are quite distinct. Researchers

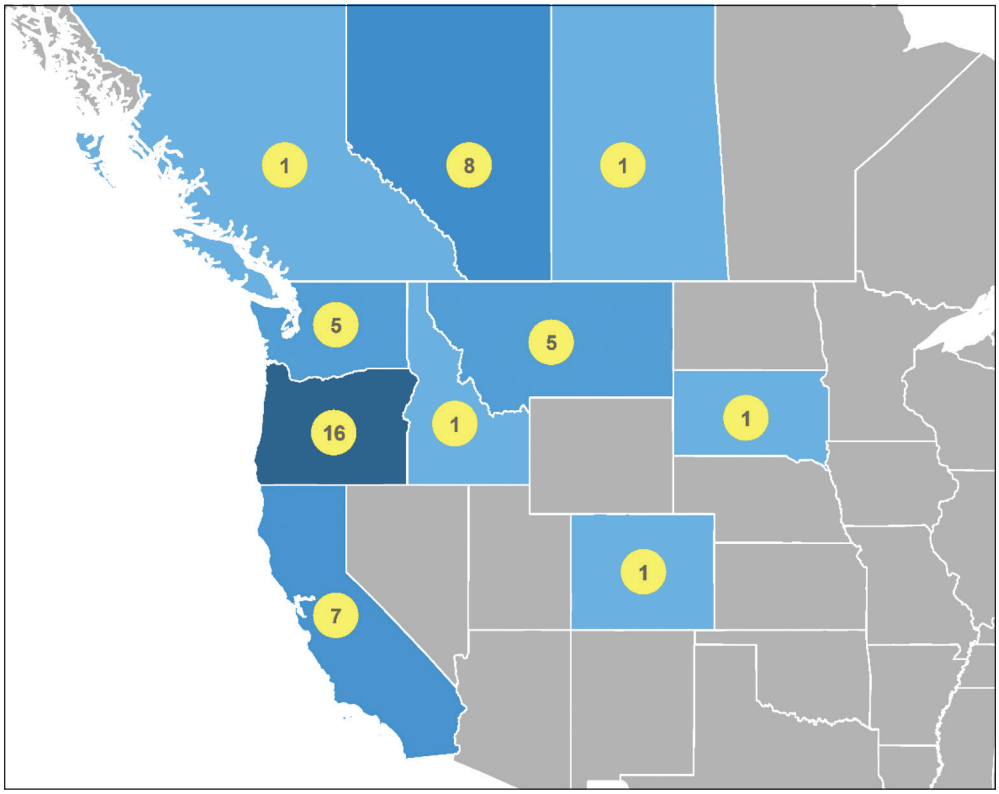


Figure 1—Salvage research locations by U.S. state and Canadian province in focus region. Most field sites featured in published studies between 2000 and 2018 were located in Oregon, particularly the Biscuit and Summit Fires.

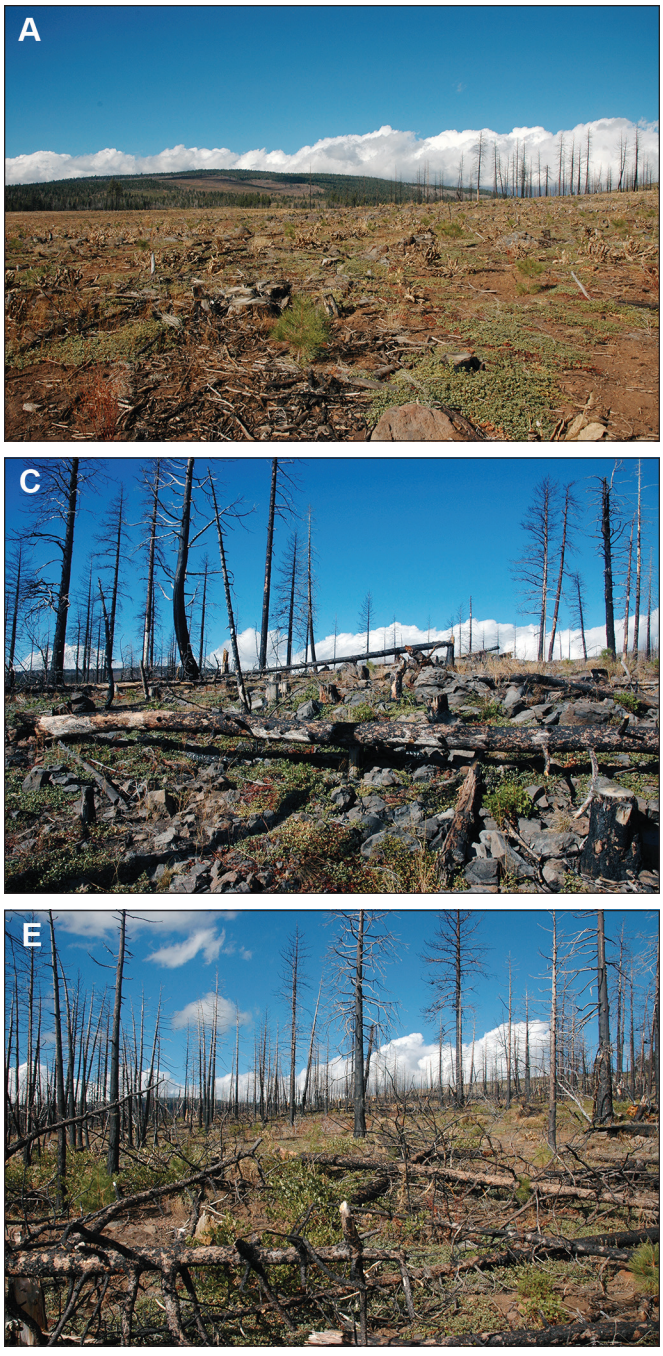
are limited by access to sites, communication with local managers, funding, and other logistical concerns when conducting field research, and these limitations are reflected in the number of fires that have received attention from scientists.

Another concern voiced by McIver and Starr (2000) is the frequent lack of unburned controls: this continues to be a common problem in salvage-logging research. Of the 43 studies reviewed here, only 14 (about a third) included unburned controls in their study design. This design shortcoming creates analytical problems for many studies. Many researchers were unable to tease out the confounding variables that affected their results. Often, the signal of a severe wildfire in the data overwhelmed the effect of postfire logging. In some cases, comparison with data from unburned controls may have aided in the clarification of these effects.

Typical of wildfire research, many of the studies reviewed here suffer from minimal knowledge of prefire conditions. Thus, confounding factors such as prefire vegetative characteristics are impossible to control in data analysis. Compounding these issues, many studies are short term in nature, which can lead to findings that are not representative of relevant ecological outcomes that occur over longer time scales. Researchers have begun to address these concerns by revisiting prior study sites, yielding valuable data on long-term trends. This practice should be continued and expanded to other previous research, as the information produced from long-term studies is critical to understanding the future trajectories of landscapes under differing management regimes and will be far more relevant to managers and policymakers.

Reducing Negative Effects of Postfire Logging

Although salvage logging is injurious to certain species guilds and habitat elements, steps can be taken to minimize these negative impacts in some situations (figs. 2 and 3). As suggested by McIver (2003), alterations to harvest methods (particularly type of equipment used and timing of operations) can substantially reduce soil disturbance and subsequent mortality of understory vegetation. Additionally, changing harvest prescriptions such that more of the large snags preferred by cavity-nesting birds remain on site may mitigate some of the effects of logging on these species, as well as provide for longevity of snag habitat (Hutto 2006, McIver and Ottmar 2007). These methods provide managers with avenues for reducing the negative effects of postfire logging, while maintaining a source of revenue for local timber economies affected by severe wildfire.



M. Ritchie, U.S. Forest Service Pacific Southwest Research Station

Figure 2—Photos of variable-retention salvage treatments from a multiyear study at the Blacks Mountain Experimental Forest, California, in fall 2006. Images were taken 4 years after the Cone Fire and 3 years after salvage operations: (A) 0 percent retention; (B) 25 percent; (C) 50 percent; (D) 75 percent; and (E) 100 percent.

D. Nemens, University of Washington



Figure 3—Fifteen years after the Storrie Fire, and 3 years after the Chips Fire, Lassen National Forest, California. The foreground shows an area where no action was taken, while postfire logging (on private timber holdings) is visible in the distance.

Directions for Future Research

Investigators in this field should consider the limitations of the current body of research and attempt to address these concerns in their work. Specifically, future research efforts should attempt to incorporate these elements:

1. Replicated study design using appropriate controls
2. Long-term experiments with repeated measurements
3. Expanded geographic diversity into understudied regions and ecosystems
4. Use of improved models, or seizing opportunities to directly measure fire behavior and severity
5. Integrated studies in which many variables are measured, in order to capture a more complete picture of impacts on the entire ecosystem.

Acknowledgments

Funding for this work was provided by the National Fire Plan. E. Knapp, D.W. Peterson, and J. Kane provided thoughtful comments and suggestions that improved the final version of this review.

Appendix: Literature Cited and Annotations

Note: Citations without annotation are for text reference only and were not reviewed in this document.

Beschta, R.L.; Frissell, C.A.; Gresswell, R.; Hauer, R.; Karr, J.R.; Minshall, G.W.; Perry, D.A.; Rhodes, J.J. 1995. Wildfire and salvage logging: recommendations for ecologically sound post-fire salvage management and other post-fire treatments on federal lands in the west. Corvallis, OR: Oregon State University. 16 p.

Brown, J.K.; Reinhardt, E.D.; Kramer, K.A. 2003. Coarse woody debris: managing benefits and fire hazard in the recovering forest. Gen. Tech. Rep. RMRS-GTR-105. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 16 p.

Brown, M. 2009. Post-fire salvage logging in central Oregon: short-term response in bats, birds and small mammals. Fire Science Brief 76. Boise, ID: Joint Fire Science Program. https://www.firescience.gov/projects/briefs/04-2-1-95_FSBrief76.pdf. (12 December 2018).

Location: Davis Lake Fire, central Oregon.
Type of study: Observational.
Variables: Breeding bird population density, bat activity, and small mammal abundance.
Treatments: Burned/unlogged, burned/moderate salvage, burned/intensive salvage.
Results:

- Reducing the intensity of harvest did not reduce impacts to species that responded negatively to postfire logging.
- Small mammal populations did not demonstrate a response to harvest, or varied with harvest intensity.
- Negative effects of salvage logging on some bird species may be mitigated by maintaining islands of unlogged snags within larger harvest units.
- Bat activity was higher in open areas created by intensive salvage harvest.

Cahall, R.E.; Hayes, J.P. 2009. Influences of postfire salvage logging on forest birds in the eastern Cascades, Oregon, USA. Forest Ecology and Management. 257: 1119–1128.

Location: Davis Lake Fire, central Oregon.
Type of study: Observational.
Variables: Density and abundance of bird populations.
Treatments: Burned/unlogged, burned/moderate salvage, burned/intensive salvage.
Results:

- Reducing the intensity of harvest did not reduce impacts to species that responded negatively to postfire logging.
- Negative effects of salvage logging on some bird species may be mitigated by maintaining islands of unlogged snags within larger harvest units.

Keywords: Birds, fire, salvage logging, ponderosa pine–Douglas-fir forest.

Campbell, J.L.; Donato, D.C.; Fontaine, J.B. 2016. Effects of post-fire logging on fuel dynamics in a mixed-conifer forest, Oregon, USA: a 10-year assessment. International Journal of Wildland Fire. 25: 646–656.

Location: Biscuit Fire, southwest Oregon.
Type of study: Observational (remeasure).
Variables: Surface fuel mass, decay rates, shrub cover.
Treatments: Unburned control, burned/unlogged, burned/moderate logging, burned/heavy logging.
Results:

- Fine surface woody fuel loads were initially higher in salvaged stands, but loadings converged with unsalvaged stands within a decade.
- Snags decayed at a significant rate while standing, indicating that some surface fuels did not fall to the forest floor.
- Cover of resprouting shrubs was high 10 years following fire regardless of treatment, representing a high fire danger not mitigated by postfire harvest.

Keywords: Biomass, coarse woody debris, dead wood, decay, decomposition, fuel succession, Klamath-Siskiyou, salvage logging, snag, wildfire.

Clark, D.A.; Anthony, R.G.; Andrews, L.S. 2013. Relationship between wildfire, salvage logging, and occupancy of nesting territories by northern spotted owls. Journal of Wildlife Management. 77: 672–688.

Location: Timbered Rock, Biscuit, and Quartz Fires, southwest Oregon.
Type of study: Observational.
Variables: Site occupancy of northern spotted owls.
Treatments: Unburned, moderate burn/unlogged, high-severity burn/unlogged, high-severity burn/logged.
Results:

- Site occupancy of spotted owls showed short-term declines subsequent to wildfire, and postfire disturbance may have contributed to these declines.

Keywords: Colonization, extinction, northern spotted owl, occupancy, salvage logging, site occupancy, southwest Oregon, *Strix occidentalis caurina*, wildfire.

Cobb, T.P.; Hannam, K.D.; Kishchuk, B.E.; Langor, D.W.; Quideau, S.A.; Spence, J.R. 2010. Wood-feeding beetles and soil nutrient cycling in burned forests: implications of post-fire salvage logging. Agricultural and Forest Entomology. 12: 9–18.

Location: Chisholm Fire, Alberta, Canada.
Type of study: Observational.
Variables: Abundance of saproxylic beetles.
Treatments: Unburned, burned, unburned/logged, burned/logged.
Results:

- Beetles were not present in burned stands subjected to salvage logging.

Keywords: Beetle frass, boreal forest, coarse woody debris, IPDM, *Monochamus s. scutellatus* (Say), nitrogen cycling, saproxylic beetles, soil microbial activity, wildfire.

Coppoletta, M.; Merriam, K.E.; Collins, B.M. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecological Applications. 26: 686–699.

Donato, D.; Fontaine, J.B.; Campbell, J.; Robinson, W.; Kauffman, J.; Law, B.E. 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science. 311(5759): 352.

Location: Biscuit Fire, southwest Oregon.
Type of study: Observational.
Variables: Surface fuel loads, tree regeneration density.
Treatments: Unburned, burned/unlogged, burned/logged.
Results:

- Salvage logging resulted in higher fine dead surface fuel loads than unlogged stands.
- Postfire tree regeneration was reduced by 71 percent in logged sites.
- Short-term fire risk was increased following salvage operations.

Donato, D.C.; Fontaine, J.B.; Kauffman, J.B.; Robinson, W.D.; Law, B.E. 2013. Fuel mass and forest structure following stand-replacement fire and post-fire logging in a mixed-evergreen forest. International Journal of Wildland Fire. 22: 652–666.

Location: Biscuit Fire, southwest Oregon.
Type of study: Observational.
Variables: Surface and aerial fuel mass, shrub cover.
Treatments: Burned/unlogged, burned/moderate, and burned/intensity harvest.
Results:

- Standing dead biomass was significantly reduced by salvage logging.
- Activity fuels remaining on site were greater following high-intensity (28 percent of felled material) than moderate intensity-harvest (14 percent of felled material).
- Cover of downed wood was three to five times greater in harvested stands.
- High-intensity salvage logging resulted in surface fuels that may require additional treatment to reduce fire risk.

Keywords: Biomass, Biscuit Fire, coarse woody debris, dead wood, fuel succession, Klamath–Siskiyou, legacy, logging intensity, postfire management, salvage logging, snag.

Dunn, C.J.; Bailey, J.D. 2015. Modeling the direct effects of salvage logging on long-term temporal fuel dynamics in dry-mixed conifer forests. Forest Ecology and Management. 341: 93–109.

Location: Multiple fires, central Oregon Cascade Range.
Type of study: Modelling.
Variables: Surface fuel loads, understory woody biomass.
Treatments: Burned/unlogged, burned/logged.
Results:

- In salvage harvest scenarios, fine woody fuel loads were greatest 17 to 18 years after high-severity fire.
- Postfire logging resulted in an increase in fine fuel loadings of 160 to 237 percent that persisted for 22 years after fire.
- 1,000-hr fuels loadings peaked 24 to 31 years following fire in untreated stands.
- 1,000-hr fuels were significantly reduced 7 years following postfire harvest.

Keywords: Fuel succession, reburn, salvage logging, hazardous fuels, snag dynamics, decomposition.

Emelko, M.B.; Silins, U.; Bladon, K.D.; Stone, M. 2011. Implications of land disturbance on drinking water treatability in a changing climate: demonstrating the need for "source water supply and protection" strategies. Water Research. 45: 461–472.

Location: Lost Creek Fire, Alberta, Canada.
Type of study: Observational.
Variables: Water quality.
Treatments: Unburned, burned, burned/logged.
Results:

- Wildfire and salvage logging contributed to increased turbidity and dissolved organic carbon in studied watersheds.
- Additional measures are needed to assure clean drinking water for downstream communities following large-scale wildfire.

Keywords: Source water supply and protection, treatability, adaptation, wildfire, climate change, integrated water management, drinking water treatment.

Everett, R. 1995. Review of recommendations for post-fire management (Beschta et al.). August 16 letter to John Lowe, regional forester. On file with: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 1133 N Western Avenue, Wenatchee, WA 98801.

Fontaine, J.B.; Donato, D.C.; Campbell, J.L.; Martin, J.G.; Law, B.E. 2010. Effects of post-fire logging on forest surface air temperatures in the Siskiyou Mountains, Oregon, USA. Forestry. 83: 477–482.

Location: Biscuit Fire, southwest Oregon.
Type of study: Observational.
Variables: Surface air temperature.
Treatments: Burned, burned/logged.
Results:

- Maximum daily surface air temperature was not affected by postfire logging.
- Salvage logging caused slight increase in nightly minimum temperatures and earlier daytime heating.

Gorton, S.; Kays, J. 1996. Legislative history of the timber and salvage amendments enacted in the 104th Congress: a small victory for timber communities in the Pacific Northwest. Environmental Law. 26: 641.

Haggard, M.; Gaines, W.L. 2001. Effects of stand-replacement fire and salvage logging on a cavity-nesting bird community in eastern Cascades, Washington. Northwest Science. 75: 387–396.

Location: Rat Creek Fire, Washington.
Type of study: Observational.
Variables: Abundance, species richness, and nesting populations of cavity-nesting birds.
Treatments: Burned/low, burned/medium, and burned/high-intensity salvage.
Results:

- Medium-intensity salvage sites had highest bird abundance, richness, and nesting population of the three treatments.
- Large-diameter snags (>48 cm) provided nesting habitat for greater number of bird species.

Hanson, J.J.; Stuart, J.D. 2005. Vegetation responses to natural and salvage logged fire edges in Douglas-fir/hardwood forests. Forest Ecology and Management. 214: 266–278.

Location: northwestern California.
Type of study: Observational.
Variables: Understory species composition and structure.
Treatments: Unburned, burned, burned/logged.
Results:

- Salvage logging resulted in significant changes to plant community along forest edges.
- Edge effects on intact forest patches were greater on salvaged sites than unsalvaged ones

Keywords: Edge effects, edge, fire, salvage logging, understory, old-growth, Douglas-fir.

Hebblewhite, M.; Munro, R.H.; Merrill, E.H. 2009. Trophic consequences of postfire logging in a wolf–ungulate system. Forest Ecology and Management. 257(3): 1053–1062.

Location: Alberta, Canada.
Type of study: Observational.
Variables: Forage (understory) biomass, spatial distribution of wolves and ungulate prey.
Treatments: Burned, burned/logged postfire, burned/logged prefire.
Results:

- Reductions in herbaceous biomass in logged units immediately post-harvest dissipated by the third year of the study.
- Elk avoided logged areas, despite increased forage abundance.
- Wolves selected open sites near roads and logged areas, increasing predation risk, and influencing elk movement and resource use.
- Postfire logging caused a top-down increase in predation risk for elk, affecting trophic interactions between elk and wolves.

Keywords: Edge effects, edge, fire, salvage logging, understory, old-growth, Douglas-fir.

Helms, J.A. 1998. The dictionary of forestry. Bethesda, MD: Society of American Foresters. 210 p.

Hutto, R.L. 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. Conservation Biology. 20: 984–993.

Hutto, R.L.; Gallo, S.M. 2006. The effects of postfire salvage logging on cavity-nesting birds. The Condor. 108: 817–831.

Location: Blackfoot-Clearwater Wildlife Management Area, Montana.
Type of study: Observational.
Variables: Nest abundance and density of cavity-nesting birds.
Treatments: Burned, burned/logged.
Results:

- Nest density was lower in sites subjected to postfire harvest.
- Sites which were unlogged had higher bird species richness.
- 50 percent of studied species were more abundant in unharvested areas.
- Six postfire specialist bird species were absent from logged sites.
- Nest abundance may be dependent on available foraging habitat.

Keywords: Black-backed woodpecker, cavity-nesting birds, fire, healthy forests, salvage logging.

Jennings, T.N.; Smith, J.E.; Cromack, K.; Sulzman, E.W.; McKay, D.; Caldwell, B.A.; Beldin, S.I. 2012. Impact of postfire logging on soil bacterial and fungal communities and soil biogeochemistry in a mixed-conifer forest in central Oregon. Plant and Soil. 350: 393–411.

Location: B&B Fire, central Oregon.
Type of study: Observational.
Variables: Soil nutrients, microbial and fungal species richness and community composition.
Treatments: Unburned, burned, burned/logged.
Results:

- Soil compaction resulting from postfire timber harvest decreased plant-available nitrogen.
- Subsoiling following harvest-related compaction decreased plant-available phosphorus.
- Bacterial and fungal richness did not vary between treatments.

Keywords: Soil microbial and fungal communities, nutrient cycling.

Johnson, E.A.; Miyanishi, K. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters. 11: 419–431.

Keyser, T.L.; Smith, F.W.; Shepperd, W.D. 2009. Short-term impact of post-fire salvage logging on regeneration, hazardous fuel accumulation, and understory development in ponderosa pine forests of the Black Hills, SD, USA. International Journal of Wildland Fire. 18: 451–458.

Location: Jasper Fire, South Dakota.
Type of study: Observational.
Variables: Surface fuel loading, understory cover, tree regeneration density.
Treatments: Burned, burned/logged.
Results:

- Fine and coarse woody debris were greatly increased in unharvested sites.
- Tree regeneration was reduced by 75 percent in salvage-logged sites because of low seed-tree retention.
- Understory vegetation did not vary between treatments.

Keywords: Exotic species, fuel load, mixed-severity, *Pinus ponderosa*, wildfire.

Kishchuk, B.; Thiffault, E.; Lorente, M.; Quideau, S.; Keddy, T.; Sidders, D. 2014. Decadal soil and stand response to fire, harvest, and salvage-logging disturbances in the western boreal mixed-wood forest of Alberta, Canada. Canadian Journal of Forest Research. 45: 141–152.

Location: Chisholm Fire, Alberta, Canada.
Type of study: Observational.
Variables: Soil nutrients, forest floor properties, foliar nutrition, understory.
Treatments: Unburned, burned, unburned clearcut, burned/logged.
Results:

- Postfire logging caused changes in soil nutrition that remain evident 10 years after harvest.
- After 10 years, forest floor properties were comparable between harvested and control sites.
- Soil and foliar nutritional differences did not affect regeneration vigor.

Keywords: Compound disturbance, salvage logging, soil carbon, soil nutrients, boreal plains ecozone, boreal mixed-wood forest.

Knapp, E.E.; Ritchie, M.W. 2016. Response of understory vegetation to salvage logging following a high-severity wildfire. Ecosphere. 7(11): e01550. https://doi.org/10.1002/ecs2.1550.

Location: Cone Fire, California.
Type of study: Replicated experiment.
Variables: Understory species richness and cover.
Treatments: Burned/logged at five levels of intensity (control to 100 percent removal)
Results:

- Postfire logging at highest intensity significantly reduced shrub cover.
- Salvage intensity did not affect understory plant species richness.
- Factors unrelated to postfire logging may have a stronger influence on changes in postfire plant communities.

Keywords: High-severity wildfire, nonnative species, *Pinus ponderosa*, postfire management, salvage logging, species diversity, species richness, variable-retention salvage.

Kronland, W.J.; Restani, M. 2012. Effects of post-fire salvage logging on cavity-nesting birds and small mammals in southeastern Montana. Canadian Field-Naturalist. 125: 316–326.

Location: Kraft Springs, Montana.
Type of study: Observational.
Variables: Density of small mammals and cavity-nesting birds.
Treatments: Burned, burned/logged.
Results:

- Deer mouse density showed a positive relationship with postfire harvest.
- Postfire logging resulted in lower densities of cavity-nesting birds, particularly hairy woodpeckers.

Keywords: Cavity-nesting birds, downed woody debris, forest management, nest survival, salvage logging, wildfire, hairy woodpecker, *Picoides villosus*, deer mouse, *Peromyscus maniculatus*, Custer National Forest, Montana.

Kurulok, S.E.; Macdonald, S.E. 2007. Impacts of postfire salvage logging on understory plant communities of the boreal mixedwood forest 2 and 34 years after disturbance. Canadian Journal of Forest Research. 37: 2637–2651.

Location: Various fires, Alberta, Canada.
Type of study: Observational.
Variables: Understory species composition, shrub abundance.
Treatments: Burned, burned/logged.
Results:

- Salvage logging increased species richness, presence of weedy species, and shrub abundance, and reduced fire specialists in the short term.
- Older salvaged stands showed minimal effects of logging.

Lee, D.E.; Bond, M.L.; Borchert, M.I.; Tanner, R. 2013. Influence of fire and salvage logging on site occupancy of spotted owls in the San Bernardino and San Jacinto Mountains of southern California. Journal of Wildlife Management. 77: 1327–1341.

Location: Various fires, California.
Type of study: Observational.
Variables: Owl extinction and colonization probabilities.
Treatments: Unburned, burned, burned/logged.
Results:

- Effects of salvage logging on occupancy dynamics were not statistically significant, but may be biologically meaningful.
- A slight decrease in the probability of owl occupancy was observed in burned sites that were subsequently logged.

Keywords: California spotted owl, fire severity, forest structure, occupancy modeling, population dynamics, *Strix occidentalis*.

Macdonald, S.E. 2007. Effects of partial post-fire salvage harvesting on vegetation communities in the boreal mixedwood forest region of northeastern Alberta, Canada. Forest Ecology and Management. 239: 21–31.

Location: House River Fire, Alberta, Canada.
Type of study: Replicated experiment.
Variables: Understory species richness and composition; tree regeneration.
Treatments: Burned, burned/single-tree retention harvest, burned/patch retention harvest.
Results:

- Aspen regeneration was greater in harvested stands.
- Understory species richness and diversity were unaffected by salvage.

- Salvage logging affected plant community composition, but prefire composition and burn severity may have greater effects.
- Variation in harvest intensity had little effect on variables studied.

Keywords: Boreal forest, mixed wood forest, vascular plants, richness, composition, fire, salvage logging, salvage harvest.

McGinnis, T.W.; Keeley, J.E.; Stephens, S.L.; Roller, G.B. 2010. Fuel buildup and potential fire behavior after stand-replacing fires, logging fire-killed trees and herbicide shrub removal in Sierra Nevada forests. Forest Ecology and Management. 260: 22–35.

Location: McNally, Star, Cleveland and Stanislaus Fires, California.
Type of study: Observational.
Variables: Surface fuel loading, understory species richness and cover.
Treatments: Burned, burned/logged, burned/herbicide treatment.
Results:

- Short-term fuel loading was greater in logged stands.
- Modelling did not predict differences in fire behavior between logged and control stands.
- Postfire salvage did not affect understory cover or species richness.

Keywords: Salvage logging, conifer plantations, fuel, fire behavior, cheatgrass.

McIver, J.D. 2003. Sediment transport and soil disturbance after postfire logging. Hydrological Science and Technology. 19: 335–348.

McIver, J.D.; McNeil, R. 2006. Soil disturbance and hill-slope sediment transport after logging of a severely burned site in northeastern Oregon. Western Journal of Applied Forestry. 21: 123–133.

Location: Summit Fire, Oregon.
Type of study: Replicated experiment.
Variables: Soil disturbance, sediment transportation.
Treatments: Burned, burned/partial harvest, burned/full harvest.
Results:

- Soil compaction, displacement, and erosion were greater in harvested stands.
- Sediment transport out of salvaged units was minimal.
- Favorable site conditions and logging practices designed to reduce soil impacts likely limited effects of postfire harvest.

McIver, J.D.; Ottmar, R. 2007. Fuel mass and stand structure after post-fire logging of a severely burned ponderosa pine forest in northeastern Oregon. Forest Ecology and Management. 238: 268–279.

Location: Summit Fire, Oregon.
Type of study: Replicated experiment.
Variables: Surface fuel loading.
Treatments: Burned, burned/logged commercial, burned/fuel reduction.
Results:

- Ladder tree height and tree species composition were not affected by logging.
- Surface fuel mass was greatest in fuel reduction stands, particularly in slash component.
- Modelling of fuel bed predicted a 15-year duration of dissimilarity in slash fuels.
- Projections of 1,000-hr fuel dynamics predicted heavier accumulations in unlogged stands.
- Fire effects models did not predict a difference in tree mortality between treatments, partly because of reliance on flame length as cause of tree death.

Keywords: Salvage logging, reburn hypothesis, restoration.

McIver, J.D.; Ottmar, R. 2018. Fuel mass and stand structure 13 years after logging of a severely burned ponderosa pine forest in northeastern Oregon, U.S.A. Forest Ecology and Management. 424: 505–518.

Location: Summit Fire, Oregon.
Type of study: Replicated experiment.
Variables: Surface fuel loading, tree regeneration.
Treatments: Burned, burned/logged commercial, burned/fuel reduction.
Results:

- 13 years after harvest, discrepancies in slash fuel loading dissipated.
- Logged stands continued to lack snags and coarse woody debris after 13 years.
- Regeneration density was highly variable, but higher on average in unlogged stands.

Keywords: Salvage logging, postfire logging, reburn hypothesis, restoration logging, disturbance, wildfire.

McIver, J.D.; Starr, L. 2000. Environmental effects of postfire logging: literature review and annotated bibliography. Gen. Tech. Rep. PNW-GTR-486. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 72 p.

Miller, J.D.; Thode, A.E. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment. 109: 66–80.

Morgan, P.; Moy, M.; Droske, C.A.; Lewis, S.A.; Lentile, L.B.; Robichaud, P.R.; Hudak, A.T.; Williams, C.J. 2015. Vegetation response to burn severity, native grass seeding, and salvage logging. Fire Ecology. 11(2): 32–58. doi: 10.4996/fireecology.1102031.

Location: School Fire, Washington.
Type of study: Observational.
Variables: Understory species richness and abundance.
Treatments: Unburned, burned/logged, burned/seeded, burned/seeded/logged; replicated with three burn-severity classes.
Results:

- Species richness and diversity were reduced by salvage logging.
- Burn severity and postfire seeding had a greater effect on vegetation response than logging.
- Differences between treatments were initially substantial, but declined after 6 years.

Keywords: Fire effects, mixed-conifer forests, plant succession, post-fire rehabilitation, salvage logging.

Morissette, J.; Cobb, T.; Brigham, R.; James, P. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Canadian Journal of Forest Research. 32: 2169–2183.

Location: Hawk Fire, Saskatchewan, Canada.
Type of study: Observational.
Variables: Songbird abundance, species richness and diversity.
Treatments: Unburned, burned, burned/logged.
Results:

- Songbird community composition was distinct in all three treatments.
- Differences in bird species assemblage were greatest between burned

and salvaged sites.
- Generalists and species associated with open habitats were more abundant in logged areas.
- Cavity and canopy nesters, insectivores, and resident species abundance were negatively affected by salvage logging.
- Postfire salvage may be a greater disturbance to songbird communities than fire.

Newton, M.; Fitzgerald, S.; Rose, R.R.; Adams, P.W.; Tesch, S.D.; Sessions, J.; Atzet, T.; Powers, R.F.; Skinner, C. 2006. Comment on "Post-wildfire logging hinders regeneration and increases fire risk." Science. 313: 615–615.

Peterson, D.L.; Agee, J.K.; Aplet, G.H.; Dykstra, D.P.; Graham, R.T.; Lehmkuhl, J.F.; Pilliod, D.S.; Potts, D.F.; Powers, R.F.; Stuart, J.D. 2009. Effects of timber harvest following wildfire in western North America. Gen. Tech. Rep. PNW-GTR-776. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 51 p.

Peterson, D.W.; Dodson, E.K. 2016. Post-fire logging produces minimal persistent impacts on understory vegetation in northeastern Oregon, USA. Forest Ecology and Management. 370: 56–64.

Location: Summit Fire, Oregon.
Type of study: Replicated experiment.
Variables: Understory plant cover, species richness, diversity, community composition.
Treatments: Burned, burned/logged commercial, burned/logged fuel reduction.
Results:
- No significant effect of postfire logging was observed 15 years following treatments.
- Understory species appear resilient to disturbance.
- Low-impact harvest methods may have minimized negative effects on understory.

Keywords: Postfire logging, salvage logging, understory vegetation, species richness, biodiversity, postfire forest management.

Peterson, D.W.; Dodson, E.K.; Harrod, R.J. 2015. Post-fire logging reduces surface woody fuels up to four decades following wildfire. Forest Ecology and Management. 338: 84–91.

Location: Various fires, Oregon and Washington.
Type of study: Observational.
Variables: Surface fuel loading.
Treatments: Burned, burned/logged.
Results:

- Postfire logging created a temporary pulse of increased fine and medium fuels that lasted 5 to 7 years following harvest.
- In the long term, all woody fuel loadings were lower in salvage-logged stands.
- Coarse woody fuels were reduced by logging for nearly 40 years.

Keywords: Ponderosa pine, Douglas-fir, post-fire logging, salvage logging, fuel succession, forest restoration.

Poirier, V.; Paré, D.; Boiffin, J.; Munson, A.D. 2014. Combined influence of fire and salvage logging on carbon and nitrogen storage in boreal forest soil profiles. Forest Ecology and Management. 326: 133–141.

Location: Various fires, Quebec, Canada.
Type of study: Observational.
Variables: Soil organic carbon (SOC), total soil nitrogen (N), soil structure.
Treatments: Unburned, burned, burned/logged.
Results:

- SOC was lower in organic layer in logged stands compared with burned only.
- Logging increased SOC and N in mineral horizons.
- Whole-soil SOC and N stocks of burned soils were unchanged by salvage logging.

Keywords: Soil organic carbon, total soil nitrogen, soil horizons, wildfire, salvage logging, black spruce forest.

Powers, E.M.; Marshall, J.D.; Zhang, J.; Wei, L. 2013. Post-fire management regimes affect carbon sequestration and storage in a Sierra Nevada mixed conifer forest. Forest Ecology and Management. 291: 268–277.

Location: Storrie Fire, California.
Type of study: Observational.
Variables: Carbon storage and sequestration.
Treatments: Low-severity burn, burned, burned/logged/planted, burned/logged/planted/intensive management.

Results:

- Postfire salvage logging reduced total ecosystem carbon storage.
- Belowground carbon storage in mineral soil was lowest in intensively managed treatment.
- Total carbon sequestration did not vary significantly among treatments.

Keywords: Carbon flux, carbon storage, forest management, fire, climate change.

Ritchie, M.W.; Knapp. E.E. 2014. Establishment of a long-term fire salvage study in an interior ponderosa pine forest. Journal of Forestry. 112: 395–400.

Location: Cone Fire, California.
Type of study: Replicated experiment.
Variables: Snag dynamics, surface fuel loading, tree regeneration.
Treatments: Burned/logged at five levels of intensity, including unlogged control.
Results:

- Transition of snags to surface fuels was rapid.
- Stands with higher snag retention levels (basal area > 60 ft²/acre) exceeded historical surface fuel loads after 10 years.
- White fir and incense-cedar snags had greater longevity than pine snags.
- Regeneration was minimal, and seedling density appeared unrelated to treatment.

Keywords: Snag dynamics, biomass, regeneration.

Ritchie, M.W.; Knapp, E.E.; Skinner, C.N. 2013. Snag longevity and surface fuel accumulation following post-fire logging in a ponderosa pine dominated forest. Forest Ecology and Management. 287: 113–122.

Location: Cone Fire, California.
Type of study: Replicated experiment.
Variables: Snag dynamics, surface fuel loading.
Treatments: burned/logged at five levels of intensity, including unlogged control.
Results:

- Fuel loading of coarse materials increased with snag retention level.
- Greatest loading of 1,000-hr fuels occurred in control units.
- More than 80 percent retained snag biomass had transitioned to surface fuel by year 8.
- Pine snags were more susceptible to breakage and decay than white fir or incense-cedar.

Keywords: Coarse woody debris, snag dynamics, salvage logging.

Rost, J.; Hutto, R.L.; Brotons, L.; Pons, P. 2013. Comparing the effect of salvage logging on birds in the Mediterranean Basin and the Rocky Mountains: common patterns, different conservation implications. Biological Conservation. 158: 7–13.

Location: Various fires, Montana and Catalonia, Spain.
Type of study: Observational.
Variables: Species richness and abundance of birds.
Treatments: Burned, burned/logged.
Results:

- Species that are dependent on snags were negatively affected by salvage logging.
- Logging had positive effect on open-habitat species in Mediterranean sites.

Keywords: Catalonia, conifer forests, fire specialists, forest management, Montana, wood harvesting.

Rothermel, R. 1972. A mathematical model for predicting fire spread in wildland fuels. Res. Pap. INT-115. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 40 p.

Saab, V.A.; Russell, R.E.; Dudley, J.G. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. The Condor. 109: 97–108.

Location: Foothills Fire and Star Gulch Fire, Idaho.
Type of study: Observational.
Variables: Nest density and success of open space and cavity-nesting (bark-foraging) birds.
Treatments: Burned, burned/partially logged.
Results:

- Nest densities of cavity nesting (bark foraging) were higher in unlogged than logged burn.
- Logged burn had higher nest density of two open-space-foraging species vs. unlogged burn.
- Mountain bluebird nest density was higher in unlogged than logged burn, while western bluebirds did not show an effect of treatment.
- Hairy woodpecker nest survival was reduced in logged burn vs. unlogged during early postfire period.

Keywords: Cavity-nesting birds, nest densities, nest survival, ponderosa pine forests, postfire salvage logging, wildfire.

Silins, U.; Bladon, K.D.; Kelly, E.N.; Esch, E.; Spence, J.R.; Stone, M.; Emelko, M.B.; Boon, S.; Wagner, M.J.; Williams, C.H. 2014. Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity. Ecohydrology. 7: 1508–1523.

Location: Lost Creek Fire, Alberta, Canada.
Type of study: Observational.
Variables: Water chemistry, algal production.
Treatments: Unburned, burned, burned/logged.
Results:

- Phosphorous concentrations were highest in logged watersheds.
- Although wildfire had a greater effect on measured variables, salvage logging added incremental impacts.
- Wildfire and salvage logging caused a cascading series of effects on the ecohydrology of studied watersheds.

Keywords: Forest fire, natural disturbance, hydrologic recovery, stream ecology, phosphorus, sediment, algae macroinvertebrates.

Slesak, R.A.; Schoenholtz, S.H.; Evans, D. 2015. Hillslope erosion two and three years after wildfire, skyline salvage logging, and site preparation in southern Oregon, USA. Forest Ecology and Management. 342: 1–7.

Location: Timbered Rock Fire, Oregon.
Type of study: Observational.
Variables: Sediment transport, vegetative cover.
Treatments: Burned, burned/logged.
Results:

- Erosion was more pronounced in salvage-logged sites in year following harvest.
- In second year, no differences in erosion were detected.
- As little soil disturbance was observed, increased erosion in harvested sites was most likely due to vegetation control prior to replanting salvaged areas.

Keywords: Vegetation control, plot scale measurements, postfire erosion, Pacific Northwest.

Thompson, J.R.; Spies, T.A.; Ganio, L.M. 2007. Reburn severity in managed and unmanaged vegetation in a large wildfire. Proceedings of the National Academy of Sciences of the United States of America. 104: 10743–10748.

Location: Biscuit Fire and Silver Fire, Oregon.
Type of study: Observational.
Variables: Burn severity (differenced normalized burn ratio (dNBR) from remote sensing data).
Treatments: Burned, burned/logged/planted, replicated across continuous dNBR indices of burn severity of both fires.
Results:

- Sites that burned at high severity in Silver Fire tended to burn again at high severity in Biscuit Fire.
- Harvest of fire-killed trees reduced large fuels but did not decrease reburn severity.
- Replanting of conifers in harvested areas may have increased burn severity in salvaged-logged stands.

Keywords: Public land management, salvage logging, Biscuit Fire, landsat, landscape ecology.

Thorn, S.; Bässler, C.; Brandl, R.; Burton, P.J.; Cahall, R.; Campbell, J.L.; Castro, J.; Choi, C.-Y.; Cobb, T.; Donato, D.C.; Durska, E.; Fontaine, J.B.; Gauthier, S.; Hebert, C.; Hothorn, T.; Hutto, R.L.; Lee, E.-J.; Leverkus, A.B.; Lindenmayer, D.B.; Obrist, M.K.; Rost, J.; Seibold, S.; Seidl, R.; Thom, D.; Waldron, K.; Wermelinger, B.; Winter, M.-B.; Zmihorski, M.; Müller, J. 2018. Impacts of salvage logging on biodiversity: a meta-analysis. Journal of Applied Ecology. 55: 279–289.

Location: Various fires, worldwide.
Type of study: Meta-analysis.
Variables: Species richness and community composition of 24 taxonomic groups.
Treatments: Disturbed, disturbed/logged (including fire).
Results:

- Salvage logging negatively affected richness in eight taxonomic groups.
- Post-disturbance harvest had disproportionally negative impacts on saproxylic organisms.
- Species that use open habitats had generally positive responses to logging.

Keywords: Bark beetle, climate change, dead wood, disturbed forest, fire, natural disturbance, post-disturbance logging, salvage logging, saproxylic taxa, windstorm.

Wagenbrenner, J.W.; MacDonald, L.H.; Coats, R.N.; Robichaud, P.R.; Brown R.E. 2015. Effects of post-fire salvage logging and a skid trail treatment on ground cover, soils, and sediment production in the interior western United States. Forest Ecology and Management. 335: 176–193.

Location: Tripod, Kraft Springs, Red Eagle, and Hayman Fires, Washington, Montana, and Colorado.
Type of study: Observational.
Variables: Ground cover, soil disturbance, runoff, sediment production.
Treatments: Burned, burned/logged replicated across various harvest methods.
Results:

- Soil compaction increased in salvage-logged sites.
- Harvested stands in areas with greater disturbance produced more sediment.
- Vegetative cover was negatively associated with salvage, and vegetation recovery was delayed in these sites.
- Sediment production did not increase with logging in larger swales.
- Treatment of skid trails with logging slash resulted in decreased sediment yields but did not affect soil properties.

Keywords: Erosion, wildfire, water repellency, soil compaction, salvage logging, mitigation.

Wagenbrenner, J.W.; Robichaud, P.R.; Brown, R.E. 2016. Rill erosion in burned and salvage logged western montane forests: effects of logging equipment type, traffic level, and slash treatment. Journal of Hydrology. 541: 889–901.

Location: Red Eagle, School, and Terrace Mountain Fires, Montana, Washington, and British Columbia, Canada.
Type of study: Observational.
Variables: Vegetative cover, runoff, sediment production, soil disturbance.
Treatments: Burned, burned/logged, replicated across various harvest methods.
Results:

- Erosion was more pronounced in logged stands, but effects diminished over time.
- Runoff rates were higher in logged sites.
- Equipment used for harvest did not have measureable effects.
- Using logging slash to cover skid trails did not affect runoff or sedimentation.

Keywords: Salvage logging, wildfire, runoff, soil compaction, soil water repellency, sediment.

Pacific Northwest Research Station

Website	http://www.fs.fed.us/pnw/
Telephone	(503) 808–2100
Publication requests	(503) 808–2138
FAX	(503) 808–2130
E-mail	pnw_pnwpubs@fs.fed.us
Mailing address	Publications Distribution Pacific Northwest Research Station P.O. Box 3890 Portland, OR 97208–3890



Federal Recycling Program
Printed on Recycled Paper

U.S. Department of Agriculture
Pacific Northwest Research Station
1220 SW 3rd Ave., Suite 1400
P.O. Box 3890
Portland, OR 97208–3890

Official Business
Penalty for Private Use, $300

USDA
United States Department of Agriculture

The Ecology and Management of Moist Mixed-Conifer Forests in Eastern Oregon and Washington: a Synthesis of the Relevant Biophysical Science and Implications for Future Land Management

Peter Stine, Paul Hessburg, Thomas Spies, Marc Kramer, Christopher J. Fettig, Andrew Hansen, John Lehmkuhl, Kevin O'Hara, Karl Polivka, Peter Singleton, Susan Charnley, Andrew Merschel, and Rachel White



Forest Service
Pacific Northwest Research Station
General Technical Report PNW-GTR-897
September 2014

The **Forest Service** of the U.S. Department of Agriculture is dedicated to the principle of multiple use management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forests and National Grasslands, it strives—as directed by Congress—to provide increasingly greater service to a growing Nation.

The U.S. Department of Agriculture (USDA) prohibits discrimination in all its programs and activities on the basis of race, color, national origin, sex, religion, age, disability, sexual orientation, marital status, family status, status as a parent (in education and training programs and activities), because all or part of an individual's income is derived from any public assistance program, or retaliation. (Not all prohibited bases apply to all programs or activities.)

If you require this information in alternative format (Braille, large print, audiotape, etc.), contact the USDA's TARGET Center at (202) 720-2600 (Voice or TDD).

If you require information about this program, activity, or facility in a language other than English, contact the agency office responsible for the program or activity, or any USDA office.

To file a complaint alleging discrimination, write USDA, Director, Office of Civil Rights, 1400 Independence Avenue, S.W., Washington, D.C. 20250-9410, or call toll free, (866) 632-9992 (Voice). TDD users can contact USDA through local relay or the Federal relay at (800) 877-8339 (TDD) or (866) 377-8642 (relay voice users). You may use USDA Program Discrimination Complaint Forms AD-3027 or AD-3027s (Spanish) which can be found at: http://www.ascr.usda.gov/complaint_filing_cust.html or upon request from a local Forest Service office. USDA is an equal opportunity provider and employer.

Authors

Peter Stine is a biogeographer and **Christopher Fettig** is a research entomologist, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 1731 Research Park Drive, Davis, CA 95618; **Paul Hessburg** is a research ecologist, **John Lehmkuhl** is an emeritus scientist, **Karl Polivka** is a research fish biologist, and **Peter Singleton** is an ecologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 1133 N. Western Ave., Wenatchee, WA 98801; **Thomas Spies** is a research forester, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331; **Susan Charnley** is a research social scientist, and **Rachel White** is a science writer/editor, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 620 SW Main St., Suite 400, Portland, OR 97205; **Marc Kramer** is an associate professor, University of Florida, 3165A McCarty Hall, Gainesville, FL 32611; **Andrew Hansen** is a professor, Montana State University, Landscape Biodiversity Lab, 310 Lewis Hall, Bozeman, MT 59717; **Kevin O'Hara** is a professor, University of California–Berkeley, Department of Environmental Science, Policy, and Management, 130 Mulford Hall #3114, Berkeley, CA 94720; and **Andrew Merschel** is faculty research assistant, Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331.

Cover photographs: (upper left and lower right) Okanogan-Wenatchee National Forest, Washington, by John Marshall; (lower left) Columbia River Gorge, Oregon, by Miles Hemstrom; (upper right) Deschutes National Forest, Oregon, by Tom Spies.

Abstract

Stine, Peter; Hessburg, Paul; Spies, Thomas; Kramer, Marc; Fettig, Christopher J.; Hansen, Andrew; Lehmkuhl, John; O'Hara, Kevin; Polivka, Karl; Singleton, Peter; Charnley, Susan; Merschel, Andrew; White, Rachel. 2014. The ecology and management of moist mixed-conifer forests in eastern Oregon and Washington: a synthesis of the relevant biophysical science and implications for future land management. Gen. Tech. Rep. PNW-GTR-897. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 254 p.

Land managers in the Pacific Northwest have reported a need for updated scientific information on the ecology and management of mixed-conifer forests east of the Cascade Range in Oregon and Washington. Of particular concern are the moist mixed-conifer forests, which have become drought-stressed and vulnerable to high-severity fire after decades of human disturbances and climate warming. This synthesis responds to this need. We present a compilation of existing research across multiple natural resource issues, including disturbance regimes, the legacy effects of past management actions, wildlife habitat, watershed health, restoration concepts from a landscape perspective, and social and policy concerns. We provide considerations for management, while also emphasizing the importance of local knowledge when applying this information at the local and regional level.

Keywords: Disturbance ecology, landscape restoration, land management, resilience, stewardship.

Executive Summary

One priority of the USDA Forest Service is to restore resiliency to forest and range ecosystems, enabling them to cope with an uncertain future.

Millions of hectares of Western forests have been negatively affected by drought and by insect and disease outbreaks, and are overloaded with fuel, priming them for unusually severe and extensive wildfires. In light of these trends, public support for forest restoration has grown. One priority of the USDA Forest Service is to restore resiliency to forest and range ecosystems, enabling them to cope with an uncertain future. Natural resource managers and policymakers are awash in information from a growing body of science, with little time to sort through it, let alone assimilate the many different sources and interpretations of the best available science.

Regional research and management executives requested a review of the large body of scientific information on eastside moist mixed-conifer (MMC) forests within the context of the broader forest landscape in eastern Oregon and Washington. This focus was motivated by a lack of up-to-date management guidelines, scientific synthesis, and consensus among stakeholders about management direction in the diverse MMC type.

Understanding complex ecological and social processes and functions across landscapes requires an integrated assessment that combines multiple scientific disciplines across spatial and temporal scales. Accordingly, this synthesis compiles existing research, makes connections across disparate sources, and addresses multilayered natural resource issues. It has been prepared to assist land managers in updating existing management plans and on-the-ground projects that are intended to promote resilience in MMC forests and riparian areas. We consider management flexibility at the local scale critically important for contending with specific legacy effects of management and the substantial ecological variation in MMC forest conditions, as well as for adapting management to local social and policy concerns.

Our hope is that this synthesis will serve as a reference that provides a condensed and integrated understanding of the current state of knowledge regarding MMC forests, as well as an extensive list of published sources where readers can find further information. We also hope to enhance cross-disciplinary communication and enrich dialogue among Forest Service researchers, managers, and external stakeholders as we address common restoration concerns and management challenges for MMC forests in eastern Oregon and Washington.

Key sections of this synthesis include:

- A description of MMC forests and their context in the broader landscape of eastern Oregon and Washington.
- Key concepts of restoration and the landscape perspective.
- A comprehensive summary of pre-Euro-American settlement conditions in MMC forests.

- A description of the socioeconomic context in the region.
- A summary of human impacts on MMC forests.
- Broad management implications of research findings.
- A practical list of management considerations for diagnosing restoration needs and designing landscape approaches.

Moist Mixed-Conifer Forests

Mixed-conifer forests are a major component of the dry-to-wet conifer forest complex that is widely distributed across eastern Oregon and Washington. Among other factors, these forests are important for carbon sequestration, watershed protection, terrestrial and aquatic wildlife habitat, and outdoor recreation, and they provide economic opportunities through provisioning of a wide variety of forest products. MMC forests cover a large area east of the crest of the Cascade Range in Oregon and Washington, where grand fir, white fir, and Douglas-fir are the dominant late-successional tree species. MMC forests can be considered intermediate between drier conifer forests where pine was historically dominant and fire was typically frequent and low in severity, and wetter or cooler mixed-conifer forests where fire was less frequent and burned at higher severities. The MMC forest type is in a central position along a complex moisture, composition, and disturbance gradient of conifer forests in this region. This forest type is diverse and difficult to define, but potential vegetation types and current conditions can be used to help identify places where stands and landscapes need restoration. Historically, the forest landscape (from dry to wet) was a mosaic driven by variation in climate, soils, topography, and low- to mixed- and occasional high-severity fire.

Decades of wildfire suppression and exclusion, domestic livestock grazing, and selective and clearcut timber harvesting have interacted to alter the structure, composition, and disturbance regimes of these forests. MMC forests have become denser, have lost large individuals of fire-resistant tree species, and, on many sites, have become dominated by dense patches of shade-tolerant tree species that are less resistant to fire and less resilient to drought. These vegetation changes and management activities have shifted fire regimes toward less frequent, but larger and more severe fires, which tend to simplify the landscape into fewer, larger, and less diverse patches resulting in more homogenous conditions. Currently, many mixed-conifer forests are denser and more uniform in structure, and contain more live and dead fuel than they did historically. But the relative effects of human-caused changes, like fire suppression and timber harvesting, on these forests differ widely across the region. Thus, it is important to develop local, first-hand knowledge of the historical and contemporary disturbance regimes of these forests.

Key Management Considerations

As we reviewed the scientific literature, our primary objective was to synthesize the large body of information into succinct findings that are supported by credible research and relevant to practitioners and others interested in management of MMC forests. Some of our findings are that:

- **Historical range of variation (HRV) is useful as a guide but not as a target.** Returning to it is no longer feasible or practical in some places because of changing climate, land use, and altered forest structure and composition. The contemporary concept of restoration goes beyond the oft-stated goal of reestablishing ranges of resource conditions that existed at some time in the past (e.g., prior to Euro-American settlement). Our ecological process-oriented approach supports restoration of conditions that may have occurred in the past under certain circumstances. However, the objective of ecological restoration is to create a resilient and sustainable forest under current and future conditions. It must be forward looking. Managers have some capacity to influence the future range of variability (FRV) to achieve desired future ecosystem conditions for a landscape.
- **Disturbance regimes have been significantly altered after 150 years of Euro-American land use.** Wildfires (along with insects, pathogens, and weather) were the dominant disturbance process shaping historical forest structure and composition. Low-, mixed-, and high-severity fires occurred in MMC forests, varying in size and occurrence across ecoregions. Small and medium fires were the most numerous, but large fires accounted for the majority of the area burned. Forests today neither resemble nor function as they did 150 years ago.
- **Moist mixed-conifer forests are more vulnerable to large, high-severity fire and insect outbreaks.** Widespread anthropogenic changes have created more homogenized conditions in this forest type, generally in the form of large, dense, and multilayered patches of fire-intolerant tree species. These changes have substantially altered the resilience mechanisms associated with MMC forests.
- **Patterns of vegetation structure and composition in an eastside forest landscape shaped by intact disturbance regimes are diverse and differ over space and time.** Resilience in these forests depends on this ecological heterogeneity. Euro-American settlement and early management practices put these landscapes on new and rapidly accelerating trajectories of change

in vegetation composition and structure. Despite the change and variability, topography, soils, and elevation constrain these vegetation patterns and provide a template for understanding and managing landscape patterns. For example, south-facing aspects and ridges tended to burn more often and less severely than north-facing aspects and valleys. Landscape restoration strategies can capitalize on these tendencies.

- Several wildlife species of conservation concern require structural complexity typical of mature and old forests, which are currently limited or at risk. With no action, maintaining adequate area and spatial patterns of old-forest habitats will be a challenge with the anticipated increases in severe fire and insect infestations expected in response to changed forest conditions and climate change. Restoration at a landscape scale will encounter challenges in retaining existing old-forest patches while transitioning to a more heterogeneous and resilient forest condition.
- Community-based collaborative groups can facilitate restoration in east-side national forests. One of the major constraints to increasing the pace and scale of restoration treatments on lands administered by the National Forest System (NFS) in eastern Oregon has been the lack of social agreement about how to achieve it. The Forest Service promotes collaboration as a means for helping diverse stakeholder groups come together and find an agreeable path forward. The creation of local groups and the Forest Service's Collaborative Forest Landscape Restoration Program both offer innovations and demonstrate opportunities to improve capacity for restoration through collaborative processes.

Potential Applications

In the midst of complicated social and political forces, forest managers make decisions that require the application of complex scientific concepts to project-specific conditions. Decisions often must balance risks (e.g., elimination of fuels hazards vs. preservation of old-forest conditions) while acknowledging and allowing for uncertainties. Decisionmakers also must weigh tradeoffs associated with alternative courses of action to obtain multiple-use policy and land management objectives. We acknowledge this difficult task and the concurrent need to have access to and thoughtfully apply the best available scientific information.

It is not the role of the research community to direct management decisions. However, synthesis of research, identification of core scientific findings, and discernment of management implications in specific contexts are appropriate roles.

Research also has a role of working alongside managers to learn from successes and failures. We provide considerations for management and emphasize that their application to local and regional landscapes requires the skill and knowledge of practitioners to determine how best to apply them to a local situation with its particular management history. Legacy effects do matter, and one size does not fit all.

In chapter 5, we synthesize principle findings gleaned from the body of scientific literature (summarized in chapter 4) as they pertain to management of MMC forests. These constitute the "take-home" messages that are intended to assist land managers in the execution of their work.

The social agreement and institutional capacity for restoring MMC forests is every bit as important as the scientific foundation for doing so. The ability to institute the kinds of changes managers will consider is directly a function of the capacity of the larger community to form working partnerships and a common vision.

Some of the potential changes in forest management evoked within this document represent a departure from "business as usual." Land managers will decide how to proceed, and this will depend in large part on budget, policy, local circumstances, and ultimately the judgment of line officers. However, there are some ideas and observations from past work, both research and management, that suggest the need for some prudent adjustments in management approach.

Contents

1 **Chapter 1—Introduction**
1 **Purpose and Scope of This Synthesis**
4 **Current Management Context and Restoration Mandate**
8 **Structure of This Report—Where to Find Sections of Interest**
9 **Chapter 2—Definition of Moist Mixed-Conifer Forests and the Regional Context**
17 **Chapter 3—Ecological Principles of Restoration and Landscapes**
18 **The Concept of Resilience**
21 **Ecological Principles for Landscape Planning and Management**
29 **Chapter 4—Scientific Foundations**
29 **Ecological Composition, Patterns, and Processes Prior to Euro-American Settlement (Before About 1850)**
31 Where Is the MMC Forest Located?
39 Vegetation Classification and Disturbance Regimes
53 Landscape Concepts
60 Natural Disturbance Factors
75 Animals of the Moist Mixed-Conifer Ecosystem
87 Aquatic Habitats
95 **Human Impacts to Moist Mixed-Conifer Systems: Influences of the Last 100 to 150 Years**
97 Timber Harvest and Associated Activities
98 Fire Exclusion and Natural Fire Dynamics
99 Grazing
100 Land Development
102 Climate Change
108 Changes in Vegetation
115 Changes in Disturbance Factors: Insects and Disease
115 Effects of Altered Disturbance Regimes, Land Use, and Climate Change on Animal Populations and Habitats
128 **Current Socioeconomic Context**
130 Wood Processing Infrastructure and Business Capacity for Forest Restoration
133 Biomass Utilization
135 Tribal Concerns
137 Recreation
139 **Summary of Key Scientific Findings and Concepts**
139 Landscapes
141 Disturbances
142 Vegetation

144 Wildlife and Fish
146 Management Applications in the Field
147 **Chapter 5—Management Considerations**
147 **Key Concepts to Consider in Management of MMC Forests**
157 **Stand Management—Silvicultural Tools and Their Role in Landscape Management**
165 **Chapter 6—Social Agreement and Institutional Capacity for Restoring Moist Mixed-Conifer Forests**
165 **Social Acceptability of Restoration Treatments Among Members of the Public**
168 **Collaboration**
170 **Institutional Capacity**
170 Create Landscape Management Demonstration Areas
171 Incorporate the "All-Lands" Initiative
172 Revisit Current Management Constraints; Eastside Screens
175 **Chapter 7—Conclusions**
178 **Acknowledgments**
178 **Metric Equivalents**
178 **Literature Cited**
229 **Appendix 1—List of Practical Considerations for Landscape Evaluation and Restoration Planning**
235 **Appendix 2—Regional-Scale Fire Regimes Group Classification for Oregon and Washington**
238 **Appendix 3—Reconstructed Historical Vegetation Conditions Within Sampled Areas of the Blue Mountains Province**
250 **Glossary**

Chapter 1—Introduction

> There is and always will be uncertainty and unpredictability in managed ecosystems, both as humans experience new situations and as these systems change because of management.
>
> Surprises are inevitable. Active learning is the way in which this uncertainty is winnowed. Adaptive management acknowledges that policies must satisfy social objectives but also must be continually modified and be flexible for adaptation to these surprises. Adaptive management therefore views policies as hypotheses—that is; most policies are really questions masquerading as answers. Since policies are questions, then management actions become treatments in the experimental sense. The process of adaptive management includes highlighting uncertainties, developing and evaluating hypotheses around a set of desired system outcomes, and structuring actions to evaluate or "test" these ideas.
>
> —Lance Gunderson (2000), *Annual Review of Ecology and Systematics*

Purpose and Scope of This Synthesis

Fire-prone mixed-conifer forests east of the crest of the Cascade Range in Oregon and Washington (hereafter, "the east side") provide clean water, recreation, wildlife habitat, and many other important ecosystem goods and services (fig. 1). However, over the last century, many of these forests have become denser and less resilient to disturbance as a result of human activity, altered disturbance regimes, and climate warming. In the last few decades, many of these forests have also become further drought stressed and increasingly vulnerable to high-severity fire (Westerling et al. 2006) and insect outbreaks as a result of climate change (Preisler et al. 2012).

In the Pacific Northwest, research and management executives from the USDA Forest Service recently highlighted the need to update management guidance, scientific synthesis, and consensus among stakeholders regarding these challenges. This synthesis responds to this need. In particular, executives asked us to focus on eastside moist mixed-conifer (MMC) forests (see definition in chapter 2), within the context of the broader forest landscape on the east side. We have written this synthesis for a diverse audience of forest planners, managers, and engaged citizens.

For this effort, we convened a team of government and university scientists to review the literature, synthesize knowledge and management options, and compile a bibliography. Team members were selected based on their experience and expertise, spanning a range of disciplines including aquatic ecology and fish biology, climate change, disturbance ecology, fire and forest ecology, landscape ecology, silviculture, social science, and wildlife biology.

John Marshall



Figure 1—A moist mixed-conifer forest, Glass Creek Watershed, Okanogan-Wenatchee National Forest, eastern Washington.

We focused the synthesis on the ecology of MMC forests but acknowledge that decisionmakers must address major issues surrounding the needs and values of human communities, so these decision processes are addressed as well. The forests of the east side represent complex patchworks of temperature, moisture, productivity, climate, and disturbance regimes, and their associated forest types (fig. 2), so we occasionally discuss forest types that adjoin the MMC type to improve overall context. The synthesis specifically addresses:

- Vegetation, landscape, and disturbance ecology.
- Wildlife habitats and populations; and aquatic ecosystems and associated species.
- Landscape approaches and perspectives.
- Silvicultural approaches.
- Climate change influences and climate futures.

Research findings summarized here can make a valuable contribution to restorative management, but it will be up to managers and program leaders to consider the unique ecological conditions of each landscape and to determine how this information guides specific land management decisions. To that end, findings here are intended to conceptually frame—not prescribe—land management. Such guidance is available in the new Forest Service Planning Rule (36 CFR Part 219), an important new administrative rule that applies current science to planning and



John Marshall

Figure 2—A mixed-conifer landscape, Middle Fork of Gold Creek, Okanogan-Wenatchee National Forest, eastern Washington.

We consider management flexibility at the local site level critically important for contending with specific legacy effects of management and the substantial ecological variation in moist mixed-conifer forest conditions, as well as for adapting management to local policy concerns.

management. We consider management flexibility at the local site level critically important for contending with specific legacy effects of management and the substantial ecological variation in MMC forest conditions, as well as for adapting management to local policy concerns.

In related dry mixed-conifer and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forest types, research and social license to begin restoration is relatively more advanced (e.g., see Franklin et al. 2013, Jain et al. 2012), and managers are proceeding with restoration treatments (e.g., see Hessburg et al. 2013, OWNF 2012). However, we include the pine and dry mixed-conifer types in our discussions because these dry and MMC types are entwined spatially and ecologically in eastern Oregon and Washington.

Current Management Context and Restoration Mandate

Federal and state forest managers are charged with maintaining and restoring diverse, resilient (see "Glossary"), and productive forests in these fire-prone landscapes. Restoration can increase the resilience of eastside MMC forests, and reduce the ecological costs of high-severity wildfire and economic costs of fire suppression activities and postfire rehabilitation, along with the ecological and socioeconomic threats to adjoining state, private, and tribal lands. But achieving these goals is challenging without sufficient investment. Twentieth-century harvesting of large trees has reduced commercial operability in many eastside forests (e.g., see Rainville et al. 2008), and the value of remaining commercial products is often insufficient to cover the costs of restoration.

Developing and implementing sound management strategies requires up-to-date knowledge of biological and physical processes that regulate forest ecosystem structure and function. We also require information on how humans have modified these processes, especially disturbance processes, which are a key to sculpting habitat and structural patterns (e.g., see Spies 1998). In this context, a number of factors are particularly relevant to eastside MMC forests:

- The processes and patterns of eastside forests have been altered over the past 100 to 150 years (depending upon location) by the combined cumulative effects of mining, livestock grazing, road and railroad construction, conversion of grasslands and shrublands to agriculture, timber harvesting, fire suppression and exclusion, urban and rural development, invasions of alien plant and animal species (including pathogens, insects, and aquatic organisms), expanding infestations of native diseases and insects, and anthropogenically induced climate change.

- In many areas (e.g., those not burned in recent decades), today's dry and MMC forests are denser, have more small trees and fewer large fire-tolerant trees, and are dominated by shade-tolerant and fire-intolerant tree species. These conditions have reduced the fire and drought tolerance of these forests. Large increases in surface and canopy fuel loads are widespread, resulting in greater risk of large and often severe wildfires, especially during extreme fire weather conditions. Furthermore, high stand densities increase competition for growing space among trees, thereby reducing the amount of water and nutrients available to individual trees and increasing their susceptibility to some insect and disease disturbances. These changes threaten the long-term sustainability of dry and MMC forests in general, and in particular the long-term survival of remaining large and very large trees that persist in overcrowded conditions.
- Climate change is already transforming forests in eastern Oregon and Washington because it is linked to ongoing drought as well as elevated levels of tree mortality attributed to insects, diseases, and wildfire. This transformation is occurring at a brisk pace, and the window of opportunity for effecting change in this trajectory is relatively short (likely a few decades).

Mandated conservation of threatened or endangered species, some of which have been threatened by landscape alterations (first bullet above), has added ecological and regulatory complexity to forest management. For example, in the eastern Cascades, restoration of dry and MMC forests, fire regimes, and fuel patterns is often constrained by the need to minimize disturbance in areas around active nest locations of the northern spotted owl (NSO) (*Strix occidentalis caurina*), to conserve its dense, late-successional and old-forest nesting, roosting, and foraging habitats.

Currently, many landscapes of the east side have late-successional forest patterns that are out of sync with past and current fire regimes and are ecologically unsuited to providing large contiguous areas of late-successional habitat over time. In addition, much of the structural diversity in those stands is relatively short-lived because of the dominance of shade-tolerant tree species. Conservation of habitat for old forest species including NSO, northern goshawk (*Accipiter gentilis*), and pileated woodpecker (*Dryocopus pileatus*) needs to address the sustainability and continuous recruitment of that habitat. The revised recovery plan for the NSO (USFWS 2011) has called for an active management approach for sustaining and recruiting old forest habitats in fire-prone forests of eastern Washington and Oregon. Similar considerations are also an issue for species outside of the range of the NSO, particularly northern goshawks and pileated woodpeckers.

Forest environments throughout the east side are ecologically and physiographically variable: rates of change in forest conditions and effects of historical influences vary with forest type, cultural geography, and physiographic region. Although broad-scale direction can have value at times, one-size-fits-all solutions generally will not work. Instead, considerations of local conditions, land use histories, and biophysical and landuse classifications can help address this variability.

Managers report that maps of forest types across the east side are inconsistent in their classifications of vegetation associations. This creates a significant challenge for managing that vegetation for myriad uses and habitats. Managers also lack adequately detailed characterizations of how each forest type has been affected by natural, human, and climatic influences.

The relative merits of active versus passive management of forests to achieve ecological and socioeconomic goals are subject to fierce debate, which is driven by wide-ranging and often competing or conflicting societal values and is not likely to subside. Many citizens have expectations for sustainable delivery of ecosystem services from forests on public lands. Delivery is confounded by uncertainties regarding the long- versus short-term effects of various management practices on goods, services, and values.

In the Western United States, Forest Service priorities focus on restoring ecosystems, managing wildland fires, and strengthening communities while providing jobs (Chief of the Forest Service address to the Pinchot Institute, 2013). Restoration on public lands[1] implies reenabling forests and grasslands and their associated species to adequately cope with increased climate-related stresses, and enhancing their recovery from climate-related disturbances, while continuing delivery of forest-derived values, goods, and services to citizens. **A central purpose of restoration then is to reestablish the adaptive and resilient capacities of landscapes and ecosystems in each unique physiographic region. A second, related purpose is to restore the adaptive capacity and social resilience of associated human communities, while restoring ecological systems.** The first purpose is served by restoring ecological patterns and processes that are in synchrony with the biota, geology, and climate. The second is served by enabling human communities to derive benefit from forest goods and services while conducting restoration and maintenance activities.

A central purpose of restoration is to reestablish the adaptive and resilient capacities of landscapes and ecosystems in each unique physiographic region.

[1] The USDA Forest Service has defined restoration as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed. Ecological restoration focuses on reestablishing the composition, structure, pattern, and ecological processes necessary to facilitate terrestrial and aquatic ecosystem sustainability, resilience, and health under current and future conditions" (USDA FS 2013).

The concept of restoration includes, but is larger than, the goal of reestablishing the historical range of variability (HRV). A process-oriented approach supports restoring ranges of conditions that have occurred in the past (e.g., eradicating invasive species and reconnecting fragmented habitats of threatened or endangered species), in environments where the future climate will strongly resemble the recent climate, and where the results are socially understood and acceptable. Where the future climate is not expected to resemble the recent climate, the objective of ecological restoration would be to create resilient forests and rangelands that are adapted to the future climate. This idea is captured in the related notion of future range of variability, or FRV, as coined by several authors (Binkley and Duncan 2010, Hessburg et al. 2013, Keane et al. 2009, Moritz et al. 2011, Weins et al. 2012). In addition to being forward-looking, contemporary concepts of ecological restoration may emphasize social context and the connectivity and interactions among people, societies, and the biophysical elements of ecosystems. For some landscapes, it will simply be impossible and inadvisable to return them to prior conditions (Harris et al. 2006), while for others it may be well advised.

To effectively implement restoration goals across eastside mixed-conifer forests, managers can consider applying already completed assessments of conditions across the eastside landscape (e.g., the Interior Columbia Basin Ecosystem Management Project and Eastside Forest Ecosystem Health assessments), perhaps expanding on them, and then prioritizing the location and nature of treatments that would be most beneficial to ecosystems and to people. This will involve both regional and local landscape assessment.

In some places, there may be a need to increase the pace and scale of restoration to address a variety of immediate threats—including fire, climate change, bark beetle infestations, and others—for the health of public forest ecosystems, watersheds, and natural-resource-dependent communities. However, for these efforts to be sustainable, both ecological and socioeconomic vantage points would be best considered in the context of regional and local landscape patterns and processes, because in the long run the natural system must support the social system.

Structure of This Report—Where to Find Sections of Interest

Overview of contents—This report progresses from a review of the relevant science to a presentation of management considerations.

Chapter 2 discusses how MMC types fit within a regional coniferous mosaic. In this chapter, the reader will understand our definition of MMC forests, what forest types are typically included within this classification, and generally where they are located.

Chapter 3 presents ecological concepts that are foundational to landscape restoration.

Chapter 4 explains and summarizes the detailed scientific information that constitutes our synthesis. We provide a large number of citations to guide the reader through the scientific literature. Major findings are also summarized in chapter 4. Appendix 3 is provided to complement chapters 4 and 5.

Chapter 5 is the core of this report, in which the reader will find relevant management concepts gleaned from the scientific literature. We also provide a list of considerations that can help guide a landscape evaluation process. This list arises from recent experiences of eastside land managers who have adopted a landscape perspective and are conducting landscape evaluations. Silvicultural options and innovations are discussed as they relate to landscape prescriptions and their component stand-level prescriptions. We also present ideas about adjustments that may help increase institutional capacity to implement the ideas contained in this report. We close this section with an overview of the socioeconomic conditions that underlie most land management decisions.

Chapter 6 provides a brief discussion of the important institutional considerations that influence how these concepts might be implemented. This chapter also presents a summary discussion on the socioeconomic issues that are clearly in the foreground of any management strategy that seeks to restore lands and resources.

Chapter 7 provides brief conclusions and summary thoughts about how our findings may be incorporated into land management and project-level plans.

Chapter 2—Definition of Moist Mixed-Conifer Forests and the Regional Context

Moist mixed-conifer (MMC) forests are diverse and cover a large area east of the crest of the Cascade Range in Oregon and Washington, where grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) are the potential late-successional (climax) tree species (fig. 3). These forests grow in environments that are subsets of the white fir–grand fir and Douglas-fir "series," broad potential vegetation types used by Forest Service managers (Powell et al. 2007, Simpson 2007) to characterize the land's general ecological and vegetative capability.

Depending upon the environment and local site climate, patches of MMC forest typically occur where the current vegetation (not necessarily the same as potential natural vegetation or the vegetation that would develop under historical fire regimes) is a mixture of shade-intolerant ponderosa pine (*Pinus ponderosa*



Tom Spies

Figure 3—A mixed-conifer forest with overstory of ponderosa pine and patchy understory of post-1900 grand fir on the Sisters Ranger District, Deschutes National Forest, central Oregon.

Lawson & C. Lawson) or western larch (*Larix occidentalis* Nutt.), and shade-tolerant Douglas-fir, white or grand fir, and occasionally Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), as in the moist grand fir zone of the Blue Mountains (Powell 2007). In areas of complex, dissected topography, the MMC forest intermingles with ponderosa pine and dry mixed-conifer types and wetter or cooler conifer types (fig. 4) (Powell et al. 2007, Simpson 2007). Other conifers occasionally associated with MMC forest include lodgepole pine (*Pinus contorta* Douglas ex Loudon), western white pine (*Pinus* monticola Douglas ex D. Don), sugar pine (*Pinus lambertiana* Douglas), Shasta red fir (*Abies magnifica* A. Murray bis), Pacific silver fir (*Abies* amabilis (Douglas ex Loudon) Douglas ex Forbes), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Dry ponderosa pine and dry mixed-conifer conditions tend to occupy lower montane settings, ridgetops, and southern exposures, whereas MMC conditions typically occur in mid to upper montane settings; on northerly and sometimes southerly aspects, especially in the upper elevations; in valley bottoms; and in lower headwall positions.

The focus of this report is not so much about forests of a particular moisture class, but mixed-conifer forests where fire exclusion has altered forest composition, structure, and function from their historical range of variability. Wetter mixed-conifer forests with longer fire return intervals may also have restoration needs, but these typically are not associated with changed fire regimes and thus are not examined in this report. The historical vegetation of MMC forest was controlled by frequent to moderately frequent fires (<20 to 50 years) that burned with mixed severity, containing both low- and high-severity patches. In most parts of the MMC forest, this fire frequency has been suspended, and disturbance regimes have been altered through a combination of historical drivers including grazing, loss of Native American fire ignitions, and active fire suppression. Consequently, the current MMC forest vegetation contains a significantly greater component of shade-tolerant tree species (e.g., white or grand fir or understory Douglas-fir) than occurred in the historical vegetation. Under historical or more fire- and drought-resilient states, these shade-tolerant species would have been less common in the understory in many areas, and large fire-resilient ponderosa pine, Douglas-fir, and western larch would have dominated the canopy layer. See appendix 3 for additional information about the variety of historical forest conditions that occurred in the Blue Mountains forest province early in the 20th century. Data are adapted from the Interior Columbia Basin Assessment (Hessburg et al. 1999a, 2000a).

Dry mixed-conifer and ponderosa pine sites (ponderosa pine series, or drier grand-fir/white or Douglas-fir subseries) typically experienced frequent fire return intervals (10 to 25 years), and exhibited a relatively open forest structure. Wetter



Miles Hemstrom

Figure 4—Dry mixed-conifer and pine-oak, grading into moist mixed-conifer in a drainage, Columbia River Gorge, near Rowena, Oregon.

and cooler mixed-conifer sites experienced longer fire return intervals (>50 years), and greater frequency of higher severity fire, and would have had a component of older shade-tolerant trees in the overstory, with dense areas of multistoried forest. Because few detailed fire history studies exist for the mixed-conifer forest in general, we use potential vegetation types (PVTs, see discussion below) as a surrogate for the fire regime and the degree to which mixed-conifer forests have departed in terms of composition and structure. These potential natural vegetation types, which include both series and approximations of subseries (e.g., dry, dry-moist, moist, and moist to wet variants of grand, white, and Douglas-fir series) can be a starting place for identifying the environments and locations of MMC forest (table 1). The PVTs used by managers (e.g., series, subseries, and plant associations) are often the best available source of local information, but are only an approximate surrogate for the fire regime of a site or local landscape. Figure 5 illustrates the continuum of forest types found along an elevational gradient on the east side of the Cascade Range and the relationship of forest type to general fire regimes.

Table 1—Area of major forest potential vegetation types in eastern Oregon and Washington

	All ownerships	Federal lands			Nonfederal
		Wilderness	Other	Total	
			Hectares		
Potential vegetation type:					
Douglas-fir (dry)	1 818 129	57 050	740 450	797 500	1, 020 629
Grand fir/mixed conifer (cool/moist)	1 654 634	169 229	929 871	1 099 100	555 534
Grand fir (warm/dry)	433 195	24 283	335 693	359 977	73 218
Mixed conifer (cold/dry)	98 149	3056	73 966	77 022	21 127
Mixed conifer (dry)	1 096 662	15 495	442 618	458 114	638 548
Lodgepole pine	180 526	1646	114 442	116 087	64 439
Mountain hemlock	505 756	171 993	225 136	397 129	108 627
Pacific silver fir	172 084	59 154	84 780	143 934	28 150
Ponderosa pine	1 804 724	10 645	1 040 868	1 051 514	753 210
Subalpine fir	616 773	172 152	343 853	516 005	100 768
Western hemlock	304 794	10 214	180 064	190 278	114 516
Other potential vegetation types	18 675 361			6 136 634	12 538 727
Total	27 360 787			11 343 294	16 017 493

Source: the Integrated Landscape Assessment Project.

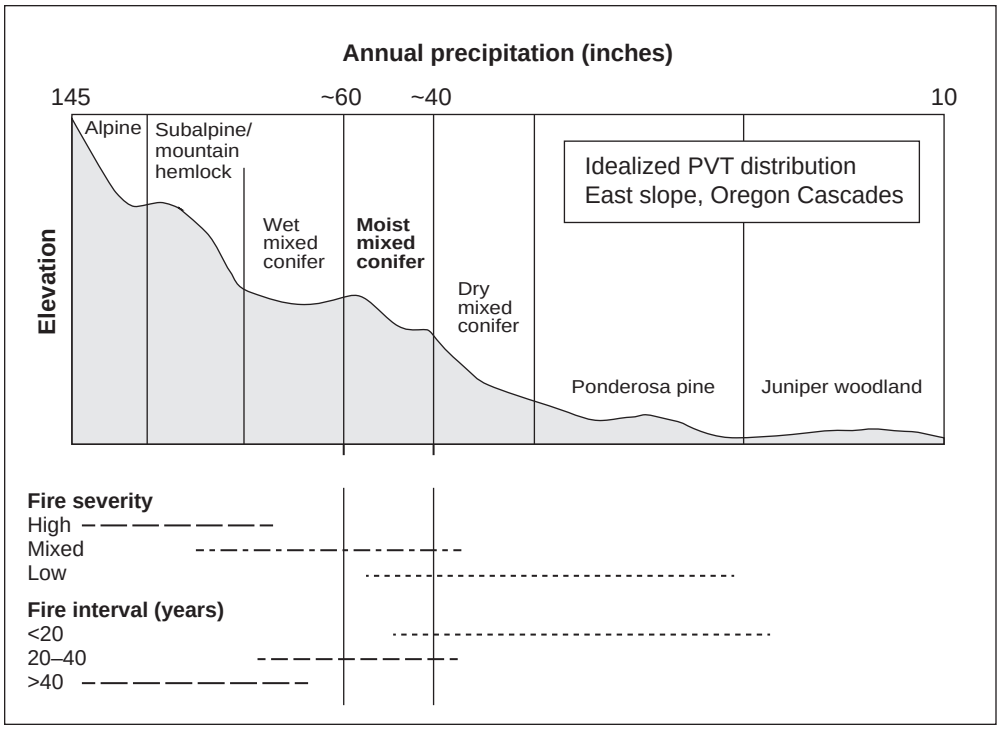


Figure 5—Continuum of forest types found along an elevational gradient on the east side of the Cascade Range and the relationship of forest type to general fire regimes. PVT = potential vegetation type.

Variation in slope, topographic position, and landscape context can create a high degree of variation in fire regimes within the same PVT. For example, for a given PVT, areas with steep or concave slopes often experience more high-severity fire than gentler and more convex slopes. Likewise, MMC PVT patches embedded within large dry forest patches or adjacent to grass or shrub patches may experience a higher fire frequency than they would if they were embedded in MMC forest. Context matters, and is critical to interpreting the native fire regime. Final determination of MMC forest for restoration purposes should be based on landscape context, local environment, and disturbance history. Figure 6 provides a conceptual model of the complex ecological setting in which we find MMC forests. There are many biological and physical conditions that will influence what kind of vegetation is found at a site.

Variation in slope, topographic position, and landscape context can create a high degree of variation in fire regimes within the same potential vegetation type.

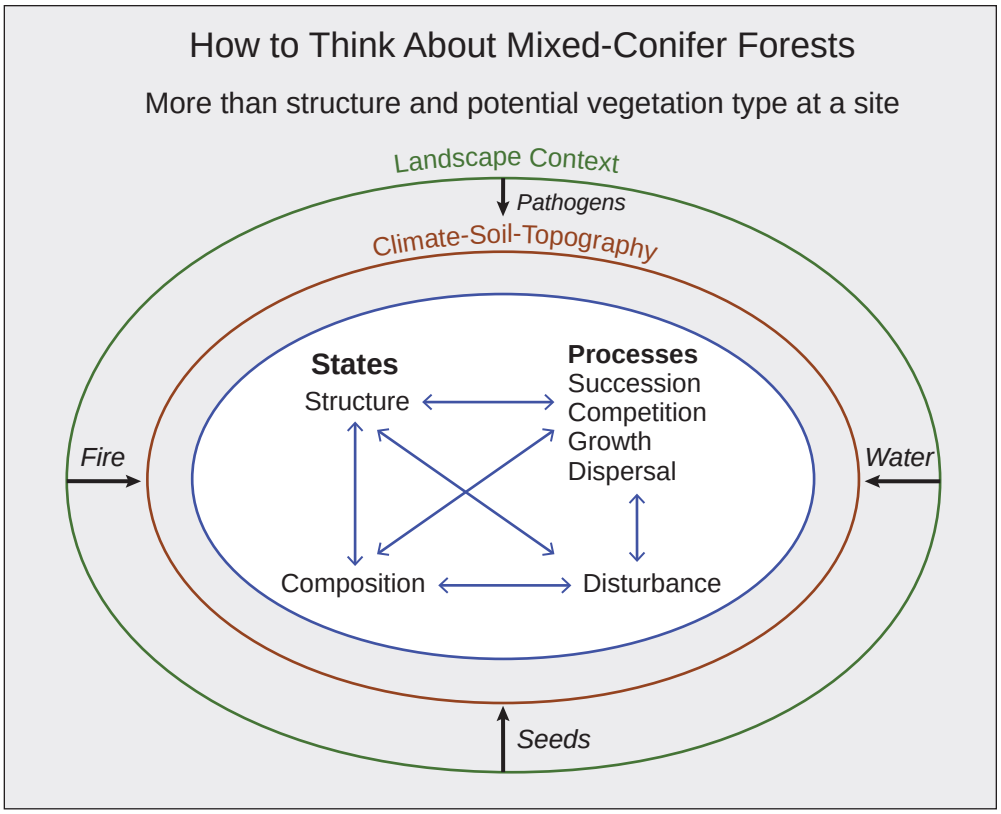


Figure 6—Conceptual model of the complex ecological setting of moist mixed-conifer forests.

The MMC type is widely distributed across the east side (fig. 7) occupying particular environments and elevations along the east slope of the Cascade Range and large patches within the northern and central portions of the Blue Mountains. It often is sandwiched between the drier mixed-conifer and pine types and cooler and wetter mixed-conifer types. Figure 7 is intended to give a general depiction of the distribution of MMC forest. No standard, peer-reviewed maps of dry, moist, or wet PVTs exist for the entire region. See "Ecological Composition, Patterns, and Processes Prior to Euro-American Settlement (Before About 1850)" in chapter 4 for more details on sources of regional information and details on vegetation in general.

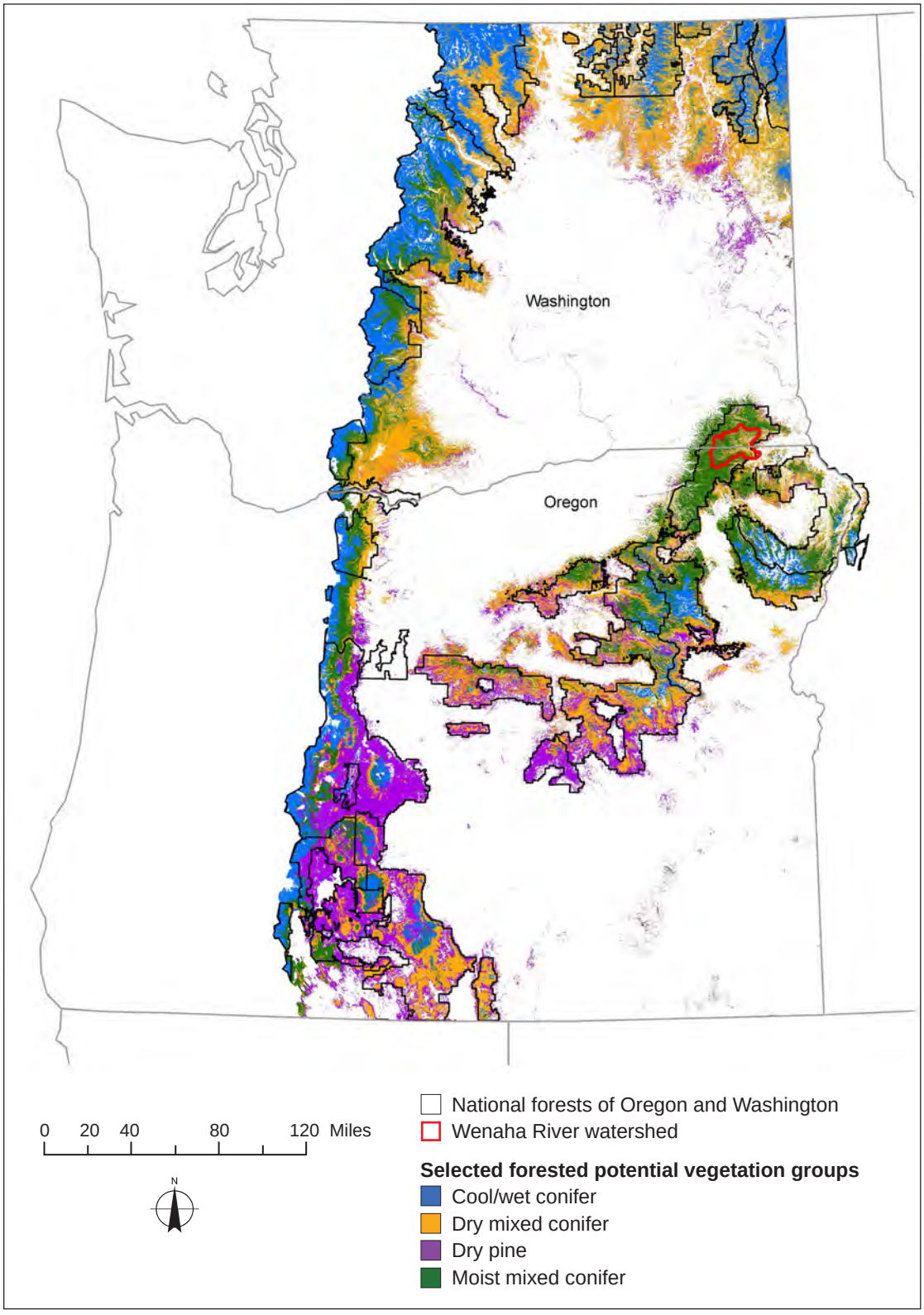


Figure 7—Map of selected potential vegetation types that support mixed-conifer forests in eastern Oregon and Washington, using data from the Integrated Landscape Assessment Project (Pacific Northwest Research Station and Oregon State University).

Chapter 3—Ecological Principles of Restoration and Landscapes

Restoration of ecological processes and patterns requires a multi-scale spatial and temporal perspective. Historically, the forests in eastern Oregon and Washington were diverse and complex in their species composition and structure (e.g., tree sizes, ages, density, layering, clumpiness). These patterns influenced the frequency, severity, and spatial extent of native insect, disease, wildfire, and abiotic disturbance processes such that signature "disturbance regimes" were apparent. However, a century or more of management has significantly altered patterns of structure and composition, and as a direct consequence, the associated disturbance regimes are highly altered as well. Figure 8 illustrates the large disparity in historical vs. current species composition and structure of forests in eastern Oregon and Washington.

Moist mixed-conifer (MMC) forests were and continue to be hierarchically structured systems with complex interactions between spatial scales. Part of what concerns us today is uncertainty driven by these cross-scale disturbance interactions. For example, very large wildfires, insect outbreaks, and changes in winter

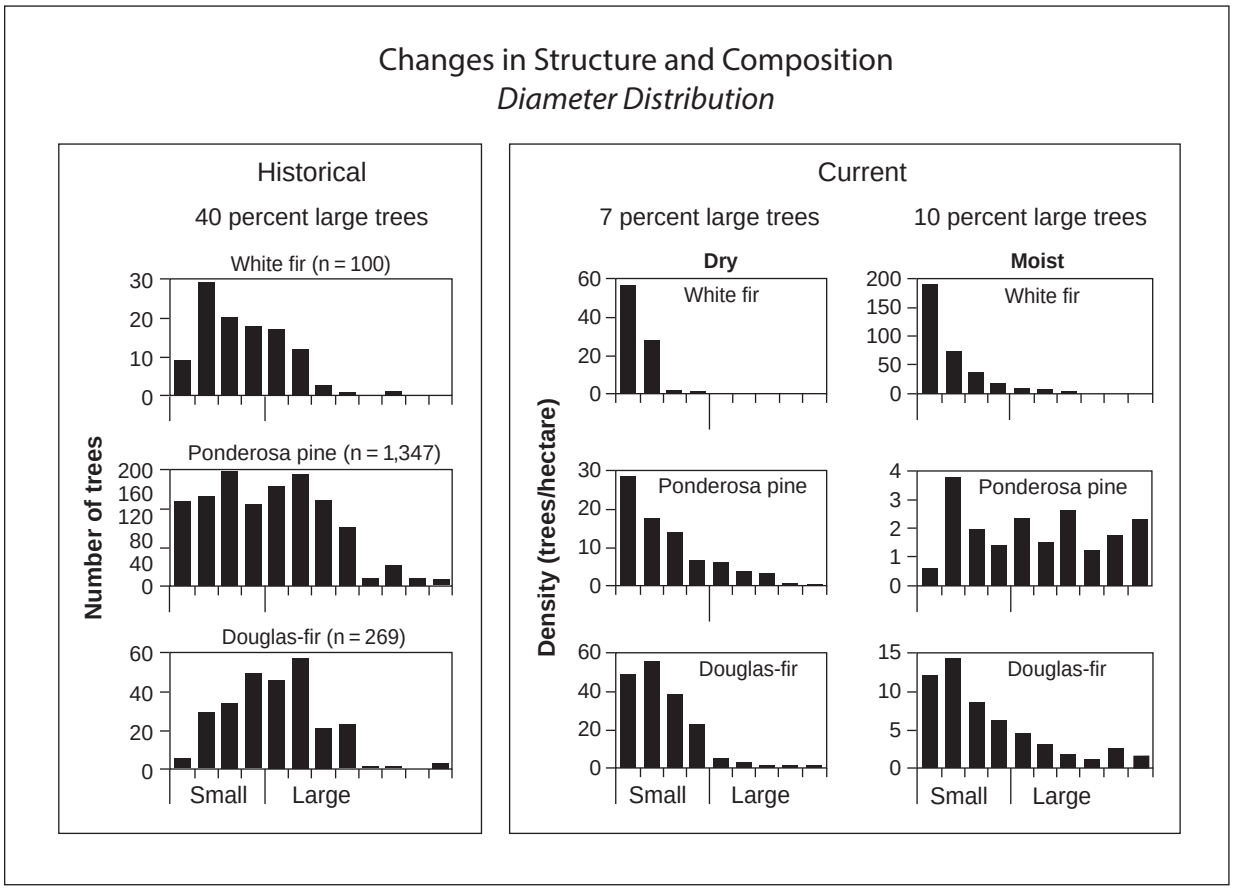


Figure 8—Disparity in historical vs. current species composition and structure of forests in eastern Oregon and Washington.

snowpack and hydrology occurring at a regional scale threaten to alter meso-scale patterns and disturbance processes of local landscapes. Simply working at meso-scale (local landscapes, e.g., watersheds and subwatersheds) does not address these concerns. The answer lies in regional- or ecoregional-scale solutions.

At a meso-scale, patterns of forest structure and composition emerge, which are primarily maintained by interactions among environments, topography, weather, soils, geomorphology, and disturbances. But other broader and finer scale patterns also exist, and these are also influential to maintaining and changing meso-scale vegetation patterns over space and through time.

Forest ecosystem responses to disturbances or weather changes are often nonlinear, or involve complex feedback loops or time lags, particularly when we allow for longer observation periods.

Forest ecosystem responses to disturbances or weather changes are often nonlinear, or involve complex feedback loops or time lags, particularly when we allow for longer observation periods. Thus, some interactions are relatively more unpredictable and may not manifest in any sort of change in the short term, until some kind of threshold is reached (Malamud et al 1998, Moritz et al. 2013, Peterson 2002). The challenge for scientists and managers seeking to restore landscape resilience is to develop a better understanding of ecological complexity that can more readily be translated into practical strategies for restoration.

Our review of recent theory, observation, and understanding in the field of landscape ecology shows it is critical to consider long-term spatial and temporal phenomena prior to drawing conclusions or developing simplified decision rules based solely on temporally short or narrow geographic observation windows.

The Concept of Resilience

The concept of resilience promises a robust alternative to management goals based on static conditions or simple applications of the historical range of variability.

The resilience of current and future forest ecosystems is a major concern of land managers today. The concept of resilience promises a robust alternative to management goals based on static conditions or simple applications of the historical range of variability (HRV). However, resilience is not an easily defined concept in a practical sense (Gunderson 2000). Furthermore, operational metrics of resilience have received little attention to date (Carpenter et al. 2001). To become more operational, resilience must be defined in terms of specific system attributes and in relation to specific disturbances or perturbations. It is important to understand that resilience is a relative term and is constrained by space and especially time. Eventually change will be significant enough that a previously resilient system will reset itself into a new state. Thus, some bounding of space and time is necessary to define resilient states.

Folke (2006) and Gunderson (2000) have identified three conceptual domains of resilience: (1) engineering resilience, which focuses on recovery or return time to a stable equilibrium (e.g., return to a particular forest structure or composition); (2) ecological resilience, which focuses on maintaining function and persistence with multiple equilibria (e.g., HRV); and (3) socioecological resilience, which focuses on reorganization, adaptive capacity, and multiscale interactions among the many community members, stakeholders, and responsible government organizations that have an interest in the outcome of land management. Although we focus mainly on ecological resilience in this report, we acknowledge that the ecological system is imbedded in a socioeconomic system that interacts with ecological systems.

The degree of alteration of an ecosystem and its dynamics (patterns of change over time and space) must be understood before we can consider if and how the system can be restored (fig. 9).

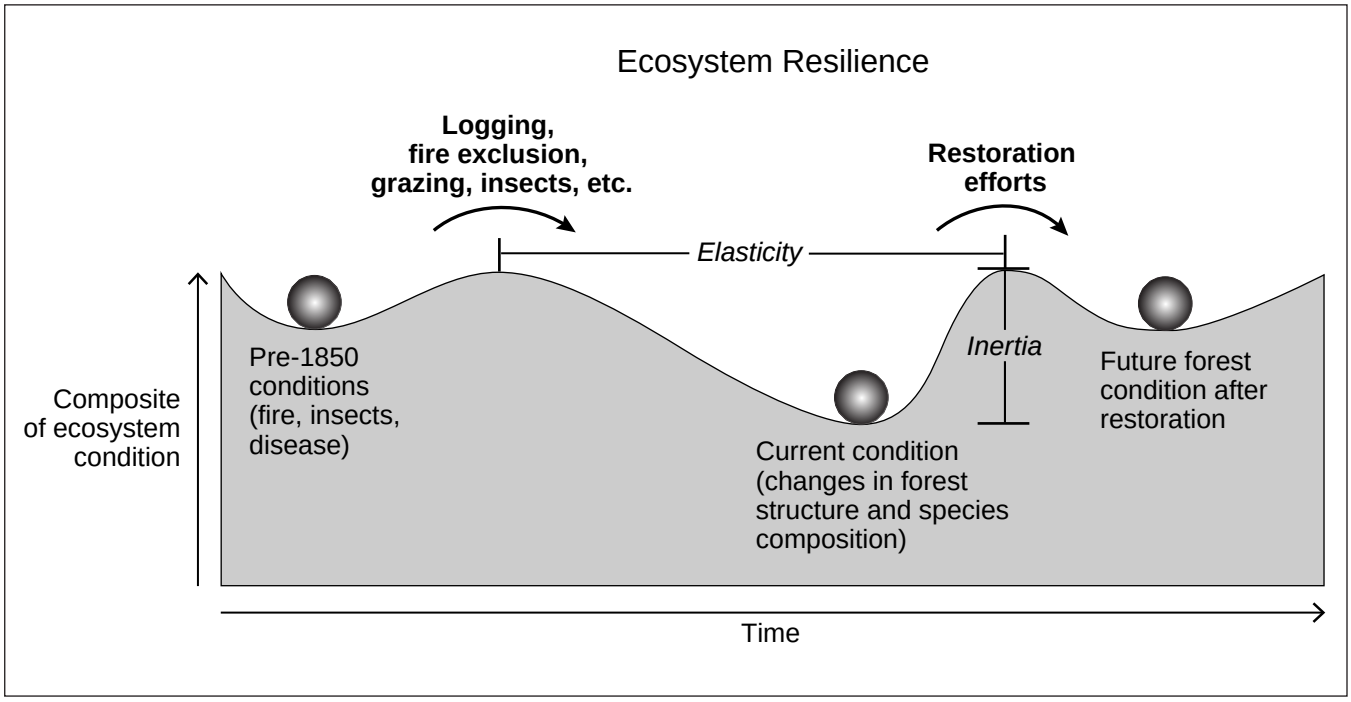


Figure 9—Ball and cup heuristic of ecosystem stability (adapted from Gunderson 2000). Valleys represent the boundaries in which ecosystems are coping with disturbances, balls represent the ecosystem, and arrows represent disturbances. Some disturbances push the system out of a past "stable" state into a different ecosystem condition. The influences of inertia and elasticity are indicated in the diagram.

Westman (1978) suggested five characteristics that depict the potential resilience of a system:

Inertia: The resistance of a system to disturbance.

Elasticity: The speed with which a system returns after disturbance.

Amplitude: A measure of how far a system can be moved from a previous state and still return.

Hysteresis: The lagging of an effect behind its cause, such as delayed response of the system to a disturbance.

Malleability: The difference between the pre- and postdisturbance conditions. The greater or lesser the malleability, the lesser or greater will be the system's resilience.

These technical terms from systems analysis illustrate the complexity of system responses to change and the challenge of restoring dynamic systems. The characteristics of resilience described here are not all measured with equal ease; some may simply be immeasurable in a short period because of a lack of historical data or reliable ecosystem models (Westman 1978). Given these limitations on data availability and the overall understanding of ecosystem interactions, we are reminded of a compelling need to employ an adaptive management approach in both research and monitoring, where we can track the results of management efforts and follow disturbances and recovery efforts over a long term. This would give managers the ability to inform subsequent management decisions with what was learned from previous management decisions and thus make appropriate adjustments. It also suggests the value and need for ecosystem models and tools that can include consideration and measurement of both inertia and resilience. Early versions of these tools have given us a better understanding of the complex dynamics of forest ecosystems and, in turn, how we can craft management strategies to achieve desired outcomes. In short, management for ecosystem resilience necessitates iterative steps to allow for adjustments at each juncture of trial and learning.

Resilience does not always result in desirable conditions on the land (Folke 2006). Degraded and nonnative vegetation can also be resilient in its own way; e.g., landscapes dominated by cheatgrass (*Bromus tectorum* L.), which is generally considered undesirable, can be resilient in the face of restoration efforts by land managers. In this example, managers have experienced significant difficulties attempting to restore sagebrush steppe ecosystems invaded by cheatgrass (Chambers et al. 2009, D'Antonio et al. 2009).

Landscapes often have considerable inertia because of alterations of pattern and process after more than a century of human activity. For example, Wallin et al. (1994) found that landscape patterns generated by past forest management or disturbance can take decades or centuries to restore (see also Heinselman 1973). Hysteresis (in a large dose) can operate in altered landscapes to create undesirable resilience or a delay in desired response to management. For example, the widespread accumulation of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and, to a lesser degree, grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) across many eastside landscapes now means that disturbance patches created by management or wildfire are more likely to regenerate to Douglas-fir and grand fir than they would have in the recent past. These relations can create significant challenges in executing successful restoration because of the large scale of the effect.

Ecological Principles for Landscape Planning and Management

Our perspective on the scientific principles underlying restoration of landscape resilience in eastside landscapes is based on three central ideas: (1) the biophysical environment (i.e., vegetation, climate, geology, and topography) and disturbances interact to control system behavior at several key spatial and temporal scales; (2) Euro-American activities have altered these ecological interactions and reduced landscape resilience; and (3) increasing resilience of desired conditions requires management actions that restore processes and patterns at these key scales. Without a broad geographic and ecosystem perspective that includes the past, present, and future role of humans and the climate, it will be impossible to restore resilient forests across a wide range of ecoregions and landscapes. Such a systems view should enable more effective application of treatments to meet restoration or resilience goals.

We use the terms **local** and **regional** to describe landscapes. We define local landscapes as variably sized areas, typically ranging in size from one to several subwatersheds (hydrologic unit code [HUC] 6 or 12-digit watersheds) (Sieber et al. 1987) (see also the National Hydrography Dataset at http://nhd.usgs.gov/), or a watershed (HUC 5 or 10-digit watershed). These subwatersheds collectively reside in a single ecological subregion (sensu Hessburg et al. 2000a), and exhibit characteristic patchworks of successional stages and topography consistent with the climate, biota, physical processes, and disturbance regimes of that subregion. Subwatersheds (i.e., HUC level 6) typically range in size from about 10,000 to 40,000 ac (4050 to 16 200 ha), but larger and smaller subwatersheds also occur. We define a regional landscape as the complete collection of all local landscapes that comprise an ecological subregion.

We define (local or regional) landscape resilience as the capacity of the ecosystems to absorb disturbance and climate change while reorganizing and changing but essentially retaining the same function, structure, identity, and feedbacks (adapted from Walker et al. 2004). Resilient landscapes maintain a dynamic range of species, vegetation patterns, and patch size distributions (broad- or meso-scale) that emerge under the constraints of the climate, geology, disturbance regimes, and biota of the area.

We are motivated by eight core ecological principles that are foundational to restoring eastside forests, including moist mixed-conifer forests.

In this chapter, we outline eight core ecological principles that are foundational to restoring eastside forests, including MMC forests. We expand on these in later chapters; however, our aim here is to highlight key ideas that motivate our thinking.

Physical and biological elements of an ecosystem interweave, creating distinctive patterns on a landscape. Climate, interacting with vegetation, disturbance, topography, soils, and geomorphology created domains of ecosystem behavior at local and regional landscape scales. During every historical climate period, a range of patterns and patch sizes of forest successional stages likely emerged. This emergent natural phenomenon is referred to as the natural range of variation (NRV), also referred to as the HRV. As the climate shifted, so did the NRV. The notion of a static NRV is a common misperception and provides a misleading objective for land managers. It does not exist. Prolonged periods of warming or cooling, wetting or drying, or combinations of these have occurred repeatedly over time. Whenever these changes have happened, they have pushed the NRV in new directions. But sudden and extensive shifts in the NRV were typically constrained, except under the most extreme climatic circumstances, by the lagged landscape memory encoded in existing patterns of living and dead vegetation. This is the quality of a natural system that we represent as landscape resilience.

Vegetation dynamics and fire regimes of MMC forests were and are among the most variable. In the historical forest, this forest type exhibited low-, mixed-, and high-severity fires; the amount of each severity type varied with the climate regime, and by physiographic region. Patterns of vegetation structure and composition and fire frequency and severity changed gradually across landscapes with variation in climate and the impacts of settlement and early management. But before management, fire regimes of MMC forests were variable, depending on topography and ecoregion. In some locations, fires occurred relatively frequently (every 10 to 30 years), in others, fire frequency was more variable (25 to 75 years). In the former, fire severity would have been primarily low- and mixed-severity, with surface fire effects dominating. In the latter case, fire severity would be primarily mixed- and high-severity, with active and passive crown fire effects dominating. In some ecoregions, the fire regimes and tree composition of the dry ponderosa pine, dry

mixed conifer, and MMC types were quite similar and there were no clear lines of demarcation. In others, the differences in these types in terms of aspect orientation, tree density, layering, and species mixes were pronounced. With the advent of fire suppression, understories of the ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and dry mixed-conifer forests were in-filled largely by ponderosa pine and shade intolerant Douglas-fir, respectively, but the MMC forests were in-filled by grand or white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) and Douglas-fir. Grand fir and Douglas-fir understories may have been transient in some historical MMC forests: if they got established during a period without fires, they may or may not have been eliminated by subsequent frequent low-severity fires. During longer intervals between fires, significant fuel ladders may have developed and mixed-severity fire effects would have been typical. On wet mixed-conifer forest sites, shade-tolerant tree species were persistent and fire intervals were long enough to allow development of old shade-tolerant trees and larger patches of dense multilayered forests within stands and landscapes.

Eastside forest patterns and influential processes are constantly shifting over space and time. However, topography, soils, and elevation constrain these patterns and provide a relatively simple template for understanding and managing landscapes for them. As a first approximation, the topographic and edaphic patterns of landscapes provide a natural template for pattern modification and restoration. For example, spatial patterns of ridges and valleys, and north- and south-facing aspects, strongly represent characteristic patterns and size distributions of historical vegetation patches. North-facing aspects and valley bottoms historically supported the densest and most complex forest structures, and when fires occurred, these sites experienced more severe fire behavior than south-facing aspects and ridges, owing to site climate and growing season factors. The same is true today. In contrast, south-facing aspects and ridges tended to burn more often and less severely than north-facing aspects and valleys. Wildfire conditions in summer were typically drier and fine fuels were conditioned for burning, even during average summer burn conditions.

Ecosystems and their component parts are organized in an interactive, hierarchical arrangement. Processes associated with the regional landscape exert a measure of control over patch dynamics of local landscapes, and ultimately, some fine-scale patterns and processes within patches. For this reason, no forest type, its disturbance regime, or its variation may be thought of in isolation. Some landscapes are dominated by one topographic aspect (e.g., north- or south-facing); consequently, vegetation on minor aspects may be different than would otherwise be expected from knowledge of their site conditions alone. In landscapes with more

southerly aspects and ridges, corresponding northerly aspects typically also see more frequent fires and lower than typical severity. Knowledge of specific context and scale can help guide patch-level decisions.

Postsettlement human activities have resulted in increasingly homogenized forests and, in turn, significant changes in the scope and effects of natural disturbances. Widespread human-caused changes to vegetation structure, composition, and fuelbeds have created more homogenized conditions in the MMC forest, generally in the form of large, dense, and multilayered patches of intermediate-aged fire-intolerant tree species. These changes have increased the area and frequency of large, high-severity fire patches, and the extent and frequency of other biotic disturbances (e.g., bark beetle and budworm outbreaks). The changes have also substantially altered the resilience mechanisms associated with the native forests. Climate and the characteristic disturbance regimes and landscape patterns regulated the composition, frequency, and size of the largest patches. Prior to Euro-American settlement, local and regional landscapes had developed over a period long enough for coarse and fine-scale patterns and species composition to be in some degree of synchrony with their physical environments and the climate system. Much of this synchrony has been lost through the cumulative effects of relatively recent human activities on the landscape. Current and future fire regimes and landscape patterns are on new trajectories trending away from a previously established resilience. To restore this coupling between patterns and processes (wildfire, insects, pathogens, and weather), forest structure, composition, and landscape patterns must be modified at a scale that is consistent with the scale of the current vulnerabilities. Pattern modifications should be consistent with the inherent disturbance regimes of large landscapes and forest types, and with the climate regime.

Rare ecological events can have a disproportionately large effect on ecosystems. Rare, large-scale events (disturbance, climatic, biotic, geologic) can significantly affect future landscape dynamics, especially if their frequency, size, or severity are unprecedented for the climatic, biotic, and environmental conditions. Large wildfires, dramatic climatic extremes, rapid changes in plant and animal species distributions, and large insect outbreaks are examples of natural and human-caused events that are rare but can have a strong and lasting effect on future landscape patterns and processes. Typically, these events are hard to predict and some are outside the control of managers. Nevertheless, they shape current landscapes and can be anticipated when developing and gaging the extent and timing of risk mitigation strategies. To a modest degree, managers can, through cumulative smaller actions, prepare landscapes in a manner that reduces the likelihood or impact of these large and rare events. However, to be effective, the timing and extent of the actions must match the level of inertia that supports the large-scale

events. For example, large areas of eastern Oregon and Washington are susceptible to chronic western spruce budworm (*Choristoneura occidentalis*) infestation owing to the wide prevalence of Douglas-fir, grand fir, and white fir in large, dense, multilayered patches. Changing this situation would require the reduction in the prevalence, complex layering, and density of these host tree species over a very large area to match the scale of the vulnerability to this disturbance.

Resilience depends on ecological heterogeneity and varies with spatial and temporal scale. At no time were all patches of a landscape resistant to fires or other disturbances. At any given time, some patches within a landscape were always susceptible to insect attack, stand-replacing fires, pathogen infections, or a combination of these. In some ecoregions, as much as 25 to 35 percent of the forest had been recently burned by high-severity fire, and a significant area was in an early-seral condition (grass, shrub, or seedling/sapling) or was recently burned and recovering (e.g., see the tables in app. 3). This is how forest habitats with complex structure and age classes continuously emerged on the landscape and were retained despite ongoing disturbances. In other ecoregions, where surface fire effects stemming from low- and mixed-severity fires were clearly dominant, fine-scale patterns in forest composition, structure, and tree age created a fine-scale mosaic of susceptibility to disturbance. This is how forest habitats with fine-scale structure and age classes continuously emerged on this landscape. The interplay of fine- and coarse-scale drivers (e.g., disturbance, topography, soils, and microclimate) across the regional landscape created fine-, meso-, and coarse-scale forest habitats with complex structure and age classes. In this way, local and regional landscapes, but not all stands or patches, were resilient.

Completely natural or historical landscape patterns cannot be the goal for current and future climate and landscape conditions. However, the past (e.g., HRV) can be an important guide to creating resilient forests. Knowledge of how forests and landscapes changed in response to disturbances and climate variation in the past is valuable for providing future forests and landscapes that have desired ecological patterns and processes. Where human-driven changes (e.g., fire suppression, grazing, past logging) have significantly altered forests relative to HRV, it will take significant inputs of human energy (i.e., ecologically motivated management) to create desired landscape conditions.

The size, diversity, and complexity of eastside mixed-conifer landscapes necessitate a prioritized approach to management. Though generalized, this concept, as well as those listed above, are critical to restoring resilience in these forests. These concepts have a strong ecological foundation, focus on restoring a more natural coupling of pattern and process, and can help managers create conditions that

conserve options, are adaptable, and can be implemented with available skills and abilities common on the staff of a forest or district (or equivalent). Developing this characterization of a forest, although new to contemporary forest management, is not overly difficult and will enable a much more effective treatment strategy at the stand level where managers typically do their on-the-ground work.

Topography as a Template for Landscape Heterogeneity

Previous research efforts have highlighted the predictive importance of topography (and more broadly, geomorphology) in landscape management (e.g., see Underwood et al. 2010). Studies and assessments from mixed-conifer forests (e.g., Hessburg et al. 2005, 2007; North et al. 2009; Taylor and Skinner 2003) have established that patterns of forest condition and fire behavior are strongly affected by topographic and physiographic features. Variability in soils also contributes to landscape heterogeneity, usually at a finer spatial scale. There are simple rules-of-thumb that can be gleaned from this work and applied to landscape management.

Simple partitioning of the landscape into basic topographic positions is a straightforward method for parsing the forest into subunits with different inherent growth potential and disturbance regimes.

Simple partitioning of the landscape into basic topographic positions, such as drainage bottoms, ridgetops, or south- and north-facing slopes, is a straightforward method for parsing the forest into subunits with different inherent growth potential and disturbance regimes. Aspect patches of all sizes can be used to tailor treatments to the landscape; these can be readily generated in a geographical information system (GIS). There are now a number of easy-to-use GIS tools for doing this on any landscape using standard digital elevation model (DEM) data. The following provides a brief overview of some of the insights that topography provides.

South-facing aspects and ridges tended to burn more often and less severely than north-ridges, and fine fuels were typically conditioned for burning, even during average summer burn conditions. One can imagine that ridges, with their more exposed conditions and open grown forests, provided a rather elaborate network of natural fuel breaks owing to high lightning ignition frequency and limited fuel accumulations. This was typically not the case on north-facing aspects and in valleys, hence their reduced fire frequency. Although exceptions to these generalizations abound, landscape restoration can capitalize on these general tendencies without using a one-size-fits all approach. Instead, landscape restoration can apply a rule-of-thumb approach, as follows.

Managing south-facing aspects and ridgelines. In application, southerly aspects and ridges could be managed to support fire-tolerant species in clumped and gapped distributions by: (1) favoring very large-, large-, and medium-sized trees so that they occupied, e.g., 40 to 50 percent of the tree cover in the majority of these patches, and represented, e.g., 50 to 60 percent of their total area; (2) stocking to support a dominance of surface fire behavior stemming from low- and mixed-severity fires, and tree densities that support endemic but not epidemic bark beetle populations (i.e., resulting in the mortality of only a few trees over time); (3) maintaining tree species composition that strongly discourages the spread and intensification of root diseases, while allowing their presence; and (4) maintaining stocking on south slopes and ridges by low and free thinning and similar methods, especially by prescribed burning at regular intervals. Size class and canopy cover dominance would certainly vary from place to place, but ranges of conditions could be calibrated from historical reconstructions and modified as needed by incorporating expected climate changes. Prescribed burning and thinning activities could discriminate against the most severe dwarf mistletoe infestations. This would adequately mimic historical fire influence, but allow some of the most ecologically beneficial aspects of dwarf mistletoe infestation. Where fire- and drought-tolerant species are not dominant on south slopes and ridges, managers can regenerate them using methods that are best adapted to local site conditions.

Managing north aspects and valley bottoms. In application, north aspects and valley bottoms tend to support a mix of fire-tolerant and fire-intolerant tree species in relatively dense, often multilayered arrangements. Stocking can support surface and crown fire behavior stemming from mixed- and high- with occasional low-severity fires. Landscape patchiness of denser north aspect and valley bottom forest conditions can help constrain the frequency, severity, and duration of defoliator and bark beetle outbreaks. Ideal stocking on north slopes and valleys would reflect species compositions that encourage or allow the spread of root disease as a natural process; mixed fire-tolerant and fire-intolerant species compositions should adequately restrain the spread of root diseases while allowing ecologically beneficial fine-scale habitat and forage conditions stemming from root disease centers. Stocking on north slopes and valleys may be maintained by free selection thinning or similar methods, especially where density is quite high and layering is simple. Where fire-tolerant species are not present in north-facing slopes and valley bottom settings, they may be regenerated using methods that are adapted to local site conditions, depending on other local habitat constraints. Some patches may be dominated by drought- and fire-intolerant species without harm to the larger landscape.

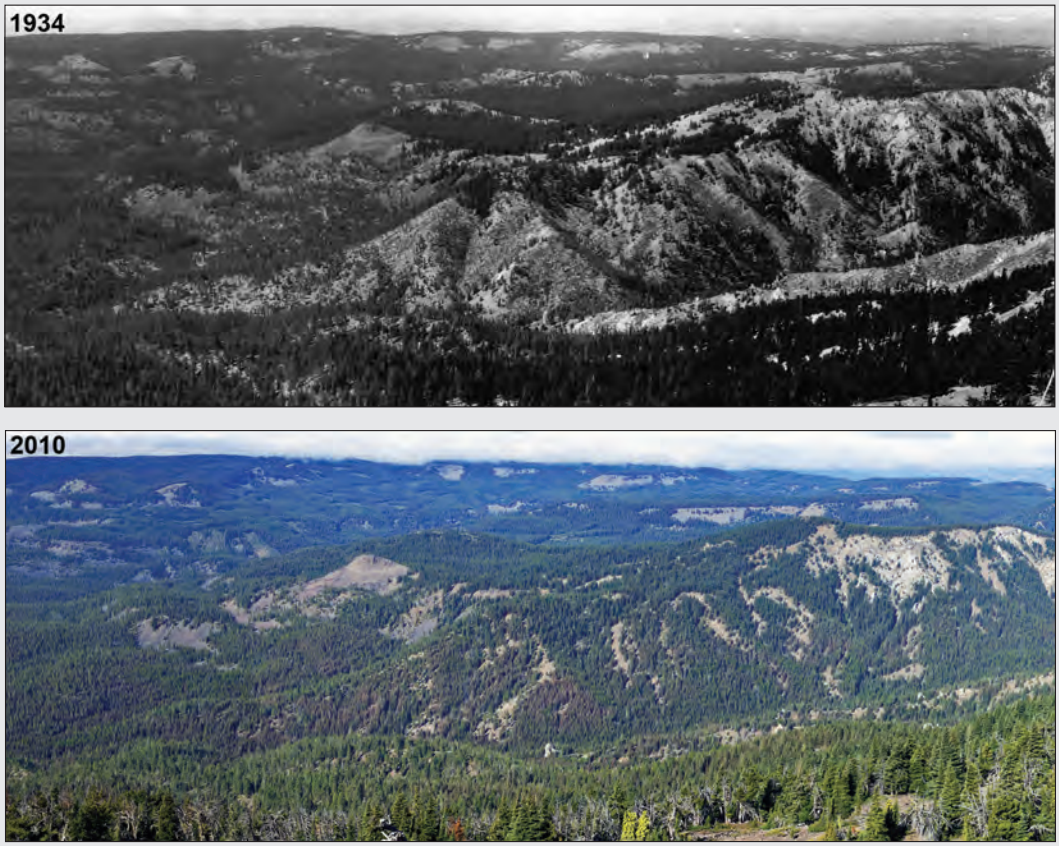
Forest types and their fire regimes are interconnected. Disturbance regimes and their variations in each forest type offered a regulating influence in adjacent but differing forest types. For this reason, no forest type and its disturbance regime and variation may be thought of in isolation. Some landscapes have significantly more north- or south-facing aspects than others;

(continued on next page)

(from page 27)

consequently, variations emerge that increase landscape complexity and these should be noted. In landscapes with more southerly aspects and ridges,north-facing aspects typically see more frequent fires and lower than typical severity. The converse is also true. These ideas can help shift the focus away from an overly simplistic topographically driven landscape template.

Figure 10 illustrates this intrinsic landscape pattern driven by topographic position with two photographs of Mission Peak on the Wenatchee National Forest. The photo from 1934 shows very little tree growth on the south-facing slopes and ridgetops with dense forest on the north-facing slopes and drainage bottoms. Because of fire exclusion, the forests have filled in as shown by the 2010 photo.



John Marshall

Figure 10—The Mission Peak area on the Okanogan-Wenatchee National Forest; a comparison between 1934 and 2010 of forest density and structure.

Chapter 4—Scientific Foundations

Ecological Composition, Patterns, and Processes Prior to Euro-American Settlement (Before About 1850)

The mountains of Oregon and Washington exert strong orographic control on climate, vegetation, disturbance, and land use across the region. Steep precipitation and temperature gradients have a significant influence on the vegetation east of the Cascade Divide (Franklin and Dyrness 1988) (fig. 11). Moist mixed-conifer (MMC) forest patches frequently occur within a broader continuum of mixed-conifer forest types (fig. 12) and within topographic locations juxtaposed with mixed conifer or ponderosa pine vegetation types, or grassland and shrubland patches (fig. 13) (Hessburg et al. 1999a, 2000b; Spies et al. 2006). This mosaic of landscape composition and physiognomic conditions can alter the disturbance regime as well as the functioning of these patches across broader spatial scales. For example, the frequent fire regimes of grassland and shrubland influence adjacent forests by increasing their fire frequency. This occurs because grass and shrub patches often function as "conveyor belts," readily spreading wildfire to adjacent patches. Likewise, dry mixed-conifer patches that experience frequent surface fires can also influence adjacent MMC patches. However, when MMC forest is surrounded by cold or wet forest types, the fire regime may be influenced by this context; and fires may tend to be less frequent and more severe.



B. Nguyen

Figure 11—At the regional scale, the moisture gradient is structured by large-scale topographic features, such as the Cascade Mountains, and a prevailing south-southwest storm track.

Illustration by Stevie Ruda

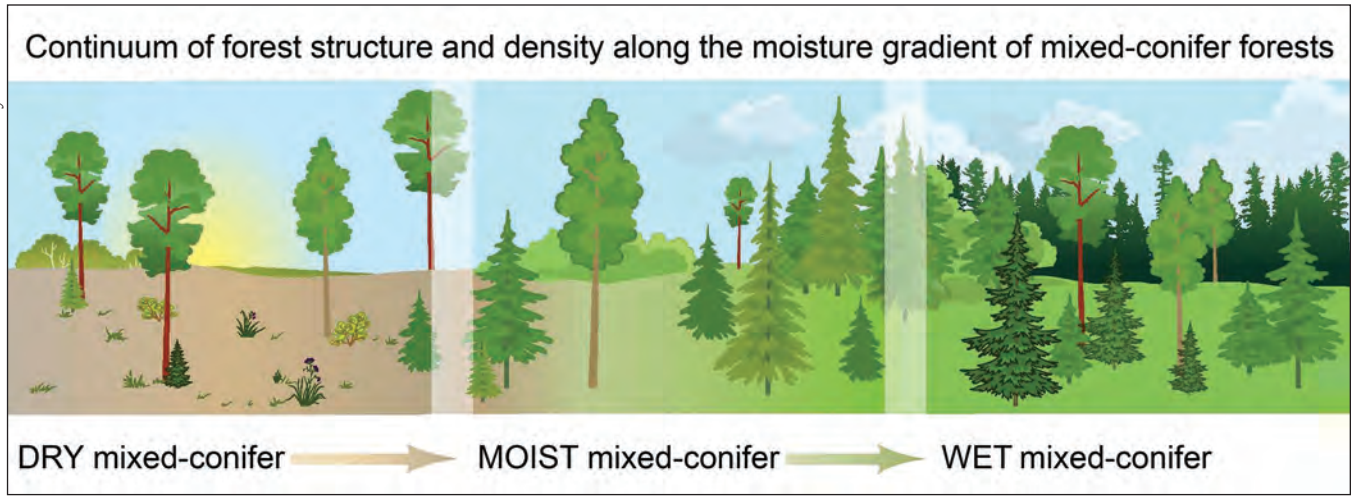


Figure 12—A simple schematic illustrating a typical landscape gradient of different forms of mixed conifer, from the dry type through the moist types to the wet types.

Miles Hemstrom



Figure 13—A common gradient of grasslands/shrublands to dry forests and moist forests. Blue Mountains near Pendleton, Oregon.

Where Is the MMC Forest Located?

No standardized, peer-reviewed maps of the potential vegetation subseries covering the MMC forest are published for the entire region. The Region 6 Area Ecology Program has developed plant association classifications and maps for individual subregion ecology areas, but the names and environmental conditions of the plant associations differ. Currently the region is using the vegetation classification represented in the Integrated Landscape Assessment Program (a partnership jointly managed by the Forest Service Pacific Northwest Research Station and Oregon State University's Institute of Natural Resources) for defining MMC forest distribution and abundance (fig. 7, table 2). The map we presented is intended solely for the purpose of initial regional-scale planning and analysis and has limited spatial accuracy for project planning. Local classifications and maps that are spatially accurate at a patch scale are more appropriate for defining the distribution of the MMC forest for project level planning and management.

Local classifications and maps that are spatially accurate at a patch scale are more appropriate for defining the distribution of the moist mixed-conifer forest for project level planning and management.

Other classification strategies also exist (e.g., Henderson et al. 2011, Simpson 2007) for vegetation zones that have resulted in different depictions of this forest type across the region. Confounding this issue, national forests often have their own local maps of potential vegetation types (PVTs) that they use for management, and the scale of these maps varies from forest to forest. These maps do not correspond to the regional maps shown here. We suggest that any future regionwide strategy for MMC forest be underpinned with a single map that uses a regionally coherent classification standard and mapping protocol. The map would accurately identify the major areas that support the MMC type, and its relation to other types. This regional map would enable cross-forest data sharing and landscape assessment and management coordination. Local forest-level maps would then be needed to estimate departure from historical dynamic and threats to forest resilience.

Mixed-Conifer Plant Association Classification

The plant associations of series associated with mixed-conifer forest can be placed into different moisture/fire regime groups using published and unpublished information (table 2). We present these as a first approximation for defining the occurrence of different mixed-conifer-disturbance regime types and aid to communication. As stated elsewhere, potential vegetation types (e.g., series, subseries, and associations) are only approximate indicators of fire regime, a concept which is best applied at landscapes scales (larger areas that are mosaics of local climate, topography, soils and vegetation).

(continued on next page)

(from page 31)

We grouped plant associations of the grand fir, Douglas-fir, and Shasta red fir (*Abies magnifica* A. Murray bis) series into subgroups based on moisture and historical fire regime: dry-low severity, moist-dry-low- to mixed-severity, moist-mixed severity, and moist to wet-high-severity (table 2). Associations in the subalpine fir and Shasta red fir series were included if ponderosa pine is an overstory component in the series or if plant association guides mentioned that low-severity fires were part of the historical fire regime. We assigned plant associations to a mixed-conifer moisture-fire regime group based on published information and expert opinion about the historical disturbance regime, environmental setting, and species composition. Plant associations in dry environments where historical fire regimes were predominately low severity and ponderosa pine was common in both the overstory and understory were classified as dry mixed-conifer.

Plant associations were classified as MMC forest if the following conditions were met: (1) mixed-severity fire regime; (2) intermediate environmental setting; and (3) Douglas-fir or grand fir are the most common understory tree species and are co-dominant in the overstory with ponderosa pine or other early-seral dominant, or those tree species are predicted to be dominant in the overstory and understory community based on the primary indicator plant species. Plant associations that could not be classified as dry or moist because of broad variability in historical disturbance regimes and species composition were classified as moist-dry. We expect the variability in the moist-dry group represents associations where dry and MMC forest intermingle on the landscape. The moist to wet classification was given to all plant associations with an infrequent, high-severity fire regime and species composition that were inconsistent with our definition of eastside mixed-conifer forest. Some of these associations would be classified as "moist" in some subregions but their historical fire regimes are still dominated by high-severity fire at relatively longer intervals. In these latter associations, ponderosa pine was usually absent in all strata; early-seral species including lodgepole pine, Douglas-fir and western larch were often even-aged; and shade-tolerant fire-intolerant species were common in the overstory. Plant associations in these moist to wet environments may still merit restoration due to past timber management activities, but fire does not play the same role as it does in dry and MMC forests, and it is unlikely that fire exclusion has modified structure, composition in these wetter types.

Table 2—Mixed-conifer plant associations grouped by moisture and approximate fire regime (app. 2)

National forest (NF)/region[a]	Vegetation series/ plant association	Extent[b]	Species composition[c]	Source[d]
Dry with low-severity fire—*characterized by low-severity fires and relatively short return intervals of less than 35 years. Natural fire regimes in order of prevalence are I, III A, III B, and IV A.*				
Blue and Ochoco Mountains	Douglas-fir/elk sedge	Widespread	PSME, PIPO, ABGR	Johnson and Clausnitzer 1992
Blue and Ochoco Mountains	Grand fir/elk sedge	Widespread	ABGR, PIPO, PSME	Johnson and Clausnitzer 1992
Blue and Ochoco Mountains	Grand fir/pinegrass	Widespread	ABGR, PIPO, PSME, LAOC, PICO	Johnson and Clausnitzer 1992 Johnson and Simon 1987
Blue and Ochoco Mountains	Grand fir/birchleaf spirea	Intermediate	ABGR, PSME, LAOC, PIPO	Johnson and Clausnitzer 1992
Blue and Ochoco Mountains	Douglas-fir/mountain snowberry	Minor	PSME, PIPO, JUOC	Johnson and Clausnitzer 1992 Johnson and Simon 1987
Blue and Ochoco Mountains	Douglas-fir/common snowberry	Widespread	PSME, PIPO, LAOC, JUOC	Johnson and Clausnitzer 1992 Johnson and Simon 1987
Blue and Ochoco Mountains	Douglas-fir/pinegrass	Widespread	PSME, PIPO, ABGR	Johnson and Clausnitzer 1992 Johnson and Simon 1987
Blue and Ochoco Mountains	Douglas-fir/birchleaf spirea	Intermediate	PSME,PIPO	Johnson and Simon 1987
Colville NF	Ponderosa pine–Douglas-fir/bluebunch wheatgrass	Minor	PIPO, PSME	Williams et al. 1995
Colville NF	Douglas-fir/snowberry	Intermediate	PSME, PIPO, LAOC	Williams et al. 1995
Colville NF	Douglas-fir/mountain snowberry	Minor	PSME, PIPO, LAOC	Williams et al. 1995
Colville NF	Douglas-fir/pinegrass	Widespread	PSME, LAOC, PIPO	Williams et al. 1995
Deschutes, Mount Hood NFs	Douglas-fir/bitterbrush	Intermediate	PIPO, PSME, CADE, JUOC	Simpson 2007
Deschutes, Mount Hood NFs	Douglas-fir/greenleaf manzanita	Intermediate	PIPO, PSME, CADE	Simpson 2007
Fremont-Winema, Mount Hood NFs	Douglas-fir/common snowberry	Intermediate	PSME, PIPO, QUGA, JUOC	Simpson 2007
Fremont-Winema, Mount Hood NFs	Douglas-fir/mahala mat	Intermediate	PIPO, PSME, CADE	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/pinegrass	Minor (in east Cascades)	PIPO, PSME, ABGR	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/common snowberry	Widespread	PIPO, ABGR, PSME	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/greenleaf manzanita	Widespread	PIPO, ABGR, PICO	Simpson 2007
Fremont-Winema NF	Grand fir/wooly wyethia	Minor	PIPO, ABGR, PICO	Simpson 2007
Fremont-Winema NF	Grand fir/mahala mat	Intermediate	PIPO, ABGR, CADE, JUOC	Simpson 2007
Mount Hood NF	Douglas-fir/elk sedge	Widespread	PIPO, PSME, QUGA, ABGR	Topick et al. 1988
Mount Hood NF	Douglas-fir/western fescue	Intermediate	PSME, PIPO, ABGR, QUGA	Topick et al. 1988
Mount Hood NF	Douglas-fir/snowberry	Intermediate	PIPO, PSME, ABGR	Topick et al. 1988
Mount Hood NF	Douglas-fir/pinemat manzanita	Minor	PIPO, PSME, ABGR	Topick et al. 1988
Mount Hood NF	Grand fir/elk sedge	Widespread	PSME, ABGR, PIPO	Topick et al. 1988
Mount Hood NF	Grand fir/snowberry	Most widespread	PSME, ABGR, PIPO	Topick et al. 1988
Okanogan NF	Ponderosa pine–Douglas-fir/bluebunch wheatgrass	Widespread	PIPO, PSME	Williams and Lillybridge 1983

Table 2—Mixed-conifer plant associations grouped by moisture and approximate fire regime (app. 2) (continued)

National forest (NF)/region[a]	Vegetation series/ plant association	Extent[b]	Species composition[c]	Source[d]
Okanogan NF	Douglas-fir/pinegrass	Most widespread	PSME, LAOC, PIPO, PICO, POTR5	Williams and Lillybridge 1983
Okanogan NF	Douglas-fir/bearberry	Intermediate	PSME, PICO, PIPO, LAOC	Williams and Lillybridge 1983
Okanogan NF	Douglas-fir/mountain snowberry	Intermediate	PSME, PIPO, LAOC	Williams and Lillybridge 1983
Wenatchee NF	Oregon white oak/bluebunch wheatgrass	Minor	QUGA, PIPO	Lillybridge et al. 1995
Wenatchee NF	Oregon white oak/pinegrass–elk sedge	Minor	QUGA, PIPO, PSME	Lillybridge et al. 1995
Wenatchee NF	Oregon white oak/California hazel–common snowberry	Minor	QUGA, PIPO, PSME, POTR5	Lillybridge et al. 1995
Wenatchee NF	Ponderosa pine/pinegrass–bluebunch wheatgrass	Minor	PIPO, PSME	Lillybridge et al. 1995
Wenatchee NF	Ponderosa pine/bitterbrush–bluebunch wheatgrass	Intermediate	PIPO, PSME	Lillybridge et al. 1995
Wenatchee NF	Douglas-fir/elk sedge	Intermediate	PSME, PIPO	Lillybridge et al. 1995
Wenatchee NF	Douglas-fir/bitterbrush–bluebunch wheatgrass	Widespread	PIPO, PSME	Lillybridge et al. 1995
Wenatchee NF	Douglas-fir/bitterbrush–pinegrass	Widespread	PIPO, PSME	Lillybridge et al 1995
Wenatchee NF	Douglas-fir/bluebunch wheatgrass	Widespread	PSME, PIPO	Lillybridge et al. 1995
Wenatchee NF	Douglas-fir/pinegrass–bluebunch wheatgrass	Intermediate	PIPO, PSME	Lillybridge et al. 1995
Wenatchee NF	Douglas-fir/pinegrass	widespread	PSME, PIPO, PICO, LAOC	Lillybridge et al. 1995
Wenatchee NF	Douglas-fir/snowberry–bluebunch wheatgrass	Intermediate	PSME, PIPO	Lillybridge et al. 1995
Wenatchee NF	Douglas-fir/snowberry–pinegrass	Widespread	PSME, PIPO	Lillybridge et al. 1995
Wenatchee NF	Douglas-fir/snowberry	Widespread	PSME, PIPO	Lillybridge et al 1995
Wenatchee NF	Douglas-fir/mountain snowberry	Intermediate	PIPO, PSME	Lillybridge et al. 1995
Wenatchee NF	Douglas-fir/shiny-leaf spirea–pinegrass	Widespread	PSME, PIPO	Lillybridge et al. 1995
Wenatchee NF	Grand fir/pinegrass	Most widespread	PSME, PIPO, ABGR, PICO	Lillybridge et al. 1995
Wenatchee NF	Grand fir/mountain snowberry	Minor	PSME, PIPO, ABGR	Lillybridge et al. 1995
Wenatchee NF	Grand fir/pinemat manzanita	Widespread	PSME, PIPO, ABGR, PICO, LAOC	Lillybridge et al. 1995
Warm Springs Indian Reservation	Ponderosa pine–Douglas-fir/bitterbrush	Intermediate	PSME, PIPO CADE	Marsh et. al 1987
Warm Springs Indian Reservation	Ponderosa pine–Douglas-fir/bitterbrush-ceanothus	Widespread	PIPO, PSME, CADE	Marsh et. al 1987
Warm Springs Indian Reservation	Ponderosa pine–Douglas-fir/snowberry	Intermediate	PSME, PIPO CADE	Marsh et. al 1987
Warm Springs Indian Reservation	Ponderosa pine–Douglas-fir/bitterbrush (Mutton)	Intermediate	PIPO, JUOC, QUGA	Marsh et. al 1987
Warm Springs Indian Reservation	Ponderosa pine–Douglas-fir/snowberry (Mutton)	Intermediate	PSME, PIPO CADE	Marsh et. al 1987

Table 2—Mixed-conifer plant associations grouped by moisture and approximate fire regime (app. 2) (continued)

National forest (NF)/region[a]	Vegetation series/ plant association	Extent[b]	Species composition[c]	Source[d]
Warm Springs Indian Reservation	Ponderosa pine–Douglas-fir/greenleaf manzanita–ceanothus (Mutton)	Intermediate	PSME, PIPO, CADE, QUGA	Marsh et. al 1987
Warm Springs Indian Reservation	Ponderosa pine–Douglas-fir/snowberry (Mutton)	Intermediate	PSME, PIPO QUGA	Marsh et. al 1987
Warm Springs Indian Reservation	Ponderosa pine–Douglas-fir/prairie smoke avens–mule's ears (Mutton)	Intermediate	PIPO, PSME, JUOC, QUGA	Marsh et. al 1987
Moist-dry with low- to mixed-severity fire—*Characterized by low to moderate-severity fire with intervals intermediate between the dry and moist group. Large high-severity fires rarely occur. Natural fire regimes in order of prevalence are III A, III B, I, IIIC, and IV A.*				
Blue and Ochoco Mountains	Douglas-fir/oceanspray	Intermediate	PSME, PIPO	Johnson and Clausnitzer 1992
Blue and Ochoco Mountains	Grand fir/grouse huckleberry	Intermediate	ABGR, LAOC, PSME, LAOC, PICO, PIPO	Johnson and Clausnitzer 1992
Blue and Ochoco Mountains Wallowa-Snake Province	Douglas-fir/Rocky Mountain maple–mallow ninebark	Intermediate	PSME, PIPO	Johnson and Simon 1987
Blue and Ochoco Mountains Wallowa-Snake Province	Douglas-fir/big huckleberry	Intermediate	PSME, PIPO, LAOC	Johnson and Clausnitzer 1992 Johnson and Simon 1987
Blue and Ochoco Mountains; Strawberry Mountains	Douglas-fir/pinemat manzanita/ elk sedge	Minor	PSME, PIMO, ABLA	Johnson 2004
Blue and Ochoco Mountains Wallowa-Snake Province	Douglas-fir /mallow ninebark	Widespread	PSME, PIPO, LAOC	Johnson and Clausnitzer 1992
Colville National Forest	Douglas-fir/ninebark	Most widespread	PSME, PIPO	Williams et al. 1995
Colville National Forest	Douglas-fir/ninebark–twinflower	Widespread	PSME, LAOC, PIPO	Williams et al. 1995
Colville National Forest	Douglas-fir/big huckleberry	Intermediate	PSME, LAOC, PICO	Williams et al. 1995
Colville National Forest	Douglas-fir/dwarf huckleberry	Minor	PSME, PICO, LAOC,PIPO, PIEN	Williams et al. 1995
Colville National Forest	Grand fir/ninebark	Widespread	PSME, LAOC, PIPO, ABGR	Williams et al. 1995
Colville National Forest	Grand fir/dwarf huckleberry	Minor	PICO, PSME, LAOC, ABGR	Williams et al. 1995
Deschutes, Mount Hood NFs	Douglas-fir/chinquapin	Widespread	PSME, PIPO, CADE, PILA	Simpson 2007
Deschutes, Mount Hood NFs	Douglas-fir/oceanspray	Minor	PSME, PIPO, QUGA, JUOC	Simpson 2007
Deschutes, Mount Hood NFs	Grand fir/oceanspray	Intermediate	PSME, PIPO, ABGR	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Douglas-fir/starflower	Widespread	PSME, PIPO, CADE	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Douglas-fir/creeping snowberry	Intermediate	PSME, PIPO, CADE, QUGA	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Douglas-fir/prince's pine	Intermediate	PSME, PIPO, CADE	Simpson 2007
Fremont-Winema NF	Grand fir/creeping snowberry	Intermediate	PIPO, ABGR, PICO, PSME	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/golden chinquapin	Widespread	PSME, PIPO, ABGR	Simpson 2007

Table 2—Mixed-conifer plant associations grouped by moisture and approximate fire regime (app. 2) (continued)

National forest (NF)/region[a]	Vegetation series/ plant association	Extent[b]	Species composition[c]	Source[d]
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/western starflower	Widespread	PSME, ABGR, PIPO	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/common prince's pine	Widespread	PIPO, ABGR, PICO, PSME	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/starry false-solomonseal	Widespread	PIPO, ABGR, PICO	Simpson 2007
Mount Hood NF	Douglas-fir/oceanspray/elk sedge	Widespread	PSME, PIPO, QUGA, ABGR	Topick et al. 1988
Mount Hood NF	Grand fir/starflower	Widespread	PSME, ABGR, PIPO	Topick et al. 1988
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/long-stolen sedge	Intermediate	PIPO, PICO, ABGR	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/pinemat manzanita	Intermediate	ABCO, PICO, PIPO, PIMO	Simpson 2007
Mount Hood NF	Grand fir/chinkquapin	Minor	ABGR, PSME, PICO, LAOC, PIPO	Topick et al. 1988
Okanogan NF	Douglas-fir/ninebark	Minor	PSME, LAOC, PICO, PIPO	Williams and Lillybridge 1983
Okanogan NF	Douglas-fir/boxwood	Minor	PSME, PIPO, POTR5	Williams and Lillybridge 1983
Okanogan NF	Douglas-fir/huckleberry	Intermediate	PSME, LAOC, PICO, PIPO	Williams and Lillybridge 1983
Okanogan NF	Subalpine fir/pinegrass	Intermediate	PSME, ABLA,PICO, LAOC, PIPO	Williams and Lillybridge 1983
Wenatchee NF	Douglas-fir/huckleberry (three minor huckleberry associations)	Minor	PSME, LAOC, PICO, PIPO	Lillybridge et al. 1995
Wenatchee NF	Grand fir/pinegrass– lupine	Intermediate	PSME, PIPO, ABGR, PICO, LAOC	Lillybridge et al. 1995
Wenatchee NF	Grand fir/heartleaf arnica	Intermediate	PSME, ABGR, LAOC, PIPO, PIEN	Lillybridge et al. 1995
Wenatchee NF	Grand fir/oceanspray–pinegrass	Intermediate	PSME, ABGR, PIPO, LAOC	Lillybridge et al. 1995
Wenatchee NF	Grand fir/Cascade Oregon grape–pinegrass	Intermediate	PSME, ABGR, PICO, LAOC, PIPO	Lillybridge et al. 1995
Wenatchee NF	Grand fir/common snowberry–pinegrass	Intermediate	PSME, ABGR, PIPO	Lillybridge et al. 1995
Warm Springs Indian Reservation	Mixed conifer/snowberry/elk sedge	Intermediate	PIPO, PSME, ABGR	Marsh et. al 1987
Warm Springs Indian Reservation	Mixed conifer/ceanothus	Widespread	PIPO, PSME, ABGR, CADE	Marsh et. al 1987
Warm Springs Indian Reservation	Mixed conifer/snowberry	Widespread	PSME, PIPO ABGR	Marsh et. al 1987
Warm Springs Indian Reservation	Mixed conifer/boxwood	Intermediate	ABGR, PSME, PIPO, LAOC	Marsh et. al 1987
Warm Springs Indian Reservation	Grand fir/boxwood	Intermediate	ABGR, PSME, PIPO, LAOC	Marsh et. al 1987
Moist with mixed-severity fire—*Characterized by moderate to high-severity fire with lesser amounts of low-severity fire in comparison to the moist-dry group. Fire return intervals are usually longer than 50 years. Natural fire regimes in order of prevalence are III B, III C, III A, IV B, and IV A.*				
Blue and Ochoco Mountains				
Wallowa-Snake Province	Grand fir/big huckleberry	Widespread	ABGR, LAOC, PSME, PIEN, ABLA, PIPO, PICO	Johnson and Clausnitzer 1992
Johnson and Simon 1987				
Wallowa-Snake Province	Grand fir/Rocky Mountain maple	Intermediate	ABGR, PIEN, PSME, LAOC, PIMO	Johnson and Clausnitzer 1992 Johnson and Simon 1987

Table 2—Mixed-conifer plant associations grouped by moisture and approximate fire regime (app. 2) (continued)

National forest (NF)/region[a]	Vegetation series/ plant association	Extent[b]	Species composition[c]	Source[d]
Blue and Ochoco Mountains	Grand fir/Columbia brome	Intermediate	ABGR, PSME, LAOC, PIEN	Johnson and Clausnitzer 1992
Blue and Ochoco Mountains	Grand fir/grouse huckleberry–twinflower	Intermediate	ABGR, PIEN, LAOC, PSME	Johnson and Clausnitzer 1992
Blue and Ochoco Mountains				
Wallowa-Snake Province	Grand fir/twinflower	Widespread	ABGR, PIEN, PSME, LAOC, PICO, ABLA, PIPO, PIMO	Johnson and Clausnitzer 1992 Johnson and Simon 1987
Wallowa-Snake Province	Grand fir/queenscup beadlilly	Widespread	ABGR, LAOC, PSME, PIEN	Johnson and Clausnitzer 1992
Johnson and Simon 1987				
Colville National Forest	Grand fir/big huckleberry/queenscup beadlilly	Intermediate	PSME, LAOC, ABGR, PICO,	Williams et al. 1995
Fremont-Winema, Deschutes NFs	Mountain hemlock/golden chinquapin	Widespread	ABCO, ABPR, PICO, PIMO, PIPO, PSME, TSME	Simpson 2007
Fremont-Winema, Deschutes NFs	Shasta red fir/golden chinquapin	Intermediate	ABPR, PICO, PILA, PIMO, PIPO	Simpson 2007
Fremont-Winema, Deschutes NFs	Shasta red fir/common prince's pine	Intermediate	ABPR, PICO, PIMO, PIPO	Simpson 2007
Fremont-Winema, Deschutes NFs	Shasta red fir/pinemat manzanita	Intermediate	ABPR, PICO, PIMO, PIPO	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/twinflower	Widespread	PSME, ABGR, PIPO	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/queenscup beadlily	Widespread	ABGR, PSME, PIPO, TSME	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	Grand fir/vanilla leaf	Widespread	ABGR, PSME, PIPO, CADE, TSME	Simpson 2007
Fremont-Winema, Deschutes, Mount Hood NFs	grand fir/wild ginger	Intermediate	PSME, ABGR, PIPO, ABMA/ABPR	Simpson 2007
Mount Hood NF	Grand fir/twinflower	Widespread	ABGR, PSME, PIPO	Topick et al. 1988
Mount Hood NF	Grand fir/vanilla leaf	Widespread	PSME, ABGR, PIPO, PICO, LAOC, TSHE, ABPR	Topick et al. 1988
Mount Hood NF	Grand fir/skunk leaved polemonium	widespread	ABGR, PSME, PICO, LAOC, PIEN, PIPO	Topick et al. 1988
Okanogan NF	Subalpine fir/vaccinium	Widespread	LAOC, PSME, PICO, PIEN, ABLA	Williams and Lillybridge 1983
Wenatchee NF	Grand fir/shiny-leaf spirea–bracken fern	Intermediate	PSME, PIPO, ABGR, PIMO	Lillybridge et al. 1995
Wenatchee NF	Grand fir/vine maple–queencup beadlily	Intermediate	PSME, ABGR, PIPO	Lillybridge et al. 1995
Wenatchee NF	Grand fir/Cascade Oregon-grape	Widespread	PSME, ABGR, LAOC, PIPO	Lillybridge et al. 1995
Wenatchee NF	Grand fir/vanilla leaf	Intermediate	ABGR, PSME, LAOC, PIMO, PIPO	Lillybridge et al. 1995
Wenatchee NF	Grand fir/vine maple–prince's pine	Intermediate	PSME, ABGR, PIPO, PICO,	Lillybridge et al. 1995
Warm Springs Indian Reservation	Grand fir/snowberry	Widespread	ABGR, PSME, PIPO,	Marsh et. al 1987
Warm Springs Indian Reservation	Grand fir/vine maple	Widespread	PSME, ABGR, PIPO	Marsh et. al 1987
Warm Springs Indian Reservation	Grand fir/big leaf huckleberry	Widespread	ABGR, PSME, LAOC, PIMO	Marsh et. al 1987
Warm Springs Indian Reservation	Grand fir–Lodgepole pine/ boxwood/ pinegrass	Intermediate	PICO, ABGR PIPO, ABLA,	Marsh et. al 1987

Table 2—Mixed-conifer plant associations grouped by moisture and approximate fire regime (app. 2) (continued)

National forest (NF)/region[a]	Vegetation series/ plant association	Extent[b]	Species composition[c]	Source[d]
Moist to wet with high-severity fire—*Higher severity fire tends to dominate in most events and return intervals are usually greater than 100 years. Natural fire regimes in order of prevalence are III C and IV B.*				
Blue and Ochoco Mountains	Grand fir/oakfern	Minor	ABGR, PIEN, PSME, LAOC, ACGL, TABR	Johnson and Clausnitzer 1992
Blue and Ochoco Mountains	Grand fir/sword fern–ginger	Intermediate	ABGR, PSME, LAOC, PIEN	Johnson and Clausnitzer 1992
Blue and Ochoco Mountains				
Wallowa-Snake Province	Grand fir/Pacific yew/ queen's cup beadlilly	Intermediate	ABGR, PIEN, PSME, LAOC, TABR	Johnson and Clausnitzer 1992
Johnson and Simon 1987				
Blue and Ochoco Mountains	Grand fir/Pacific yew/ twinflower	minor	ABGR, PSME, LAOC, PIEN, TABR	Johnson and Clausnitzer 1992
Blue and Ochoco Mountains	Grand fir/false bugbane	Intermediate	ABGR, PIEN, ABLA, LAOC, PICO, TABR	Johnson and Clausnitzer 1992
Colville National Forest	Grand fir/Douglas maple/queencup beadlilly	Intermediate	PSME, LAOC, ABGR	Williams et al. 1995
Mount Hood National Forest	Grand fir–Engelmann spruce/ starry solomonplume	Minor	ABGR, PIEN, PSME, PICO	Topick et al. 1988
Mount Hood NF	Grand fir/vanilla leaf–vine maple	Widespread	PSME, PIPO, ABGR, CONU	Topick et al. 1988

Note: This table is intended as an interim classification subject to further revision as new information becomes available. Note that terms used to describe climatic environment are relative terms and have different definitions among regions. Therefore, this regional classification may differ from local classifications.

[a] National forest/region = subregion of the plant association.

[b] Extent = geographic distribution and approximate area of a plant association relative to other associations within the region.

[c] Species composition = all tree species recorded in each association, ordered by prominence within each association.
ABGR = *Abies grandis* (grand fir); ABLA = *Abies lasiocarpa* (subalpine fir); ABPR = *Abies procera* (noble fir); ACGL = *Acer glabrum* (Rocky Mountain maple); CADE = *Calocedrus decurrens* (incense cedar); CONU = *Cornus nutallii* (Pacific dogwood); JUOC = *Juniperus occidentalis* (western juniper); LAOC = *Larix occidentalis* (western larch); PICO = *Pinus contorta* (lodgepole pine); PIEN = *Picea engelmannii* (Engelmann spruce; PILA = *Pinus lambertiana* (sugar pine); PIMO = *Pinus monticola* (western white pine); PIPO = *Pinus ponderosa* (ponderosa pine); PSME = *Pseudotsuga menziesii* (Douglas-fir); QUGA = *Quercus garryana* (Oregon white oak); TABR = *Taxus brevifolia* (Pacific yew); TSHE = *Tsuga heterophylla* (western hemlock); TSME = *Tsuga mertensiana* (mountain hemlock).

[d] Source = citation for plant association description.

Vegetation Classification and Disturbance Regimes

Effective restoration depends on having an accurate classification of vegetation and its disturbance regime. There are various schemas for classifying vegetation for purposes of ecological stratification, including current vegetation, historical vegetation, and potential natural vegetation (PNV). PNV in application is organized into a taxonomic hierarchy consisting of series, subseries, and plant associations, which are named for dominant overstory and undergrowth plants (Powell 2007). The standard system of vegetation classification and mapping used by the Forest Service and other federal agencies is based on this taxonomic hierarchy. Mixed conifer is composed of grand fir, white fir and Douglas-fir series, but the distinction of dry, moist and wet mixed-conifer types (i.e., disturbance regimes) requires the use of lower levels in the hierarchy, including subseries and groups of plant associations. We provide a first approximation for how associations could be grouped into four moisture/disturbance regime classes, (equivalent to subseries; table 2), but caution that this classification is interim and subject to revision as more knowledge becomes available. In this synthesis we use the term PVT in a general way to refer to any potential natural vegetation class regardless of level in the hierarchy (series, subseries, and plant associations).

A PVT is the native, late-successional (or "climax") plant community that reflects the regional climate and the dominant plant species of an area that would occur on a site in the absence of disturbance (Pfister and Arno 1980). This approach assumes that disturbances still occur, but that the composition of the late-successional community occurring when disturbance is absent is a reasonable indicator of the biophysical environment. Hence, PVTs may be considered as approximate surrogates for the environmental conditions of a site (in terms of moisture, solar, nutrient, and temperate regimes) that exert some control on productivity, habitat potential, regeneration rates, and the frequency and severity of disturbance regimes.

Concepts of orderly succession and climax vegetation are questionable in mixed-conifer and other fire-prone eastside environments (O'Hara et al. 1996). These forests actually exhibit non-equilibrium dynamics, where the potential climax conditions were typically never realized due to myriad interacting and multi-scale disturbance processes, especially fire, that both advanced and retarded succession. Potential natural vegetation classifications can also take into account the reality that vegetation structure and composition is altered and controlled by periodic wildfire (Winthers et al. 2005). Much of the dry and MMC forests in Oregon and Washington would belong to these "fire climax" potential natural vegetation types. Despite these complexities of nature and the limits of our conceptual models,

PVTs can be a useful starting place for identifying the ecological potential, fire regime, and restoration needs for an area.

At finer scales (below subseries) the plant association is a unit defined on the basis of a characteristic range of species composition, diagnostic species occurrence, habitat conditions, and physiognomy (USDA FS 2005). A number of plant associations are included in the MMC type and some grade into the drier or wetter mixed-conifer types. See the list in table 2 for an interim assignment of plant associations to our mixed-conifer moisture/disturbance regime types.

Tree species of the MMC forest are characterized as either early-, mid-, or late-successional (late-seral), and as either shade-intolerant or tolerant, respectively. The most common early-seral forest tree species are western larch (*Larix occidentalis* Nutt.), ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), lodgepole pine (*Pinus contorta* Douglas ex Loudon), western white pine (*Pinus monticola* Douglas ex D. Don), trembling (quaking) aspen (*Populus tremuloides* Michx.; especially where a seasonally high water table exists), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and mixed conditions of these types. With the exception of Douglas-fir, each of these species is shade-intolerant, all readily regenerate after fire, and western larch, ponderosa pine, and Douglas-fir can become exceptionally fire-tolerant as they advance in age, owing to an ever thickening bark (Agee 1993). Dominant late-seral tree species are grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.; in central and southern Oregon), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), where local environmental conditions (e.g., cold-air drainage or pockets) occur that will promote dominance of these species. All are shade-tolerant and fire-intolerant. Exceptions can occasionally be found in mature grand fir and white fir, which may also possess a thick bark and occasionally occur in park-like stands (Hessburg et al. 1999a, 2000a).

Under native fire regimes, the moist mixed-conifer forest would have displayed highly variable structure and composition regionally, making it among the most diverse and complex of all forest types.

Under native fire regimes, the MMC forest would have displayed highly variable structure and composition regionally, making it among the most diverse and complex of all forest types (e.g., see the tables in app. 3 for the Blue Mountains province). The MMC forest landscape included a wide range of cover type and structural class combinations that would derive from a mixture of low- to mixed-severity fires with lesser amounts of high-severity fire in the mix (e.g., see app. 3, Hessburg et al. 2007, Perry et al. 2011). Recent studies in MMC forest in central Oregon suggest that the amount of low- and mixed-severity fire and forest structure (e.g., density) and tree layer composition in pre-Euro-American times may not have differed much from nearby dry mixed-conifer PVT (Hagmann et al. 2013, Merschel 2012).

The PVT is not the same as the current or actual vegetation, which may exist in an early-, mid-, or late-successional state or in a nonnative and human-altered state (e.g., agricultural patch, urban or rural development area, pasture, or road right-of-way). The difference between the current and potential vegetation types can be important to restoration and should be known before undertaking restoration activities. The current vegetation type needs to be considered to determine which restoration trajectories are most probable, given local site conditions, landscape context, disturbance history, and potential climate change effects.

Finally, with changing climate, PVT classifications based on the relationship of potential late-successional communities to their environment will be related to current and recent past climate conditions, but not to the future climate. Consequently, managers are best served by using a variety of sources of information about a site, including potential climate change effects, when making management decisions. Individual trees or populations exposed to climate conditions outside their climate niches may be maladapted, resulting in compromised productivity and increased vulnerability to disturbance. In some locations the future will not resemble the past with respect to potential vegetation, and assemblages of tree species that we currently recognize may be quite different in the future. This will be especially true where there is a rapid change in environment and vegetation (e.g., current ecotone edges). We suggest that a current PVT map be developed to the full extent of subwatersheds of each national forest, using regionally standardized protocols for PVT definitions and mapping.

Although it is generally accepted that the PVTs differ in their disturbance regimes, only a handful of dendroecological and landscape reconstruction studies have characterized variability in wildfire regimes in eastern Washington and Oregon (Agee 1994; Hessburg et al. 2007; Heyerdahl et al. 2001, 2013; Perry et al. 2011; Wright and Agee 2004), and have been conducted in the eastern Washington Cascades and Blue Mountains. More work is needed to better understand fire regime variability and relations with physiography. Studies of dry and MMC forests, which were characterized by highly variable low-, mixed-, and high-severity fire regimes, have been conducted in three eastern Washington ecoregions (Hessburg et al. 2007), and data are available to complete similar studies in the Blue Mountains and eastern Cascades of Oregon.

Similarly, syntheses of existing studies indicate relatively high variation in fire frequency within major plant series, especially at longer return intervals. For example, fire return intervals in the grand fir series range from 17 to 100 years (Agee 1994). Agee (1994, p. 17) stated that "the [warmer and drier] mixed-conifer forests of the Douglas-fir, white fir, and grand fir series show the most frequent

fire activity of all eastside forests, although cooler, wetter sites of the grand fir series have longer fire return intervals. Frequent fires in drier plant associations of these series are likely due to higher productivity of fine dead fuels needed to carry another fire compared to the ponderosa pine series." Hessburg et al. (2007) corroborated this finding. In dry mixed conifers, they found that low- and mixed-severity fires dominated by surface fire effects affected most of the area of this type. In the MMC type, they found that mixed-severity fires were also dominant, but crown fire effects stemming from mixed-and high-severity fires were more obvious.

High variability in fire regimes as a function of environmental and vegetation context means that the correspondence of a MMC PVT with a particular narrow range of frequency and severity of fire and other disturbances should be viewed with caution. Variation in effects of fire suppression and logging on forest structure and composition is relatively large within the MMC type, especially as it is expressed in different geographic areas of the region. Thus, it is important to develop first-hand knowledge of the historical and contemporary disturbance regimes of local landscapes, and of their expression by PVT. Other factors to be considered when assessing the local disturbance regime include topography, soil physical and chemical characteristics, overall geomorphology, disturbance and management history, and climatic variability. Figures 14 and 15 illustrate the inherent heterogeneity that typically exists on these complex landscapes. Figure 14 shows the complex spatial configuration that results simply from basic topographic position at the southern end of the Wallowa-Whitman National Forest. Figure 15 illustrates the more complex patchwork of landscape units that result from a combination of topography, simplified categories of precipitation, and soils in the Wenaha River watershed on the Umatilla National Forest. This is a simple example of the concept of using a Land Type Association (LTA) that incorporates a number of landscape features into an ecological classification system based on the associations of biotic and environmental factors, which include climate, physiography, water, soils, hydrology, and potential natural communities.

General patterns of landforms, climate, and vegetation—
The ecological dynamics of the region are set within a geological and geomorphic template that controls climate, vegetation, and disturbance. Plate tectonics and volcanism, along with glacial and fluvial processes over geologic time, have produced distinct land surface forms, environments, and biotic assemblages across Oregon and Washington. These bio-geo-climatic contexts provide the basis to classify province-scale ecoregions (fig. 16) (Bailey 1995, Omernik 1987), and ecological subregions (Hessburg et al. 2000b) that reside within them. The location of the region on the windward Pacific Coast results in a predominantly marine-type

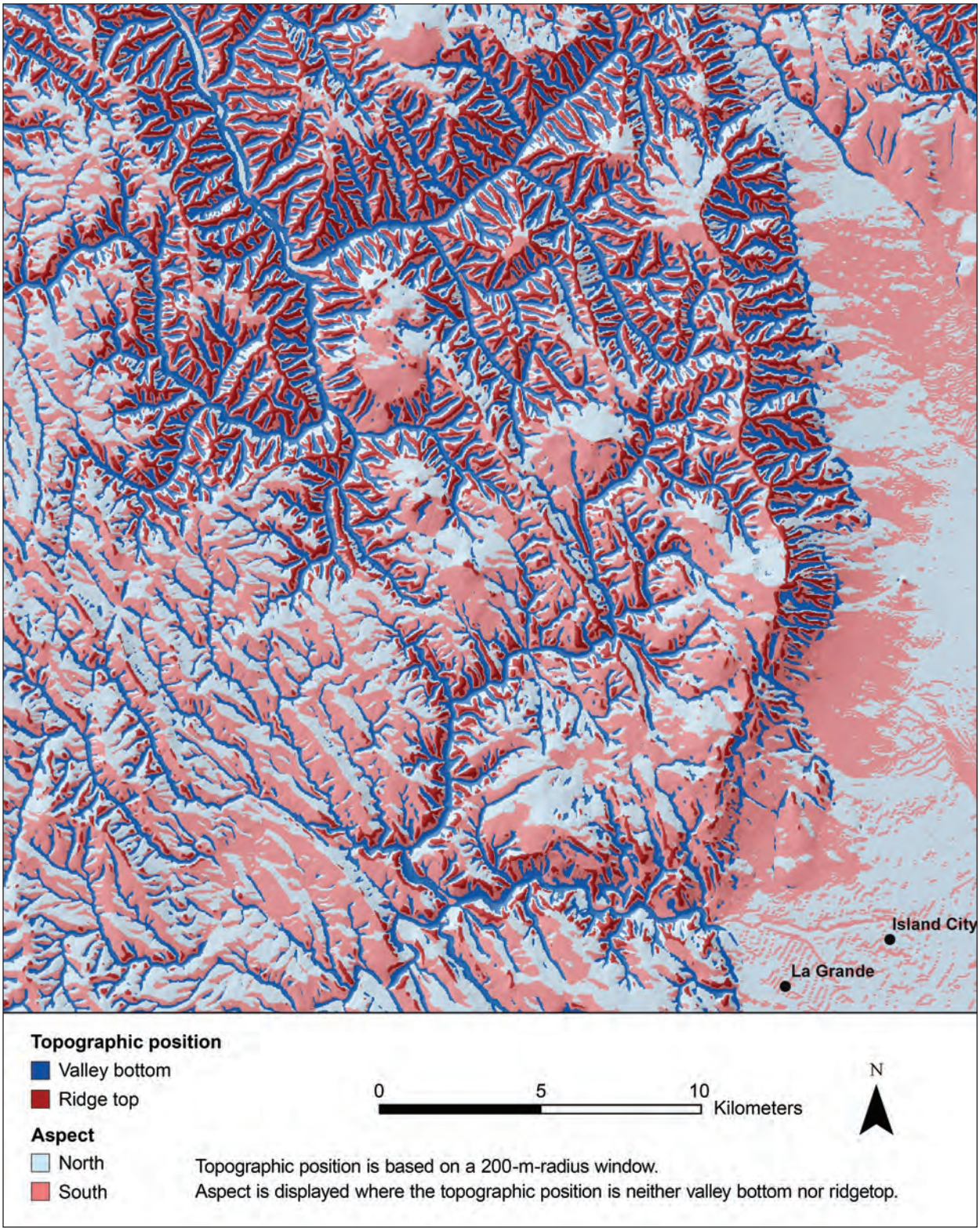


Figure 14—A map of the lower Grande Ronde Watershed on the Wallowa-Whitman National Forest in northeast Oregon, illustrating the spatial heterogeneity of the watershed simply as a function of basic topography.

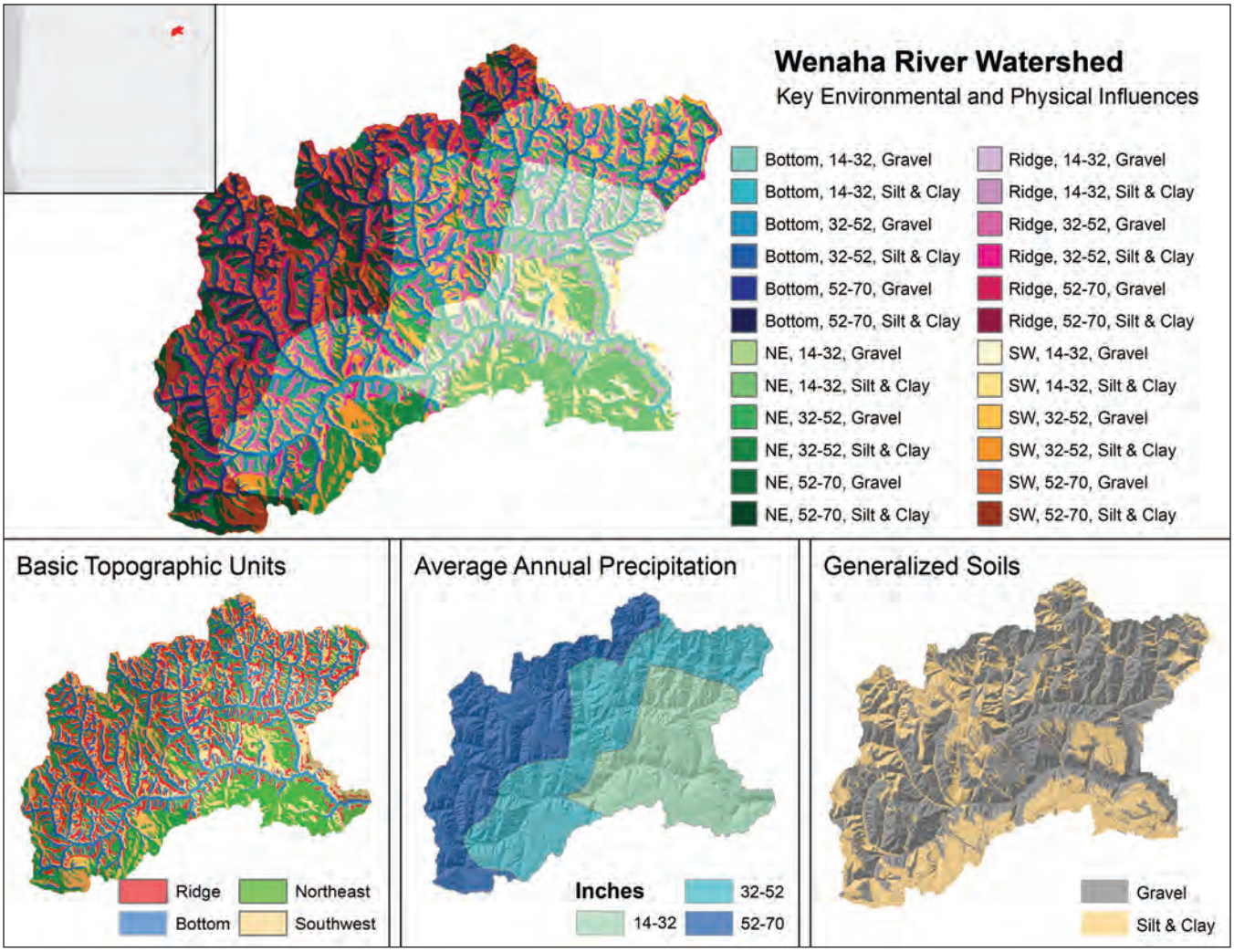


Figure 15—A map of the Wenaha River watershed on the Umatilla National Forest in northeast Oregon, illustrating the landscape complexity derived from an integration of simplified topography, soils, and climate spatial data.

climate west of the Cascade Mountains, while east of the Cascades, the climate possesses both continental and marine characteristics (Western Regional Climate Center, http://www.wrcc.dri.edu). In fall and winter, a low-pressure system in the North Pacific Ocean brings moist and mild (i.e., pacific) westerly airflow across the region, resulting in a wet season that begins in mid to late October, reaches a peak in winter (January to March), then gradually decreases later in spring. Blocking pressure in the North Pacific in summer brings a prevailing westerly and northwesterly flow of comparatively dry, cool, and stable air into the Pacific Northwest.

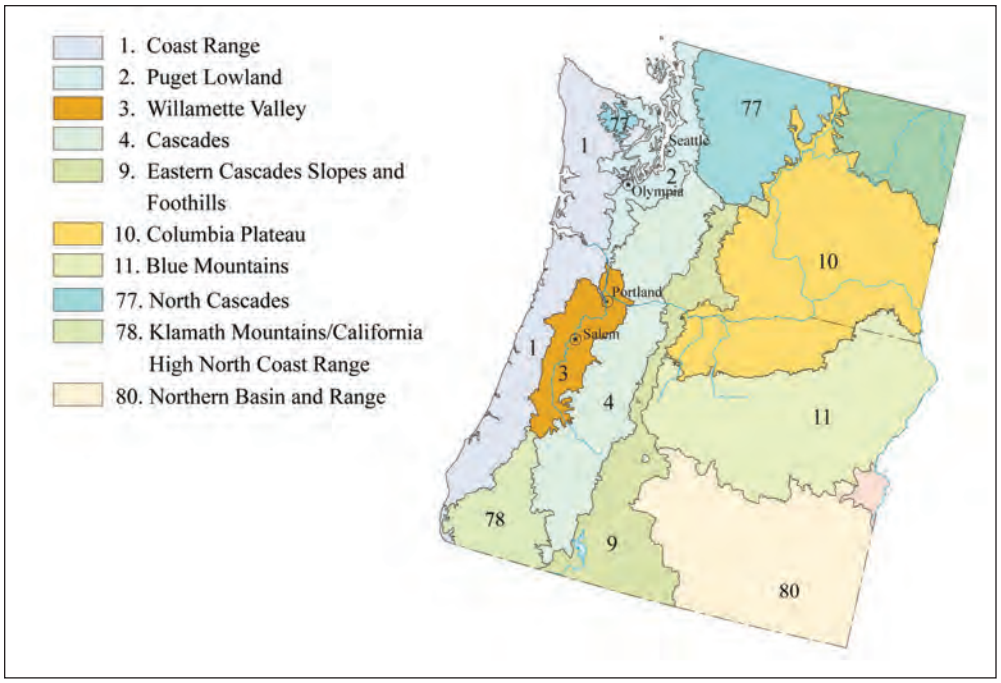


Figure 16—Ecological regions of Oregon and Washington based on the LEVEL III Ecoregions of the Continental United States, Environmental Protection Agency (revised in April 2013).

The orographic effects of the deeply dissected mountain ranges in the region result in occasionally heavy precipitation on the west slope of the Cascades and at higher elevations and relatively dry conditions on the east slope and at lower elevations (fig. 17). Temperatures vary from mild maritime conditions west of the Cascades crest to continental and temperate or Mediterranean conditions east of the Cascades.

Plant life forms and community types vary predictably across these landforms and climatic gradients. The Douglas-fir/western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) habitat type dominates west of the Cascade crest, except in the Willamette River, Umpqua River, and Rogue River valleys in the rain shadow of the Coast Mountains and portions of the Puget Trough (in the rain shadow of the Olympic Mountains), where oak savannas and dry coniferous forests occur (Franklin and Dyrness 1973). From the Cascades crest east to the west slope of the Rocky Mountains, there is a strong climate-induced stratification of vegetation types from valley bottoms to mountain tops. Sagebrush and grassland habitats dominate the Columbia Basin, the Great Basin, and the Snake River Plain. Ponderosa pine and juniper (*Juniperus* L.) habitats make up the lower forest and woodland ecotone. Douglas-fir occupies intermediate elevations, western larch and grand fir occupy still higher elevations, and Engelmann spruce and subalpine fir are found near upper tree line. Lodgepole pine inhabits subalpine environments and other low and mid-montane

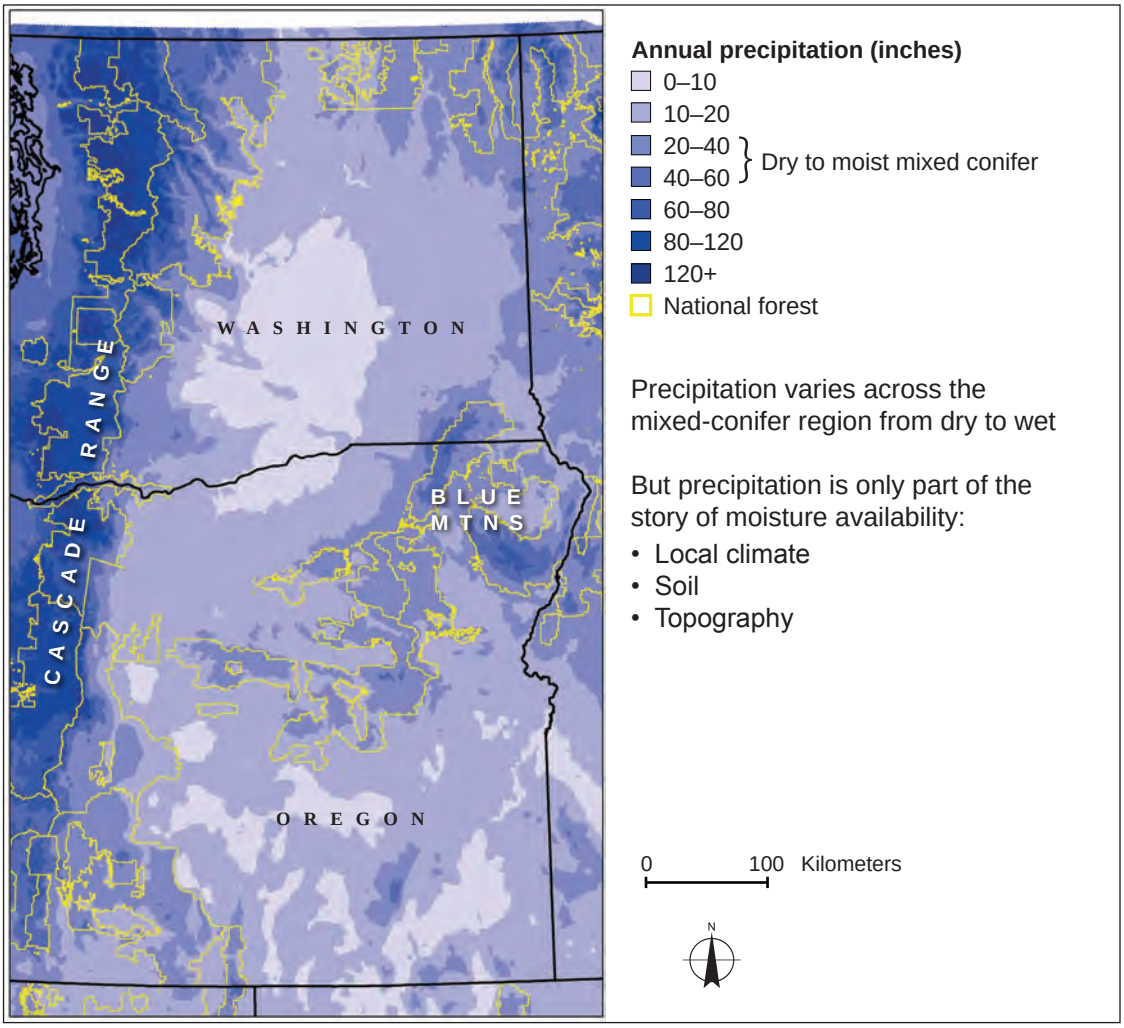


Figure 17—Generalized annual precipitation map of eastside Oregon and Washington. Note the significant rain shadow created by the Cascade Range and relatively high precipitation in some areas of the Blue Mountains.

environments that are prone to cold air pooling. Gradients extending from dry, low-elevation rangeland vegetation to moist conifer forests are especially sharp in the East Cascades, Okanogan Highlands, and Blue Mountains. In these locations, topographic controls (e.g., aspect, slope position) on vegetation composition, density, and productivity are also especially pronounced.

At the coarsest level, net primary productivity (NPP) is limited by temperature at the highest elevations, by moisture in the driest locations east of the Cascades crest, and by insolation (direct sunlight) west of the Cascades crest (Running et al. 2004). As a consequence, NPP is highest in the Coast and Cascade Ranges, intermediate in the East Cascades, Okanogan Highlands, and Blue Mountains, and lowest in the Columbia River basin and the Great Basin (Verschuyl et al. 2008).

Vegetation dynamics—
Vegetation dynamics result from the interplay between succession and disturbance processes. In the simplest case, vegetation development at a patch scale may be characterized by change in composition and structure following stand-replacement disturbance (e.g., from fire, insects, or disease). In such cases, succession can initially be relatively rapid (years to decades) and obvious, but successional change is occurring all the time, even centuries after major disturbances. The rate and nature of succession is advanced or retarded by a myriad of major and minor disturbances (O'Hara et al. 1996, Oliver and Larson 1996). In this sense, at each occurrence, disturbances may reset the vegetation condition of any patch on new trajectories that play out over space and time (Peterson 2002, Peterson et al. 1998). Patch boundaries are non-stationary as well. Patches are blended or bisected by disturbances of various kinds and combinations.

Large or severe disturbances may imprint the landscape for centuries before attenuating.

Large or severe disturbances may imprint the landscape for centuries before attenuating. The effects of small and low-intensity disturbances can be shorter in duration but still shape succession by altering site and microsite conditions that affect plant life histories by their influence on seed-fall, seed dispersal, post-dispersal seed losses, germination and recruitment, growth and mortality of juvenile and adult plants, reproduction, and a range of other factors.

Given the environmental complexity, diversity of species and processes, and variation in frequency and severity of disturbances that affect MMC forest, the number of successional pathways and development stages is quite large (fig. 18). Consequently, the structure and composition of the MMC forest across eastern Oregon and Washington was highly diverse under pre-Euro-American disturbance regimes. It was a mosaic driven by low- to mixed- and occasional high-severity fire, and the patchwork of size and age class structure and species composition differed considerably. With wildfire exclusion, domestic livestock grazing, and timber harvesting, the fire regime has shifted toward increasingly larger and more severe fires, which tend to simplify the landscape into fewer, larger, and less-diverse patches and ultimately more homogenous landscapes.

Ecological researchers are just beginning to understand ecoregional variation in the dynamics, structure, and composition of MMC forests. Given the generally sparse network of dendroecological and landscape reconstruction studies (especially in Oregon) our understanding of ecoregional and PVT-scale variation is provisional. In the eastern Cascades of Washington where high-severity fire was a component of the disturbance mix, the vegetation in MMC was a mosaic of small to very large patches comprised of early-, mid-, and late-successional forest conditions, and a broad variety of pure and mixed-cover types. In the eastern Cascades

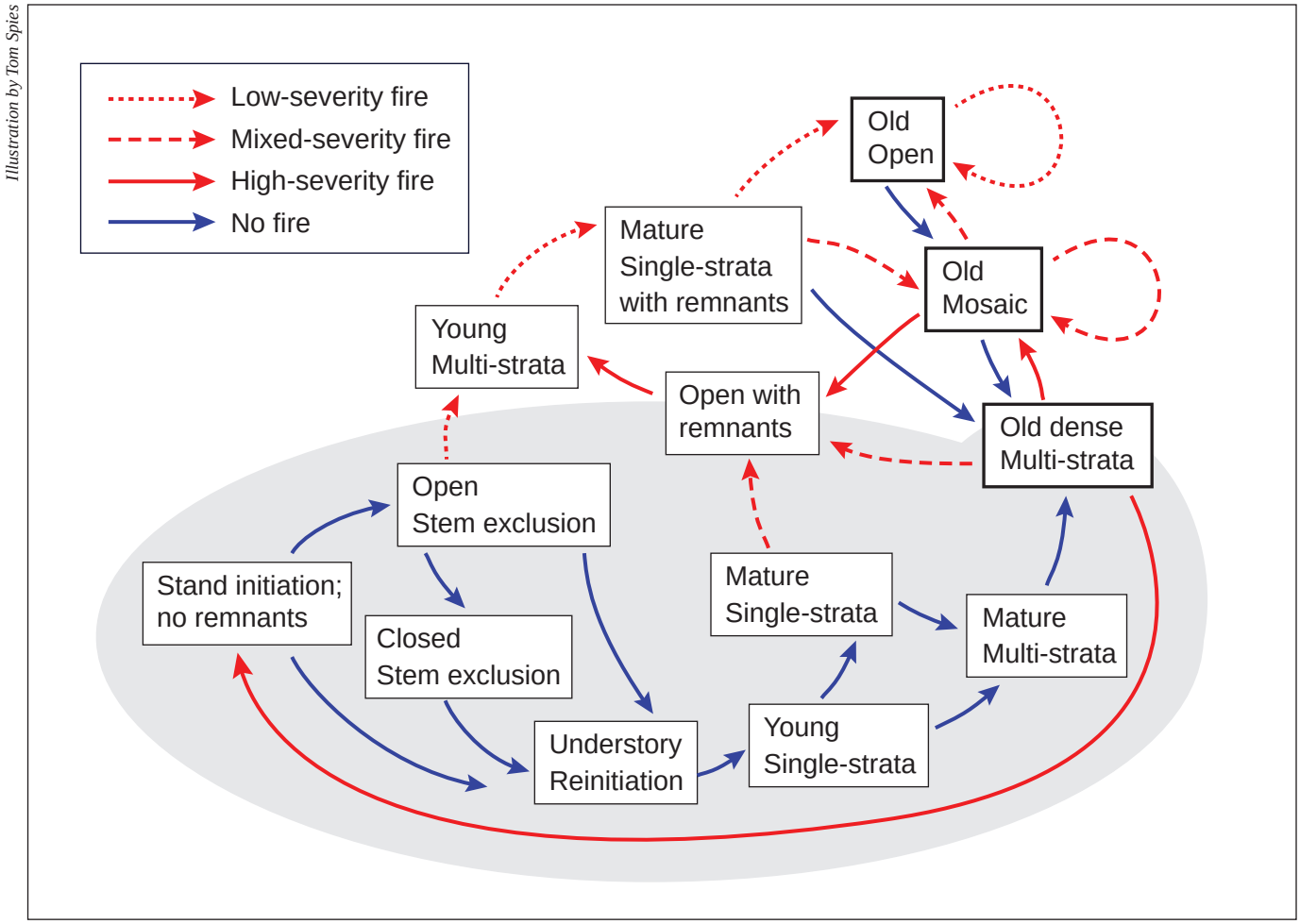


Illustration by Tom Spies

Figure 18—Conceptual model of vegetation states and transitions associated with fire severity. Under low- to mixed-severity fire regimes, moist mixed-conifer forest landscapes were dominated by patches characterized by old trees and relatively open understories or old trees in a mosaic of open and dense understory patches (bold boxes in upper right). Forest structure and composition shifted among various structurally diverse stages (boxes in upper non-gray area) depending on ecoregion, fine-scale environmental variation, and amount of high-severity fire. Under fire exclusion and even-age management, forest structure and disturbance regimes have shifted potential forest stages and pathways into the lower region of the diagram (gray area) where the amount of dense old forest, high-severity fire, and uniform young forest is much greater than it would have been under the pre-Euro-American fire regime. Some old, dense multi-strata forest would have existed under the pre-Euro-American period but it probably was a small portion of the moist mixed-conifer type across the region.

of Oregon, where the disturbance mix may have had less high-severity fire, MMC forests might have been a mosaic of large shade-intolerant forest species that can resist fire, and sparse or patchy understories of species that regenerated in areas that were disturbed by surface fires, insects, or disease, or in patches where disturbance had not occurred for several decades (Merschel 2012). On drier sites where fires were less severe and more common (<25 years), the environment may have favored growth and establishment of ponderosa pine or Douglas-fir, and understories would have been relatively open or patchy as surface fires from low- and mixed-severity fires periodically cleared them out. More work is underway and in time our understanding of this complex issue will be more complete.

Some sites within the mosaic of MMC forest would have had long intervals (>75 to 100+ years) between fires. It is on these sites that dense, multilayered forest conditions would have developed. In areas of high topographic complexity (e.g., eastern Washington Cascades and Blue Mountains) such sites are found on north-facing slopes at mid to upper elevations or at lower elevations near streams where moisture conditions would have made fuels too wet to burn except under infrequent hot dry weather conditions (Camp 1999, Camp et al. 1997). In areas of simpler topography defined by broad elevation gradients and isolated cinder cones (e.g., eastern Oregon Cascades), elevation and climate may explain the distribution of shade-tolerant species and fire regimes (Merschel 2012). Thus, many successional pathways occur in these landscapes but only a few of them would have reached old forest conditions where forests are relatively dense and dominated by shade-tolerant species, which are maladapted to fire-prone environments and droughty climate.

Despite the variation in disturbance regimes and environments, historical stand densities of large fire-tolerant trees in both dry and MMC were typically low and fell within a relatively narrow range (table 3). Of 15 estimates of historical small, medium, and large tree stand densities from different dry and MMC types and environments (based on seven total studies), 12 estimates fell within the range of 40 to 170 trees per hectare (16 to 70 trees per acre) and most of these estimates probably represent the minimum because most trees from cohorts that were regenerated in the 18th and 19th centuries were removed by disturbances. Regardless of their size, those that remain are simply the subset of survivors. Historical densities of large trees, most of them ponderosa pines and Douglas-firs, appear to fall within a relatively narrow range of low values from around 20 to 40 trees per hectare (8 to 16 trees per acre) (table 3). Figure 19 illustrates the strong contrast in historical versus current tree density in five locations in eastern Oregon and Washington.

Table 3 —Historical and current density (trees per hectare) of large diameter (typically >50 cm) trees in dry and moist mixed-conifer forest

Region	Forest description	Historical density	Current density	Source	Notes
		Mean ± standard deviation (range) and time period			
Eastern slope of the Cascade Range, southern Oregon	Mixed-dry	35 ± 15 (3–105) 1914–1922	21 ± 12 (0–45) 1997–2006	Hagmann et al. 2013	Historical density is reported for trees >53 cm diameter at breast height (dbh) based on timber inventory transects that covered 10 to 20 percent (6646 ha) of a 38 641-ha study area of ponderosa pine and dry and moist mixed-conifer forest. Current density is based on 24 current vegetation survey (CVS) plots within the study area, and density is reported for all trees >53 cm dbh. Inventory plots were assigned to habitat types (dry or moist) using mapped potential vegetation types (ILAP).
	Mixed-moist 1914–1922	35 ± 17 (3–147) 1997–2006	16 ± 15 (0–114)		
Warm Springs Indian Reservation, eastern slope of the Cascade Range, Oregon	Mixed-dry	24 ± 10 (1–62) 1922–1925	NA	Hagmann, unpublished data, 2013[a]	Historical density is reported for trees >53 cm dbh based on timber inventory transects. Plot size varied by species. Transects covered >20 percent (6952–11 327 ha) of a 32 293–ha study area of dry and MMC forest. Inventory plots were assigned to habitat types using mapped potential vegetation types (ILAP).
	Mixed-moist	26 ± 12 (0–102) 1922–1925	NA		
Eastern slope of the Cascade Range, Wenatchee National Forest, Washington	Mixed-dry/moist (estimates for several Douglas-fir potential vegetation types)	HDSG[b]—32 WDSH—2 WDTS—41 WMSH—27 1899	HDSG—77 WDSH—82 WDTS—99 WMSH—94 CDG—28 1999	Ohlson and Schellhaas 1999[c] CDG—71	For trees >40 cm (16 in) dbh. See table 5 for more information.
Blue Mountains, central Oregon	Mixed-conifer	27–32 1916–1932	NA	Forest Service inventories	Historical density reported for trees > 50 cm.
Eastern slope of the Cascade Range, central Oregon	Mixed-dry (Douglas-fir)	28 ± 19 (0–71) Early 20th century	17± 17 (0–50) 14 sample sites 2009–2010	Merschel et al. [N.d.]	Sample sites (~ 1.0 ha) were widely and randomly distributed in mature forest mapped in any of the mixed-conifer dry or mixed-conifer dry plant association groups. The number of sample sites used in each estimate is noted following the reported density. Density is reported only for shade-intolerant trees >50 cm. Historical density is based on diameter reconstruction of cut stumps, and current density is based on live trees only. Estimates refer to areas that were selectively logged, but 66 of 177 sites sampled had no evidence of logging. Period of historical density is estimated to be early to mid-20th century.
	Mixed-dry (grand fir)	30 ± 19 (17–85) Early 20th century	20 ± 15 (0–45) 16 sample sites 2009–2010		
	Mixed-moist	21 ± 17 (0–67.5) Early 20th century	12.9 ± 11 (0–45) 24 sample sites 2009–2010		
Ochoco Mountains, central Oregon	Mixed-dry (Douglas-fir)	32 ± 13.8 (5–64) Early 20th century	25.1 ± 15 (0-64) 26 sample sites 2009–2010		
	Mixed-dry (grand fir)	38 ± 19 (7.1–67) Early 20th century	19 ± 20 (0-65) 14 sample sites 2009–2010		
	Mixed-moist	18 ± 16 (0–48) Early 20th century	13 ± 13 (0-40) 14 sample sites 2009–2010		

Table 3 —Historical and current density (trees per hectare) of large diameter (typically >50 cm) trees in dry and moist mixed-conifer forest (continued)

Region	Forest description	Historical density	Current density	Source	Notes
		Mean ± standard deviation (range) and time period			
Eastern slope of the Blue Mountains, eastern Oregon	Mixed-conifer	NA	38 TPH 2012	Johnston 2013, unpublished data[d]	Density is reported for trees >50 cm in unlogged areas and provides an estimate of historical large tree density in logged areas in dry and MMC forests.
Eastern slope of the Cascade Range and foothills, Oregon and Washington	Mixed-dry	NA	21 ± 23 (n = 512) 1994–2004	Reilly 2012, unpublished data[e]	Density based on forest CVS plots distributed on a 2.5 by 2.5 km grid (5 km in wilderness areas) throughout national forests of Oregon and Washington. Sample sites include developmental stages ranging from early seral in recently disturbed areas (logging, wildfire, etc.) to mature old-growth forest. Density estimates are reported for trees >50 cm dbh. The number of CVS plots used to calculate density is reported in parentheses. CVS plots were assigned to PVTs based on ILAP.
	Mixed-moist	NA	27 ± 27 (n = 280) 1994–2004		
	Mixed-dry	NA	19 ± 16 (n = 471) 1994–2004		
Blue Mountains ecoregion, Oregon and Washington	Mixed-moist	NA	23 ± 21 (n = 1041) 1994–2004		

[a] On file with: Keala Hagmann, School of Environmental and Forest Sciences, University of Washington, Box 352100, Seattle, WA 98195.

[b] Plant association groups with respective plant associations:

HDSG (Hot/Dry/Shrub/Grass):
Pinus ponderosa/Agropyron spicatum
Pseudotsuga menziesii/Agropyron spicatum
Pinus ponderosa/Purshia tridentata/Agropyron spicatum
Pseudotsuga menziesii/Purshia tridentata/Agropyron spicatum
Pseudotsuga menziesii/Symphoricarpos albus/Agropyron spicatum

WDSH (Warm/Dry/Shrub/Herb):
Pseudotsuga menziesii/Arctostaphylos uva-ursi
Pseudotsuga menziesii/Arctostaphylos uva-ursi/Purshia tridentata
Pseudotsuga menziesii/Spirea betulifolia var. *lucida*

WDTS (Warm/Dry/Tall Shrub):
Pseudotsuga menziesii/Physocarpus malvaceus
Pseudotsuga menziesii/Physocarpus malvaceus/Linaea borealis var. *longiflora*

WMSH (Warm/Mesic/Shrub/Herb):
Pseudotsuga menziesii/Symphoricarpos albus
Pseudotsuga menziesii/Symphoricarpos albus/Calamagrostis rubescens

CDG (Cool/Dry/Grass):
Pseudotsuga menziesii/Arctostaphylos uva-ursi/Calamagrostis rubescens
Pseudotsuga menziesii/Purshia tridentata/Calamagrostis rubescens
Pseudotsuga menziesii/Spirea betulifolia var. lucida/Calamagrostis rubescens

[c] Unpublished study of stand development in mixed-conifer forest on the Malheur National Forest. On file with: James G. Johnston, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331.

[d] Ohlson, P.; Schellhaas, R. 1999. Historical and current stand structure in Douglas-fir and ponderosa pine forests. Unpublished report. Portland, OR: U.S. Department of Agriculture, Forest Service, Okanogan and Wenatchee National Forests.

[e] On file with: Matthew Reilly, Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331.

Note: see table 5 for more information. Diameter thresholds, methods of estimation, and spatial coverage used to develop estimates differs among authors.

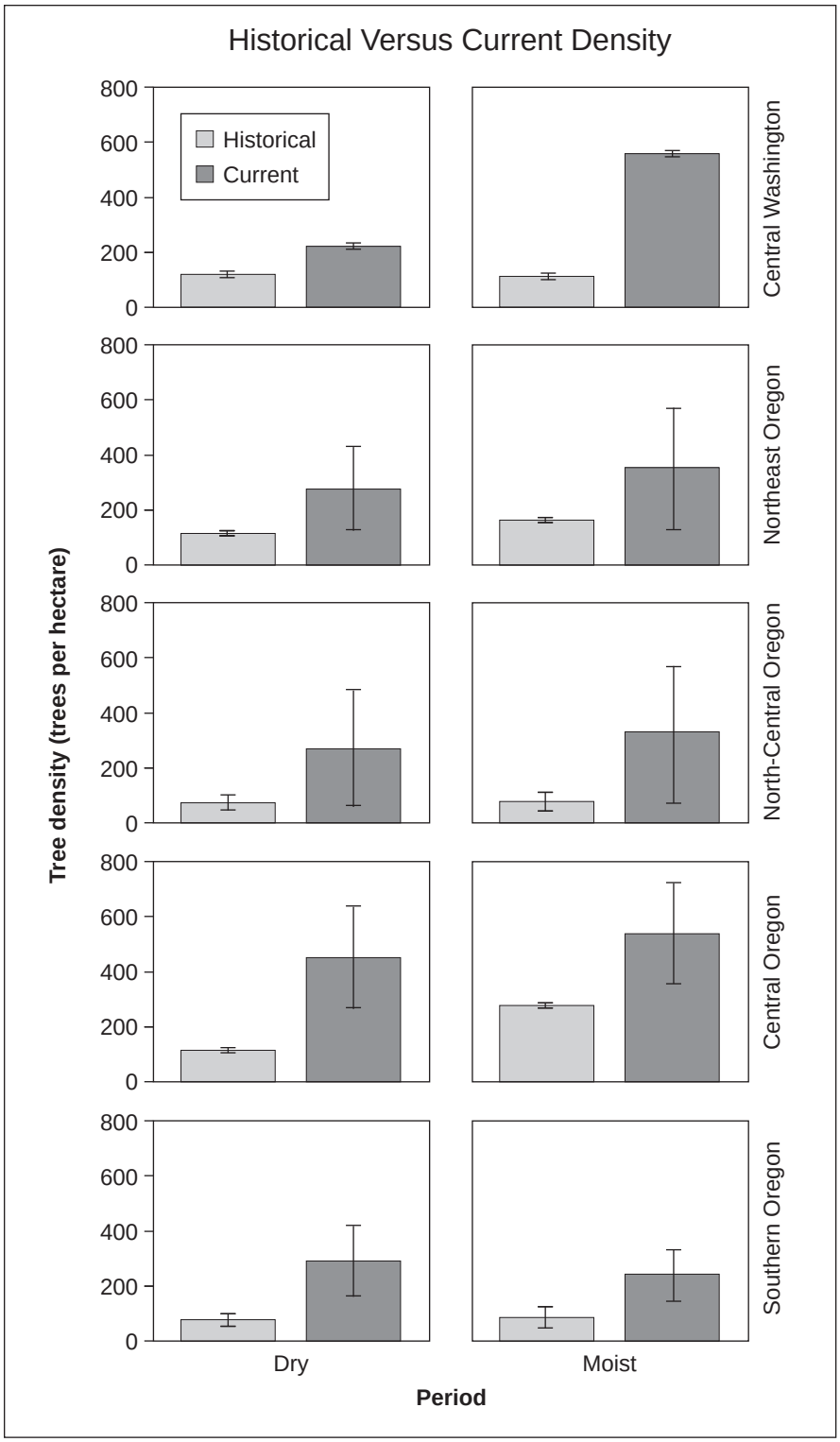


Figure 19—Historical versus current tree density in dry and moist mixed-conifer forest summarized from five study areas. Methods used to calculate density vary by reference period and study region, and diameter thresholds for tree density vary slightly among regions (10 to 15 cm). See the notes section in table 5 for citations and detailed information on how density was estimated in each region and time period.

Landscape Concepts

Provincial or regional landscapes consist of nested local landscapes, which are themselves comprised of yet smaller land units often referred to as stands or patches (Wu and David 2002, Wu and Loucks 1995). At each nested scale, species and ecosystems are controlled by spatial and temporal heterogeneity of patterns and processes. What occurs within a patch is affected by its surroundings and vice-versa. Figure 20 shows four east-west transects across montane regions of eastern Oregon and Washington and illustrates the continuous gradients of forest types that are found on these landscapes. MMC and other mixed-conifer types are thus part of a complex and intermingled landscape mosaic. The outcome of silviculture at the stand or patch level is thus inextricably linked to the interacting parts of the local and regional landscapes.

What occurs within a patch is affected by its surroundings and vice-versa.

Regional or broad-scale patterns of biota (e.g., life form zones and broad land cover types), geologic substrates (surface lithologies), geomorphic processes (land surface forms), and climatic patterns (e.g., spatial patterns of seasonal temperature, precipitation, solar radiation, and wind) constrain ecological patterns and processes occurring at a meso-scale. We call these constraints top-down spatial and temporal controls. For example, Bunnell (1995) found that the species composition of vertebrates in forest types is controlled by the disturbance regimes and mix of forest development stages found in biogeoclimatic zones in British Columbia, Canada. Changes to regional climate over relatively long time frames (100 to 1,000 years) affects relatively large spatial domains (1 million to 10 million ha). In other words, multi-century to millennial-scale changes in climate and geology can have a significant influence on species ranges. New plant and animal communities are potentially organized, new landform features emerge, and new patterns of environments and dominant disturbance regimes arise. A well-known example of landform effects in eastern Oregon is the eruption of Mount Mazama (current Crater Lake) about 7,700 years ago, which created a landscape of deep pumice deposits that control the composition and productivity of forest vegetation across central Oregon (Franklin and Dyrness 1988).

Likewise, fine-scale patterns of endemic disturbances (e.g., native insects and pathogens), topography, environments, vegetation, and other ecological processes provide critical context for patterns and processes over narrower scales or extent. These are termed bottom-up spatial and temporal controls. Bottom-up controls occur over relatively small spatial domains (1 to 100 ha), and drive processes that can vary temporally from hourly to annual time scales. For example, cool, moist, north-facing slopes can create fire "refugia" in which disturbance regimes and environment favor the development of forest containing old, fire-intolerant tree

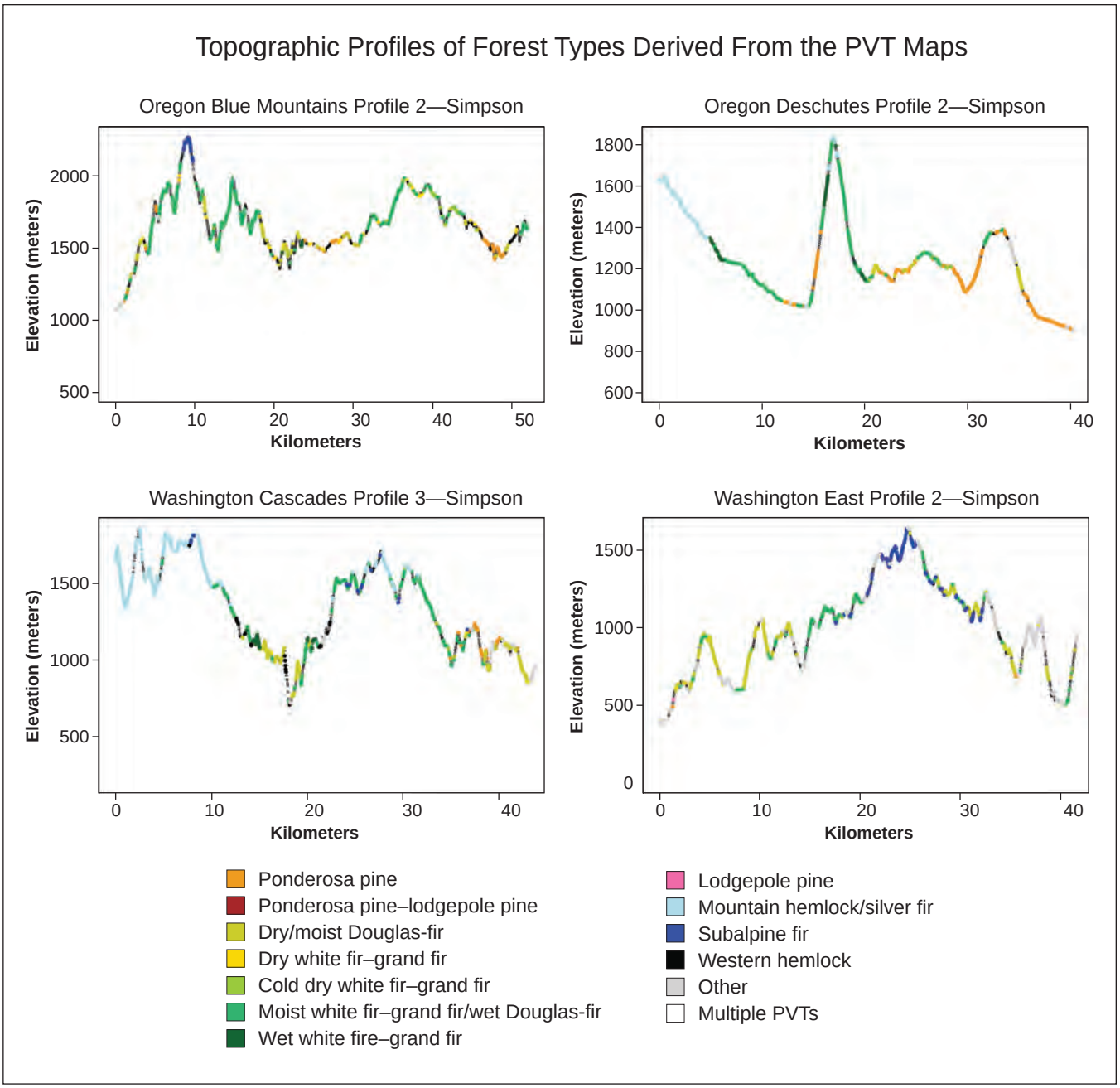


Figure 20—Profiles of predominant forest types, derived from potential vegetation types (PVTs) of Simpson (2007), across an east-west transect for four locations in eastern Oregon and Washington. Topography is exaggerated to show topographic effects.

species (Camp et al. 1997) (fig. 21). These small patches of old forest tree species can serve as seed sources that can affect rates and patterns of succession across the larger landscape (Wimberly and Spies 2001).

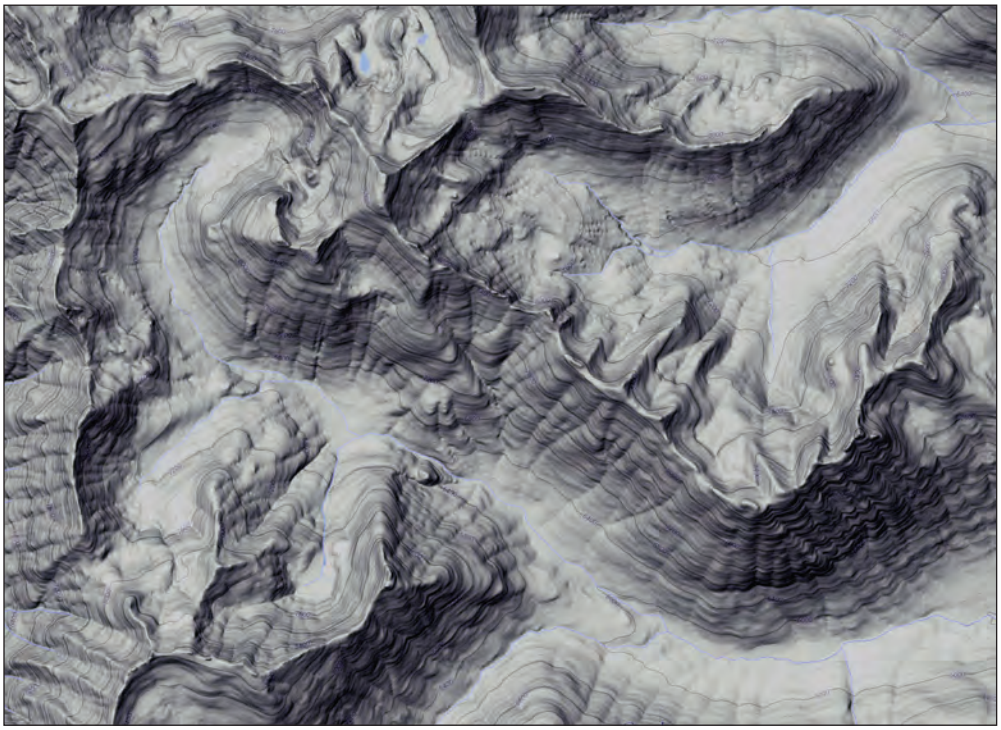


Figure 21—At the localized scale, mountainous terrain creates localized gradients in soil moisture, driven principally by differences in exposure to sunlight and wind (e.g., dry windy south-facing aspects versus cool moist north-facing hillslopes).

At all spatial and temporal scales of the hierarchy, landscapes exhibit transient patch dynamics and nonequilibrium behavior, resulting in ecosystem patterns and processes that may or may not change in linear or predictable ways. This is due to both random and deterministic properties of the supporting land and climate systems, and of ecosystem processes occurring at each level. Lower-level processes are incorporated into the next higher level of structures and processes, and this happens at all levels (figs. 11 and 21) (Wu and Loucks 1995).

Landscape patterns drive processes at local and regional landscape scales; at either scale, no two landscapes exhibit the same patterns across space or time. However, landscape patterns historically exhibited predictable spatial pattern characteristics. For example, a large sample of local landscapes (e.g., subwatersheds) comprised of dry and MMC forest in the lower and mid-montane settings, with subalpine forests in upper montane environments, reflected a predictable frequency-size distribution of cover type and structural class patch sizes (figs. 22 and 23).

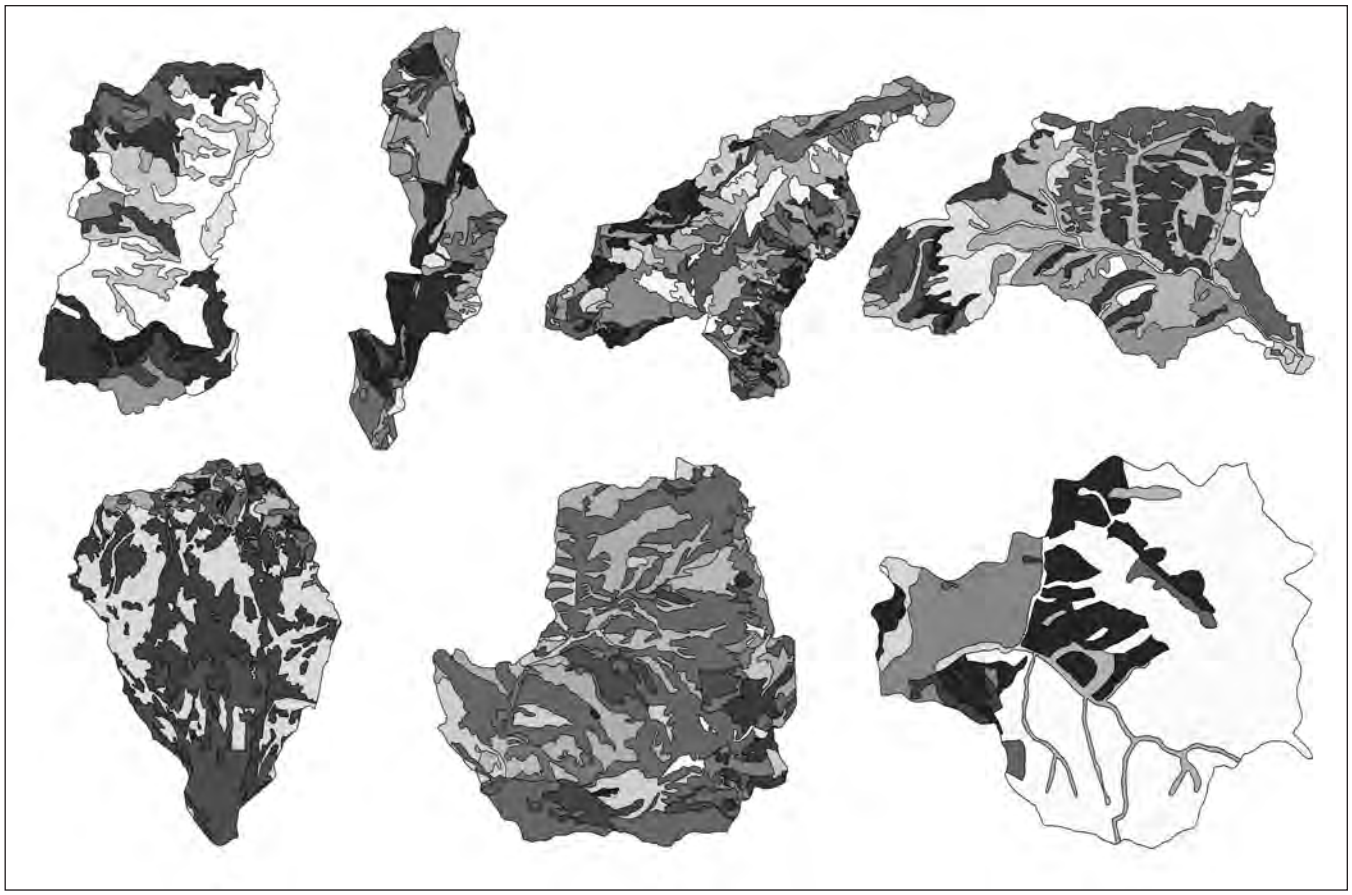


Figure 22—A sample of seven historical (ca. 1900) maps of combined cover type and structural class conditions from subwatersheds of the eastern Washington Cascades. Gray tones indicate unique cover type-structural class combinations. Note the highly variable patch sizes, with many small and fewer large patches. Despite their fewer numbers, the large patches actually make up the majority area of each subwatershed (adapted from Perry et al. 2011).

Here, think of histograms showing patch sizes in an inverse-J shaped distribution, with many small to medium-sized patches, and fewer large patches (fig. 23). Patterns and spatial arrangements of combined cover type and structural stage patch sizes (synonymous with O'Hara et al. [1996] structural classes) and their associated fuel beds provided constraint to the patch size and severity of disturbances. These patterns worked in concert with patterns of topography and weather influences to limit disturbance (Malamud et al. 1998, 2005; Moritz et al. 2010; Perry et al. 2011). This constraint probably appeared to be relatively stationary over multidecadal timeframes, but varied over multicentury periods.

As top-down controls such as regional climate or land surface forms significantly changed over large spaces and long time frames, these ranges were constantly being nudged and redefined. Moreover, because context and constraint

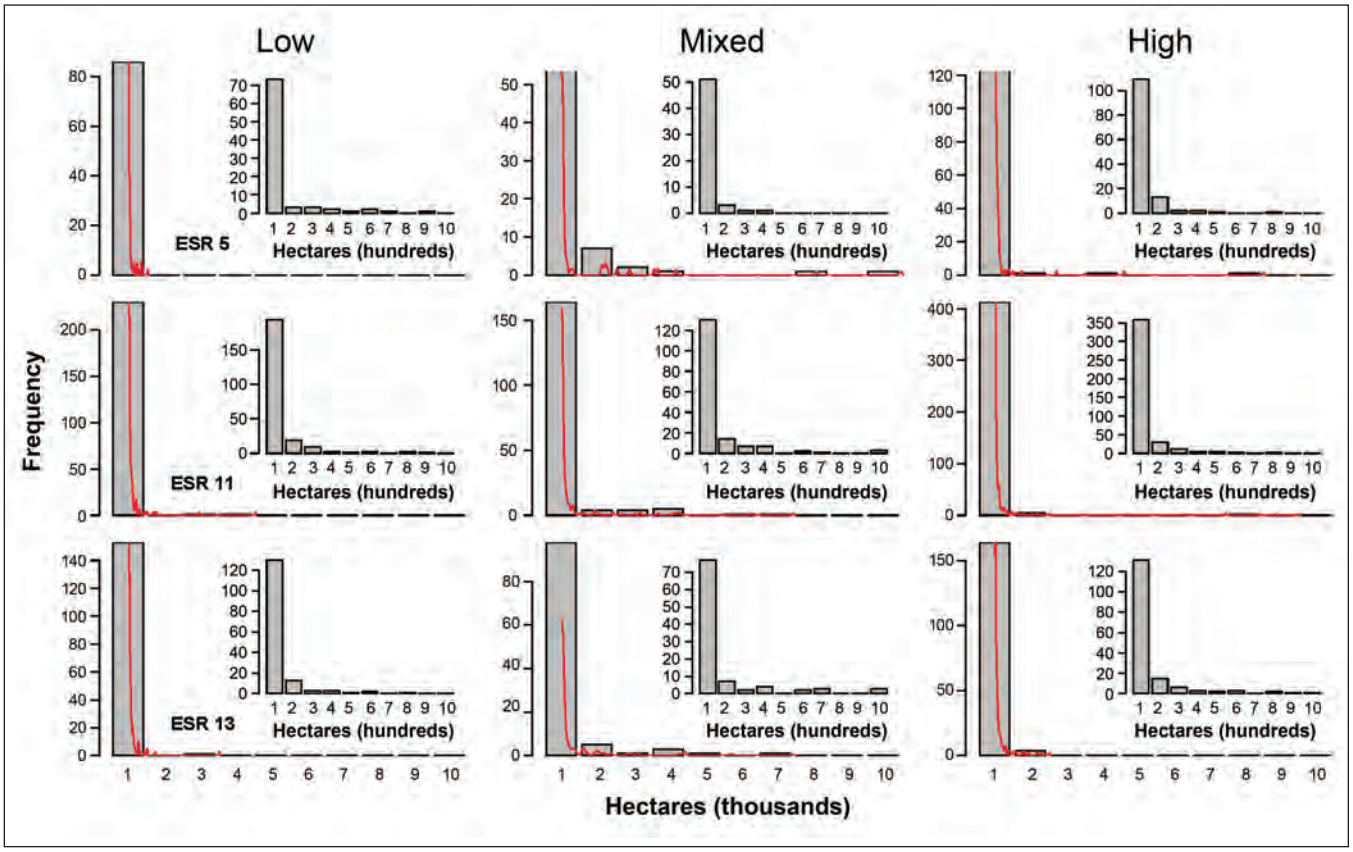


Figure 23—Frequency-size distributions of reconstructed historical (ca. 1900) fire severity patches in three ecoregions of the eastern Washington Cascades. Low, mixed, and high denote severity corresponding with <20 percent, 20 to 70 percent, and >70 percent of the overstory crown cover or basal area killed by fires, respectively. Data are from Hessburg et al. (2007). See Hessburg et al. 2000a for ecoregion details.

varied in the long term, the processes and patterns they reflected also varied over time. In a warming climate, e.g., the envelope of ecological patterns and processes at each level in the spatial hierarchy (literally the range of variation, RV) is reshaped by the strength and duration of warming (fig. 24). Reshaping of landscape patterns within a level can be figuratively represented as an envelope of conditions that drifts directionally in time (e.g., Nonaka and Spies 2005). Hessburg et al. (2000b) developed quantitative ecoregions for the interior Columbia River basin. They showed that there are strongly overlapping spatial patterns of regional climate, geology, and geomorphic processes (fig. 25). Later, they showed that these ecoregions explained some of the variance between various physiographic settings in the amount of low-, mixed-, and high-severity fires (Hessburg et al. 2004). This was first-order evidence of broad-scale spatial controls on meso-scale fire regimes.

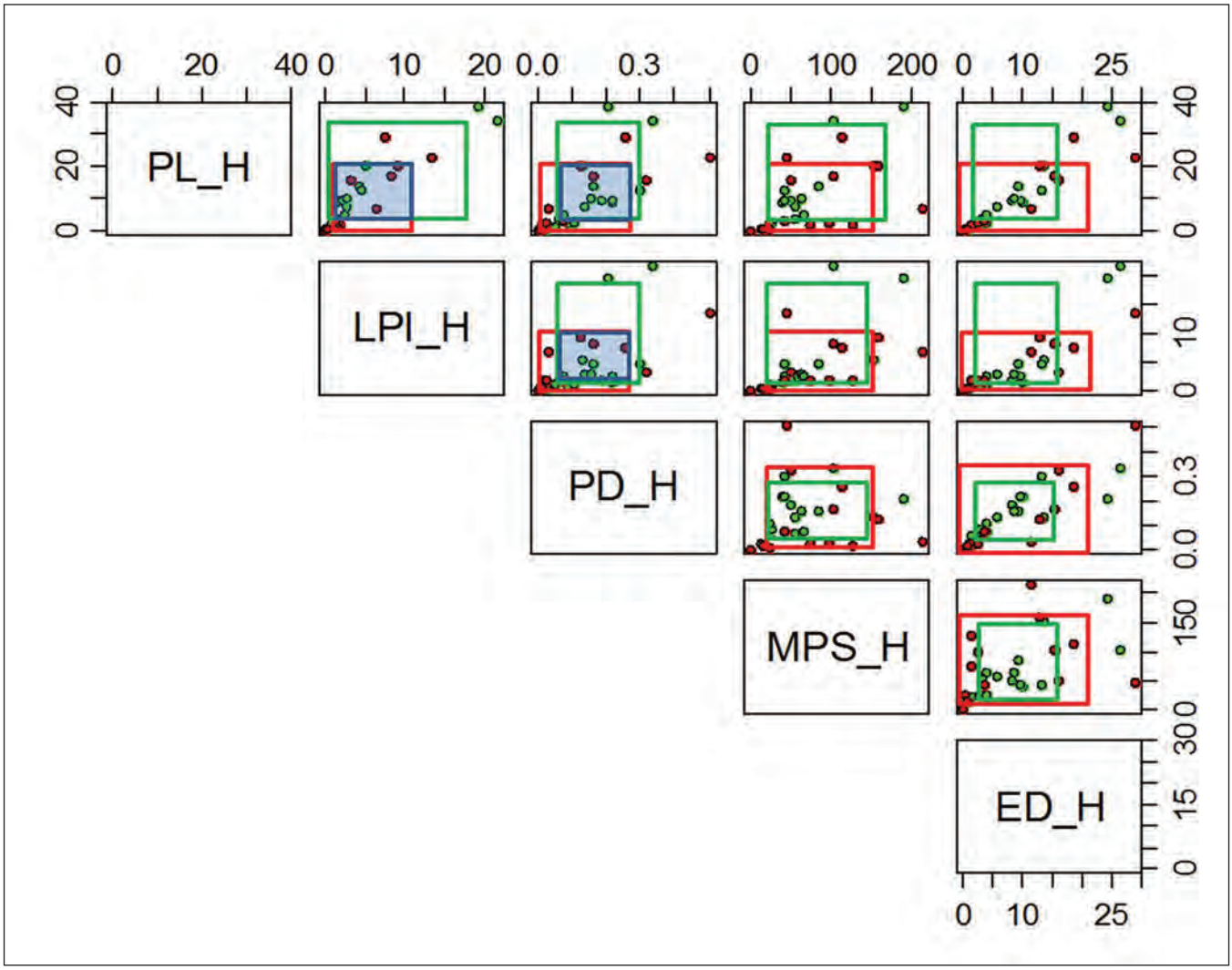


Figure 24—Comparing the historical range and variation (HRV, green dots and squares) and future range and variation (FRV, red dots and squares) with climate warming of five class metrics (paired in all possible combinations) of combined cover type–structural class patch types from a 10-percent random sample of subwatersheds of an eastern Washington Cascades ecoregion. The class metrics are the percentage of landscape area (PL_H, percent), the largest patch index (LPI_H, percent of the landscape), the patch density (PD_H, #/10,000 ha), the mean patch size (MPS_H, ha), and the edge density (ED_H, m/ha). The green square outlines the median 80 percent range of the subwatershed HRV sample. The red square outlines the median 80 percent range of the subwatershed FRV sample. Note the strong overlap between the HRV and FRV ranges in the pairwise combinations. In this example, we show paired combinations in a 2-space representation. Although impossible to graph here, one can imagine these metrics combined in a 5-space representation. In landscape analysis, any number of measures may be combined in an n-space representation to portray the HRV, the FRV, or both. In this way, departures or significant changes in spatial patterns of any contemporary landscape can be compared with the HRV and FRV to decipher the main characteristics of the changes.

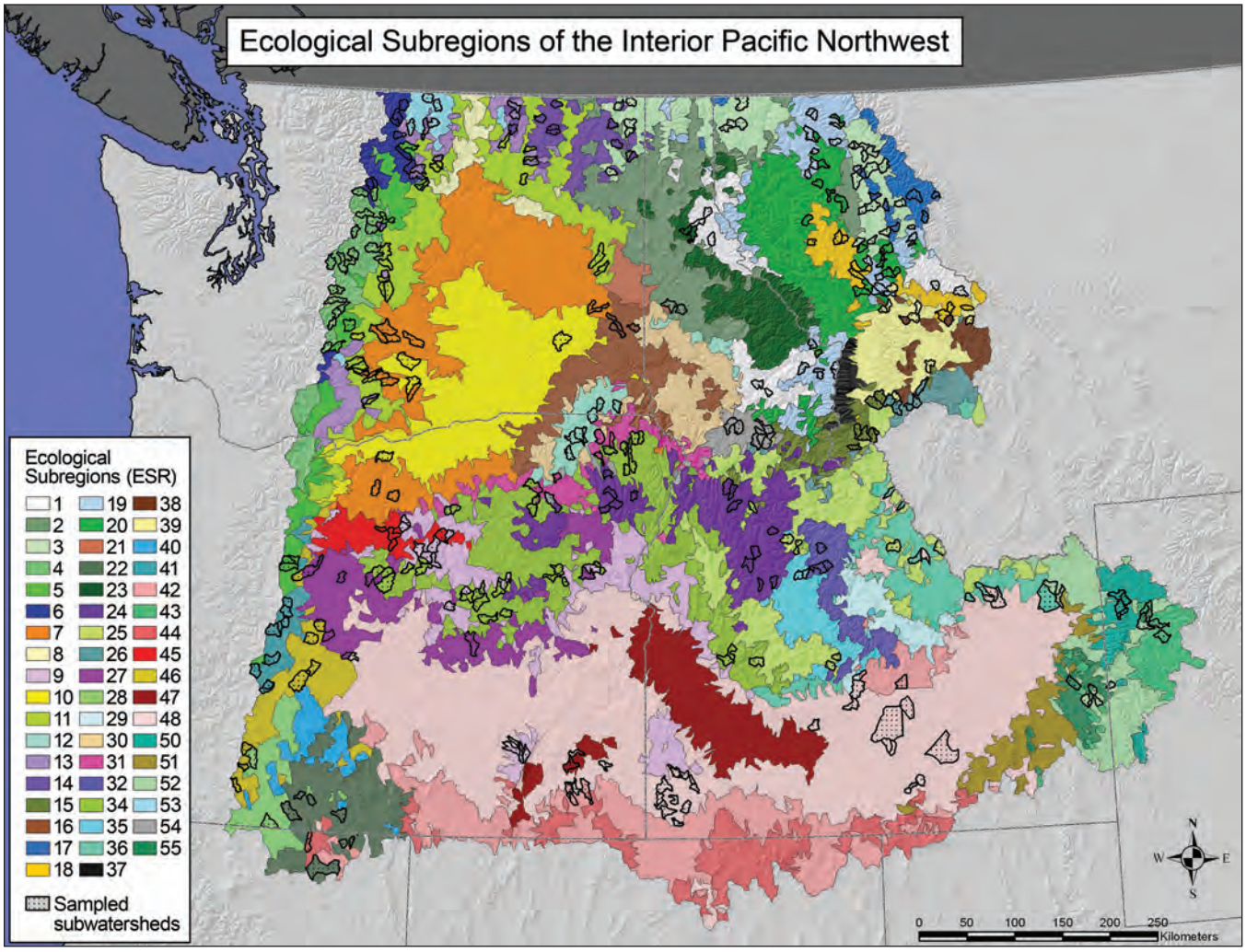


Figure 25—Ecological subregions of the interior Columbia River basin (Hessburg et al. 2000a). Names corresponding with ESR numbers are of the form: [ESR number = Bailey's (Bailey et al. 1994) ecoregion—Dominant Precipitation class(es)—Dominant Temperature class(es)—Dominant Potential Vegetation Group(s)—Dominant Solar Radiation class(es)]: 1 = M330–Wet–Warm–MF–Mod solar; 2 = M333–Moist–Warm–MF/DF–Low solar; 3 = M333–Moist–Cold–MF–Low solar; 4 = M242C–Wet–Warm–MFCF–Low solar; 5 = M242C–Moist–Warm–MF/CF–Mod solar; 6 = M242C–Wet–Cold–CF–Mod/Low solar; 7 = 342I–Dry–Warm–DS–Mod solar; 8 = M333A–Dry–Warm/Hot–DG–Mod solar; 9 = 300–Moist/Dry–Warm–DS/CS–High solar; 10 = 342I–Dry–Hot–DS/DG–Mod solar; 11 = 200/300–Dry/Moist–Warm–MF/DF–Mod solar; 12 = M330–Moist–Warm–DF–Mod solar; 13 = 200/300–Moist–Warm/Cold–MF–Mod solar; 14 = M333A–Moist–Warm/Cold–MF–Mod solar; 15 = M332–Moist/Wet–Cold–CF/DF–Mod/High solar; 16 = 330–Moist–Hot–DG–Mod solar; 17 = M333C–Wet–Cold–MF/CF–Low solar; 18 = M330–Moist–Warm–DF/DG–Mod solar; 19 = M330–Wet–Cold–MF/CF–Mod solar; 20 = M330–Moist–Cold/Warm – MF–Mod solar; 21 = 331A–Moist–Warm–DG–Low solar; 22 = 200–Moist/Dry–Warm–DF–Very high/High solar; 23 = M333D–Wet–Warm/Cold–MF–Low solar; 24 = M332–Moist/Wet–Cold–CF/DF/MF–High solar; 25 = M332–Moist–Cold–DF/CF–High solar; 26 = M332–Moist/Dry–Cold–CF–High/Mod solar; 27 = 300–Dry–Warm–CS/DF–High solar; 28 = 200 – Moist–Warm–DF/DG–High solar; 29 = M332–Dry–Cold–DS/CS–High solar; 30 = 300–Moist–Warm–DG/DF–Mod solar; 31 = 300–Moist–Warm–DF/DG–Mod solar; 32 = M332F–Moist–Cold/Frigid–CF–High/Very high solar; 34 = M332–Moist–Warm/Cold–DF/CS–High solar; 35 = M332–Moist–Cold–CF/DG–High/Very high solar; 36 = M332–Dry–Cold/Warm–DS/CS – High solar; 37 = M332B–Wet–Cold–RK/CF–Mod solar; 38 = M332–Moist–Cold–CF/DF/DG–Mod solar; 39 = M332B–Moist–Warm/Cold–DF/CF/DG–Mod solar; 40 = 200–Moist–Warm/Cold–DF–High/Very high solar; 41 = M242C–Moist–Warm–MF/DF/CF–High solar; 42 = 300–Dry–Warm–DS/CS–Very high solar; 43 = M331D–Moist–Cold–CF/DF/WD–Very high solar; 44 = 342–Dry/Moist–Warm–DS/CS–Very high solar; 45 = 342H–Dry–Warm/Hot–DS/CS–High solar; 46 = M242C – Moist–Warm–DF–High solar; 47 = 342C–Dry–Hot–DS/RS–High solar; 48 = 342–Dry–Warm–DS–High solar; 50 = M331–Moist/Wet–Cold/Frigid–CF–High solar; 51 = 300–Moist/Dry–Warm–DS/WD–High solar; 52 = M331–Moist–Cold–CF/WD – High solar; 53 = M242C–Moist–Cold–CF–Mod solar; 54 = M332–Moist–Warm–MF/DF–Mod solar; 55 = M331D–Moist – Cold–WD–High solar. Potential Vegetation Groups are: AL = Alpine; CF = Cold Forest; CS = Cool Shrub; DF = Dry Forest; DG = Dry Grass; DS = Dry Shrub; MF = Moist Forest; RS = Riparian Shrub; RW = Riparian Woodland; RK = Rock; WA = Water; WD = Woodland. Precipitation classes are: Very Dry = 0–150 mm/yr; Dry = 150–400 mm/yr; Moist = 400–1100 mm/yr; Wet = 1100–3000 mm/yr and Very Wet = 3000–8100 mm/yr. Temperature classes are: Frigid = –10––1 °C; Cold = 0–4 °C; Warm = 5–9 °C; Hot = 10–14 °C. Solar radiation classes are: very low = 150–200 W/m^2; low = 200–250 W/m^2; moderate = 250–300 W/m^2; high = 300–350 W/m^2; very high = 350–400 W/m^2. Mixed composition of attributes is indicated with a " / " and mixed attributes are listed in order of decreasing abundance. Sampled subwatersheds shown are those sampled by Hessburg et al. 2000a.

Large-amplitude and long-term changes relative to organism tolerance (often over several decades to centuries) reshape pattern envelopes by imprinting those landscapes with new disturbance and recovery patterns over large areas.

Changes that are small in amplitude and short term relative to the tolerances of dominant organisms (often multiannual to multidecadal) will do little to reshape the envelope because of the strength of system memory (inertia and elasticity; existing patterns of disturbance and recovery), expressed in successional stages and composition of vegetation. But large-amplitude and long-term changes relative to organism tolerance (often over several decades to centuries) reshape pattern envelopes by imprinting those landscapes with new disturbance and recovery patterns over large areas. For example, changes to the climate of the Southwestern United States desert biome since the last glacial maximum have been so substantial that plant and animal species ranges have fundamentally shifted and reorganized, along with their disturbance regimes (Betancourt et al. 1990).

It is informative for managers to understand the ranges of structural and compositional conditions that occur within landscapes of a region or subregion. Forest ecosystem response will be consistent with the current biophysical conditions and their disturbance regimes, including current climate forcing. For example, it is not clear how much the existing distribution of MMC forest will change with projected future climates and altered disturbance regimes. Fine-scale and gradual processes of mortality, dispersal, and range expansion are probably operating now to "adjust" patterns of species and ecosystems to the prevailing climate and disturbance trends of recent decades. Knowledge of factors controlling movement of species across landscapes provides insights to managers about how current landscape conditions will likely change, and thus how MMC forests may be able to persist under a changing climate. Multiscale research and monitoring are needed to elucidate these trends. Such information would enable a clearer vision to anticipate trends and develop tools for maintaining management options.

Natural Disturbance Factors

In this section, we highlight key disturbance factors in the MMC forest. Disturbance regimes vary across climate and environmental gradients in a relatively predictable fashion. These disturbances strongly influence vegetation composition, structure and habitat conditions, which themselves influence the variability of disturbances. These are brief synopses of complex topics, and we encourage the reader to delve deeper into the literature cited for more detail.

Wildfire—

Fire histories are not adequately documented in many moist forests in eastern Oregon and Washington. Our knowledge of past fire regimes and forest structure comes from proxy records, all of which are rich sources of data, but none of which is complete. Tree rings are one source of empirical data that can lead to

multicentury reconstructions of fire and forest history, but only over small areas. Fire and forest vegetation histories reconstructed from aerial photos from the 1930s and 1940s are another source of empirical data, and although many such reconstructions predate most logging, most represent conditions that occurred 30 to 60 years after fires were already excluded. Thus our inferences are constrained by data limitations, especially when we need to apply them to particular potential vegetation types or ecoregions.

Historical fire regimes across the region—In this region, several spatially extensive studies have reconstructed multicentury histories of low-severity fire regimes from fire scars in dry and MMC forests and inferred their climate, topographic, and land-use drivers at landscape and regional scales (Everett et al. 2000, Hessl et al. 2004, Heyerdahl et al. 2001, Kellogg et al. 2008, Wright and Agee 2004). However, few studies have focused specifically on MMC forests as we define them (Hessburg et al. 1999a, 1999c, 1999d, 2007; Heyerdahl et al. 2001; Perry et al. 2011; Tiedemann and Woodard 2002; Woodard 1977; Wright and Agee 2004). These studies suggest that mixed-severity fire was likely a dominant influence with smaller amounts of low- and high-severity fire. Current forest structure and life history strategies of trees typically found in mesic forests support our assumptions that historical fires were less frequent than in dry ponderosa pine and mixed-conifer forests and were of mixed severity (Agee 1993).

Although we have little quantitative information on the size (but see Perry et al. 2011) and frequency of past fires in MMC forests, mean fire return intervals may have much less importance than the range of fire intervals in this forest type (Halofsky et al. 2011). From only a few reconstructed fires (e.g., eight fires in Heyerdahl et al. 2001), there was a broad range of return intervals (several decades to more than 100 years, often within a single stand), but information on historical fire size was unobtainable with these methods. No studies have been designed to identify fine-scale variation in fire severity (i.e., patch size) within individual fires and only one within PVTs (see Hessburg et al. 2007). Landscape-scale reconstructions of forest structure from early to mid-20th century aerial photographs across the region also indicate that fires were of mixed severity (Hessburg et al. 2007). Perry et al. (2011) provided fire severity patch size distributions relating to dry and MMC forests in eastern Washington using the Hessburg et al. (2007) data set.

Historical fire regimes in MMC forests of this region likely varied across a broad range of spatial and temporal scales in response to regional variation in climate and physical geology, and local variation in topography and environments (Gedalof et al. 2005, Heyerdahl et al. 2001, Littell et al. 2009). These factors also control vegetation distribution, but PVT as mentioned above is only one predictor

of historical fire frequency or severity (Hessburg et al. 2007, Heyerdahl et al. 2001). Historical fire regimes have been reconstructed in MMC forests elsewhere in the Interior West, but presently we do not have enough information about spatial and temporal variation in the drivers of fire in these forests to know how well these reconstructions capture historical fire regimes throughout eastern Oregon and Washington. Low-severity fires were strongly synchronized in dry forests across the region by climate in the past (Heyerdahl et al. 2008) and the same may be true for moist forests, but the case has not been clearly made. Historical fire severity patterns have been reconstructed using dendroecological methods from about 10 percent of the total area of dry and MMC forests of the eastern Cascades in Washington. Extensive data sets are available from the Hessburg et al. (1999a, 1999b, 1999c, 1999d) Interior Columbia River Basin data archive to continue this work in the Blue Mountains and eastern Oregon Cascades.

Fire dynamics: resulting spatial patterns and tree mortality rates—Fire is a significant driver of mixed-conifer forest and aquatic ecosystems. The periodic influences of fire largely control the rates and patterns of succession and determine forest structure and composition, and aquatic and riparian condition. Despite recent contributions to the literature, there is still much scientific uncertainty and lack of consensus on the characteristics of fire regimes of mixed-conifer forests (amounts of low, mixed, and high severity), and how these varied by ecoregion. This lack of understanding (and investment in understanding) of the fire ecology of MMC forests limits the ability of managers to effectively identify appropriate steps toward ecosystem restoration. We do know that natural fire regimes in MMC forests varied somewhat predictably within areas that shared a similar climate and vegetation type, as well as topographic, edaphic (soil related), and environmental settings (Perry et al. 2011) (app. 3).

Low- to mixed-severity fires produced a highly variable mosaic of living and dead trees at multiple spatial scales, resulting in patchy regeneration in stands and landscapes, and perpetuating the low- and mixed-severity fire cycle. Low-severity fires (killing less than 25 percent of the overstory) typically occurred where fires were most frequent (e.g., every 10 to 30 years). MMC patches that experienced low-severity fire occurred in areas and slope positions that were adjacent to dry mixed-conifer and ponderosa pine woodlands. Low- and mixed-severity fire appear to be dominant in the eastern Cascades and parts of the Blue Mountains based on recent and ongoing work (Merschel 2012). Elevation and aspect influences on plant available soil moisture played important roles. Figure 26 illustrates a forest subject to a typical low-severity fire regime.



Tom Iraci

Figure 26—An example of a low-severity prescribed fire. These fires are characterized by minimal short-term ecosystem effects. The result of a low-severity fire is fuel reduction and topkill of understory vegetation.

Mixed-severity fires (killing 25 to 75 percent of the overstory) were common in the MMC forest because much of the area in these productive systems was visited by wildfires on a relatively infrequent basis (i.e., about every 25 to 75 years). This allowed for the development of a patchy vegetation mosaic, with patchy patterns of surface and ladder fuels, and both open and closed canopy conditions (app. 3). One may contrast fire severity in this way: low-, mixed-, and high-severity fires produced fine-, meso-, and broad-scale patchiness of tree structure and species composition within local and regional landscapes. Figure 27 illustrates a forest subject to a typical mixed-severity fire regime.

High-severity fires (resulting in over 75 percent overstory mortality) occurred occasionally (Agee 1990, 1993, 1994, 1998; Baker 2012; Hessburg, et al. 2007; Heyerdahl et al. 2001, 2008; Williams and Baker 2012), especially where fire return intervals exceeded 100 to 150 years. These conditions tended to occur in slope and aspect conditions adjacent to wet and cool to cold forests (e.g., western hemlock, mountain hemlock [*Tsuga mertensiana* (Bong.) Carrière], Shasta red fir, and Pacific silver fir [*Abies amabilis* (Douglas ex Loudon) Douglas ex Forbes)]) and did not appear to dominate the fire regime of MMC forests. Figure 28 illustrates a forest subject to a high-severity fire regime.

John Marshall



Figure 27—An example of the impacts of a mixed-severity fire, exhibiting a wide range of effects on the dominant vegetation. Some areas exhibit low fire severity, with little damage to overstory trees, while others exhibit moderate fire severity. Some areas exhibit high severity as indicated by complete mortality of the overstory.

John Marshall



Figure 28—An example of a high-severity fire, characterized by high levels of tree mortality, significant fuel consumption, and often extensive soil heating.

Landscape patterns: patch size and shape resulting from fire—There is still much to learn, but we know from fire history reconstructions using fire scars that small (1 to 50 ha [~2 to 123 ac]) to medium-sized (100 to 5,000 ha [~247 to 12,355 ac]) fires were most numerous, and pock-marked the landscape. They represented 85 to 95 percent of fire events, but only accounted for 5 to 15 percent of all of the landscape area burned by historical wildfires (Malamud et al. 1998, 2005) (fig. 29). The primary role of these smaller fires was to spatially isolate patterns of combustible surface and canopy fuels across the landscape (Moritz et al. 2010). In fact, the common small fires (that are currently suppressed) played a key role in shaping the larger landscape. Burned and newly recovering patches to some extent spatially interrupted the flow of larger fires, often limiting their spread. This was the primary mechanism maintaining the frequency-size distributions of wildfires. Large fires (>5000 ha [12,355 ac]) were much rarer, but they typically burned most of the landscape area that was subject to fire (75 to 95 percent).

We know from fire history reconstructions using fire scars that small to medium-sized fires were most numerous, and pock-marked the landscape.

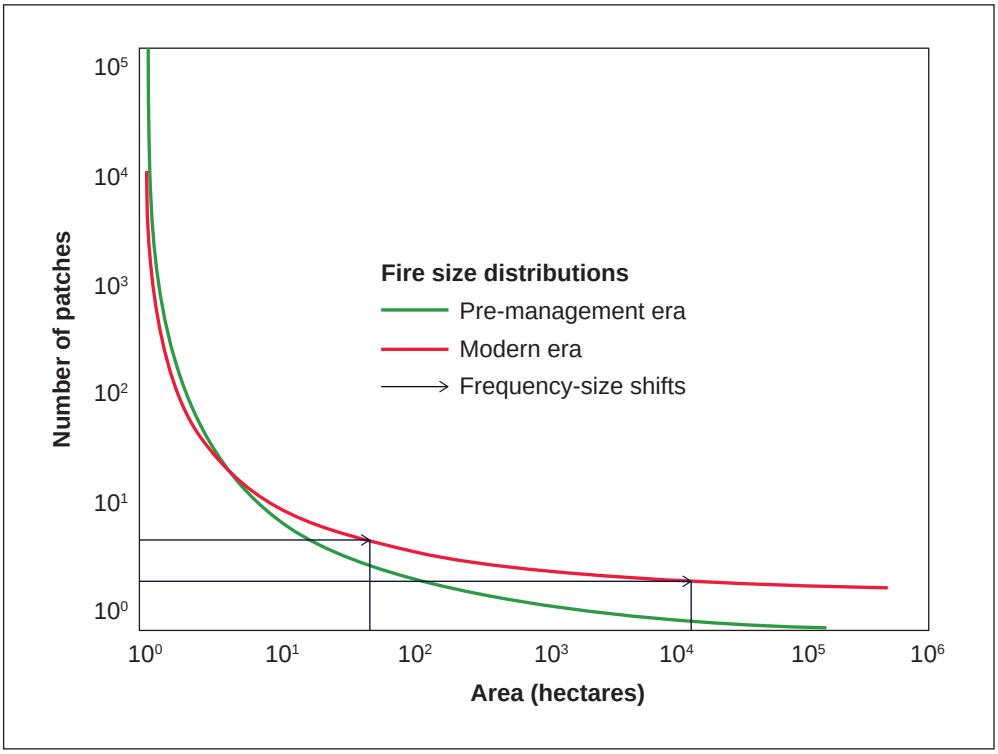


Figure 29—A comparison of fire size distributions in the pre-management and modern era. This illustrates the frequency-size shift toward larger burn patches in the modern era.

The distribution of fire event sizes approximated the negative exponential (an inverse-J distribution in the native form), and this appeared to be true regardless of fire severity (Perry et al. 2011). Overall fire frequency controlled the size of the largest fires. Numerous small- and medium-sized fires created patches of burned areas, in some stage of recovery, which reduced the likelihood of future fire spread. This mechanism likely provided a self-reinforcing type of resilience to the regional landscape. With relatively high fire frequency (as in surface fire dominated fire regimes), the largest fires were generally smaller than with relatively low fire frequency (characteristic of high-severity fire regimes).

Both landscapes and patches provided important feedbacks to wildfire frequency, severity, and size. At a landscape scale, low-, mixed-, and high-severity fires likely maintained patchworks of burned and recovering vegetation. Patches varied by size, age, density, layering, species composition, and surface fuelbed, and these landscape patterns spatially interrupted conditions that supported large disturbances, except under extreme conditions. Low- and mixed-severity fires also provided important patch level feedbacks, which encouraged subsequent low- or mixed-severity fires (Agee 2003, Agee and Skinner 2005, Hessburg and Agee 2003). Such fires frequently reduced surface fuels, which favored shorter flame lengths, and reduced fireline intensities (rate of heat release per unit length of fire front). They also increased the height to live crowns, which favored less torching, and reduced the likelihood of crown fire initiation. They decreased crown density, which reduced crown fire initiation and spread potential, favored young forest tree species, which increased tree survival during wildfires and droughts, and favored medium- and large-sized trees, which increased tree survival during wildfires. Finally, low- and mixed-severity fires produced patchy tree and surface fuel cover, which favored fire-tolerant species, and repeated low- and mixed-severity fires.

During periods of extreme weather or during rare climate events, wildfires could become very large, and fire behavior was often unrelated to the initial forest conditions, but was instead correlated with the conditioning climate or weather influences. Fire size distributions and the vegetation patchwork that supported them have been altered by a host of management and settlement influences, which we have summarized.

Insects—

In eastern Oregon and Washington, several insect species are significant disturbance factors in MMC forests, including four native bark beetle species and two native defoliating species (Hayes and Daterman 2001, Hayes and Ragenovich 2001, Torgersen 2001). In addition to these, there is one nonnative defoliating species and

one nonnative sap-sucking species of importance (table 4). The impact of these insects is influenced by other disturbances (e.g., root disease, extreme weather events, wind storms, or wildfire) while outbreaks influence the frequency, severity and extent of other disturbances.

Unlike defoliating insects, bark beetles feed on the phloem tissue beneath the bark, often directly killing the host quickly via girdling. Beetles that initiate host selection are often killed by drowning or immobilization in resin, so successful colonization requires a minimum number of beetles to "mass attack" the tree and overcome its defenses (Franceschi et al. 2005). This number varies, as more vigorous hosts require higher densities of beetles (Fettig et al. 2007). Therefore, the legacy of past disturbances influences the susceptibility of forests to future bark beetle outbreaks by affecting their structure and composition. Many bark beetle species exhibit a preference for larger diameter trees growing in high-density stands with a high percentage of host type (Fettig et al. 2007). Larger diameter trees generally provide for a higher reproductive potential and probability of survival (e.g., Graf et al. 2012, Reid and Purcell 2011) because of the greater quantity of food (phloem) available on which larvae feed. The effects of density are mediated through factors that affect host finding and colonization success, primarily microclimate, tree spacing, and changes in host vigor as mediated through the influence of growing space. Over the last decade, the majority of insect-caused tree mortality detected during aerial surveys in the region has been attributed to outbreaks of the mountain pine beetle (*Dendroctonus ponderosae*). The impact of this insect seems to be increasing in eastern Oregon and Washington, likely owing to changes in tree density and the abundance of preferred hosts (table 4), and is expected to intensify in the future (see "Climate Change" on page 102 and "Changes in Disturbance Factors: Insects and Disease" on page 115).

Defoliators consume, mine, or skeletonize the foliage of trees and may cause tree mortality depending on the species and host, and the timing, frequency and severity of feeding. Without question, the two most important defoliators in MMC forests of eastern Oregon and Washington are the Douglas-fir tussock moth (*Orgyia pseudotsugata*) and western spruce budworm (*Choristoneura occidentalis*) (table 4, figs. 30 and 31), which are notable for their infrequent, but occasional large-scale outbreaks (Torgersen 2001). Natural enemy populations (parasites, predators, and parasitoids) have a strong regulatory effect on their populations resulting in long time lags between outbreaks. In particular, western spruce budworm populations are well-coordinated with climate (Kemp et al. 1985, Volney and Fleming 2007). From the 1950s to 1980s, large-scale efforts were implemented to control Douglas-fir tussock moth and western spruce budworm outbreaks using aerially applied

Table 4—Insects considered major disturbances in moist mixed-conifer forests of eastern Oregon and Washington

Common name	Scientific name	Primary host(s) in region	Scale of outbreaks	Impacts
Bark beetles:				
Douglas-fir beetle	*Dendroctonus pseudotsugae*	Douglas-fir	Local to landscape	Mortality of individual trees or small groups of trees is typically associated with defoliation, drought, windthrow, wildfire, or root disease. Once established, outbreaks may cause large amounts of tree mortality over extensive areas.
Fir engraver	*Scolytus ventralis*	Grand fir, white fir	Local to landscape	Mortality of individual trees or small groups of trees is typically associated with drought and defoliation. Once established, outbreaks may cause large amounts of tree mortality.
Mountain pine beetle	*Dendroctonus ponderosae*	Lodgepole pine, ponderosa pine, western white pine	Local to regional	Episodic outbreaks are a common occurrence, but the magnitude and extent of recent outbreaks have exceeded the range of historic variability in much of the Western United States.
Western balsam bark beetle	*Dryocoetes confusus*	Grand fir, subalpine fir	Local to landscape	Mortality of individual trees or small groups of trees is common and associated with windthrow.
Defoliators and other:				
Balsam woolly adelgid	*Adelges piceae*	Grand fir, silver fir, subalpine fir	Local	Accidentally introduced into the United States from Europe and first detected in the Pacific Northwest in 1929. Adelgids are sap-sucking insects. Feeding causes abnormal growth responses in affected trees termed "rotholtz." Severe infestations cause growth loss, top-kill, and tree mortality.
Douglas-fir tussock moth	*Orgyia pseudotsugata*	Douglas-fir, grand fir, white fir, subalpine fir	Local to regional	Larval feeding causes growth loss, top-kill, and tree mortality. Outbreaks are often short-lived.
Larch casebearer	*Coleophora laricella*	Western larch	Local	Accidentally introduced into the United States from Europe and first detected in the Pacific Northwest in the 1950s. Larvae mine needles. Severe defoliation occurs, but larch (a deciduous conifer) withstands repeated defoliation. Growth loss is common, but tree mortality is rare.
Western spruce budworm	*Choristoneura occidentalis*	Douglas-fir, grand fir, white fir, subalpine fir, western larch	Local to regional	Early instar larvae mine needles and buds. Late instar larval feeding causes growth loss, top-kill, and tree mortality. Feeding on staminate flowers and conelets affects regeneration.



William M. Ciesla, Forest Health Management International, Bugwood.org

Figure 30—Douglas-fir tussock moth larvae.



Lia Spiegel

Figure 31—Spruce budworm larvae.

Although insect infestations affect timber and fiber production, and indirectly affect a range of ecosystem goods and services, numerous organisms depend on insect-related disturbances for their existence.

chemical and biological (bacteria- and virus-based) insecticides, but were thought to have little effect on population dynamics or levels of tree mortality (Torgersen 2011, Torgersen et al. 2005). A successful example of classical biological control has significantly limited the impact of larch casebearer (*Coleophora laricella*) in the region (Ryan 1997).

Although insect infestations affect timber and fiber production, and indirectly affect a range of ecosystem goods and services, numerous organisms depend on insect-related disturbances for their existence. Trees weakened or killed by insects and other disturbances (e.g., pathogens) can result in the transience of old forest structural conditions, and also create structure and food sources that have significant value to wildlife communities. The section "Animals of the Moist Mixed-Conifer Ecosystem" on page 75 provides some detail on the role of snags and downed logs to wildlife. Furthermore, mortality of individual or small groups of overstory trees has a significant influence on the fine-scale spatial heterogeneity of mixed-conifer forests (Fettig 2012). For example, some insects, specifically bark beetles, inflict density-dependent tree mortality (Fettig et al. 2007), and consequently maintain a mix of tree species, ages, sizes and spatial heterogeneity that influence other disturbances (e.g., wildfire).

There is some evidence that large-scale tree mortality events associated with insect outbreaks may increase fire risk and severity in affected forests. In recent years, these relationships have been studied most extensively in lodgepole pine forests affected by mountain pine beetle (fig. 32). Although there is some disagreement over predicted changes in fire behavior during and after mountain pine beetle outbreaks (reviewed most recently by Jenkins et al. 2014), most studies predict increases in surface fire rates of spread and fireline intensities resulting from increases in fine fuel loadings and reductions in sheltering (e.g., Hicke et al. 2012, Klutsch et al. 2011, Page and Jenkins 2007). During outbreaks, changes in foliar chemistry and moisture content may also increase probabilities of torching and crowning, and the likelihood of spotting (Jolly et al. 2012, Page et al. 2012). Similarly, feeding by defoliators reduces crown cover, increasing the amount of light reaching the forest floor and influencing understory and mid-story vegetative dynamics. For example, western spruce budworm outbreaks have been shown to increase surface fuel loads, yet changes in fire behavior were not significant (Hummel and Agee 2003).

The current structure and composition of dry and MMC forests is thought to be more susceptible to large-scale defoliation by Douglas-fir tussock moth and western spruce budworm in areas where fire suppression and selective harvesting of ponderosa pine and larch have favored Douglas-fir, grand fir, and white fir.



Figure 32—Mortality of lodgepole pine attributed to mountain pine beetle (*Dendroctonus ponderosae*) in northern Utah. In recent years, the effects of mountain pine beetle on fuels and fire behavior have been studied most extensively in the lodgepole pine forests of the Rocky Mountains. This species, however, now represents a significant threat to the mixed-conifer forests of eastern Oregon and Washington.

Defoliation, largely the result of infestation of these two insects, often predisposes trees to subsequent mass attack by other insects, specifically bark beetles such as the Douglas-fir beetle (*Dendroctonus pseudotsugata*).

Diseases—

In eastern Oregon and Washington, several notable forest pathogens produce significant disturbance in MMC forests, including five host-specialized dwarf mistletoes and four native root pathogens. Disturbance comes in the form of tree mortality and reduced tree growth, both of which are influential to forest succession and stand dynamics processes. Numerous stem decay organisms are also common in large and older trees of most species. These are excluded for brevity here, but we urge interested readers to delve into this literature. For a concise survey of the most common diseases and insects affecting inland Pacific Northwest forests, we refer the reader to Goheen and Willhite (2006), and recommended references therein.

Four tree-killing root diseases naturally occur in MMC forests: laminated root rot, caused by *Phellinus weirii*; Armillaria root disease, caused by *Armillaria ostoyae*; and both the P- and S-type annosum root diseases (formerly *Heterobasidion annosum*, now *H. irregular* and *H. occidentale*, respectively) (Filip 1990; Filip and Goheen 1982, 1984; Goheen and Filip 1980; Hadfield et al. 1986). Root diseases were common (<5 to 10 percent of patches affected) but not dominant in most presettlement-era MMC forests, where they provided structural diversity within patches and enhanced heterogeneity in size of openings, amount and shape of edge, and size of patches. They were likely most visible in areas with relatively infrequent fire, and less visible in areas influenced by frequent low- and mixed-severity fires (e.g., south-facing slopes and ridges), and where the dominant tree cover was ponderosa pine or western larch.

Laminated root rot infects and kills susceptible Douglas-fir, grand fir, and white fir that grow in patches missed by fire. Transmission of the fungus that causes this disease occurs via mycelial growth, when roots of susceptible host trees come in contact with those of infected trees. Because the root systems of host trees are often well rotted after they are infected, these trees usually fall over in a jackstraw arrangement (Hadfield et al. 1986). Owing to the dominance of historical wildfires and the relative rarity of root rot centers (in comparison with current conditions), historical root disease centers likely provided small to large gaps that contained root disease resistant hardwood shrubs and trees and other resistant conifer species, which enhanced plant species richness, and provided mast and a variety of habitats suitable for small mammals (Maser et al. 1979; Thomas et al. 1979a, 1979b).

Armillaria root disease also infects and kills susceptible grand and white fir, and occasionally Douglas-fir that grow in patches missed by fire. Transmission of the fungus that causes this disease occurs when roots of susceptible host trees come in contact with those of infected trees. Inter-tree transmission is facilitated by fungal mycelia and by specialized root-like fungal structures called rhizomorphs. Armillaria root disease ecology at the end of the 19th century was probably very similar to that of laminated root rot. Armillaria root disease probably played a role in forest succession and stand dynamics of many refugia dominated by grand or white fir. Refugia were found in shaded draws, on cool north slopes, in riparian areas and stream confluence zones (Camp et al. 1997), and adjacent to rock outcroppings and talus slopes, where fires burned with difficulty. This pathogen also overwhelmed low-vigor, mature, weakened, and injured trees, and those stressed by drought or lightning strike, scorched by fire, or attacked by other root pathogens (Filip and Goheen 1982, Goheen and Filip 1980). Thus, it is fairly common to find more than a single root pathogen colonizing trees.

P- and S-type annosum root disease centers were relatively uncommon in presettlement-era forests. These diseases require freshly cut stumps or wounds for windborne spores to infect and initiate new root-disease centers. Before tree harvesting, annosum root disease existed as a butt rot of trees with root collar and stem wounds. In central, southern, and northeastern Oregon, stands that have had multiple entries to harvest trees have been shown to have the highest annosum root disease and associated bark beetle-caused tree mortality (Filip et al. 1992; Schmitt et al. 1984, 1991). Most surprising in the MMC forest is the rate of increase in S-type annosum root disease (*H. occidentale*) in grand and white fir. These forests contain large increases in S-type annosum because stumps were infected by spores when stands were logged (Filip et al. 1992, Hadfield et al. 1986, Otrosina and Cobb 1989). Because S-type isolates are primarily pathogenic on true firs and spruces, the roles these stumps will play in the future incidence of disease is uncertain. Infection centers will continue to expand until fire or silvicultural activities create conditions for the reintroduction of young forest species.

Pine stump infection by P-type annosum (*H. irregular*) is often high in Douglas-fir and grand fir forests, but mortality in ponderosa pine is uncommon. With prolonged warming, however, P-type annosum may become more serious on what are now mesic white and grand fir sites.

In the current condition, all major tree-killing root diseases except P-type annosum are widespread, following landscape colonization by grand fir, white fir, and Douglas-fir (Hessburg et al. 1994). Collectively, the effects of root diseases on tree growth and mortality, and their contributions to flammable fuels are ecologically significant. At a watershed or subwatershed scale, as much as 7 to 10 percent of the area can be influenced at any one time by active infection centers.

Dwarf mistletoes have occurred for many millennia in Douglas-fir, ponderosa pine, western larch, lodgepole pine, and true firs but none was particularly threatening to the long survival of its host species (Alexander and Hawksworth 1975, Parmeter 1978, Tinnin 1981). Douglas-fir dwarf mistletoe (*Arceuthobium douglasii*) and western larch dwarf mistletoe (*A. laricis*) were probably common in mid-seral and old forests before the 20th century. Areas infested with these mistletoes tended to be the more mesic plant associations, in which fires appeared with moderate frequency. Mistletoes were probably most common on south-facing slopes, where fires were low- or mixed-severity, maintaining multiple cohorts, sizes, ages and layers of host trees. High-intensity fires would typically eliminate most (but not all) mistletoe-infested trees over large areas, and mistletoes would slowly re-invade from the perimeter at the rate of 3 to 4.5 m (10 to 15 ft) a decade (Hawksworth 1958, 1960; Parmeter 1978; Wagener 1965), or from islands of infested trees that

escaped burning. Especially in ponderosa pine and Douglas-fir, severe mistletoe infections provide an abundance of mistletoe brooms, fine fuels, resinous stems, branches, and cankers. Even low- and moderate-intensity fires would often torch these trees, destroying severely infected trees and infection centers (Koonce and Roth 1980, Parmeter 1978, Weaver 1974). No doubt active and passive crown fires were initiated in areas of severe mistletoe infestation.

Dwarf mistletoe in Douglas-fir was probably more common on northerly aspects and in riparian areas, where the interval between fires was longer. Under historical fire regimes, Douglas-fir dwarf mistletoe was probably widely distributed but at low to moderate severity (Arno 1988, Fischer and Bradley 1987, Harrington 1991). Mature Douglas-fir, with thick outer bark and crown bases elevated well above the forest floor, were quite resistant to surface fires. Douglas-fir dwarf mistletoe was well distributed in scattered, thick-barked overstory trees that had developed on young forest dominated landscapes under the influence of low-intensity fire, but further influence was minimal because understory Douglas-fir stocking was minimal.

Conversely, young Douglas-fir had thin, resinous outer bark and crowns close to the forest floor, two characteristics that increased vulnerability to surface fires. When mistletoe brooms occurred on young trees, the likelihood of tree torching was increased (Harrington 1991, Tinnin 1984, Tinnin and Knutson 1980). Under the right wind and weather conditions, fires crowned from mistletoe-infected understories. In addition, mistletoe brooms in Douglas-fir nullified benefits of inter-tree competition and natural branch pruning by maintaining a flammable link with the forest floor. In patches where Douglas-fir was abundant in the understory, e.g., in northerly aspects, Douglas-fir dwarf mistletoe was probably quite abundant.

Given the range of fire frequency and severity in historical MMC forests, the western larch mistletoe was likely the most prevalent and influential in terms of tree growth and mortality. Western larch dwarf mistletoe was perhaps the most widespread of mistletoes in old forest stands. Of all the dwarf mistletoes, larch mistletoe survived fire in overstory western larch with the greatest constancy (Bolsinger 1978), perhaps because of larch's exceptional resistance to damage by fire (Lotan et al. 1981), its resistance or tolerance to both tree-killing and opportunistic root pathogens (Filip and Schmitt 1979, Hadfield et al. 1986), and the lack of primary bark beetle associates. Larch mistletoe brooms are weak and brittle and frequently break off when still relatively small. Under historical fire regimes, branch litter accumulating under infected hosts caused lethal fire scorching of some infected trees (Alexander and Hawksworth 1975). According to Tinnin et al. (1982), the increased burn potential accentuated the advantage of fire-adapted species such as western larch.

Dwarf mistletoes create brooms in trees, sometime quite large, and this produces critically important habitat structure for many species of wildlife. Brooms are used for nesting, roosting, and hiding cover (e.g., see Bull and Henjum 1990, Bull et al. 1989, Forsman 1983, Sovern et al. 2011). Birds and squirrels also contributed to reintroduction of mistletoes to large host patches (Hawksworth et al. 1987). Mistletoes would persist in residual ponderosa pine and western larch overstory trees by virtue of their resistance to fire, or from irregularities in fuel continuity or arrangement, or fire behavior, and the spread of these mistletoes to newly regenerating patches would be much quicker (Parmeter 1978). The presence of mistletoe brooms is a prime example of a long-standing struggle between objectives to manage for wood production (i.e., foresters would be inclined to remove diseased trees) and objectives to maintain or enhance wildlife habitat (wildlife specialists would advocate keeping these trees).

At least 40 percent of all of the Douglas-fir, western larch, ponderosa pine, and lodgepole pine forests east of the Cascade crest are infected with dwarf mistletoe (Bolsinger 1978). Infections are more widely distributed and have had a greater impact on tree health than ever before, except where large wildfires have recently occurred. Because of fire exclusion and selective timber harvesting, many remaining forests are densely stocked and multilayered, conditions that are conducive to spread of mistletoes. Conifers such as Douglas-fir or ponderosa pine with severe mistletoe infections exhibit declining crown vigor and reduced resistance, and are eventually attacked and killed by bark beetles and opportunistic root pathogens like Armillaria root disease (Hadfield et al. 1986, Morrison et al. 1991).

Animals of the Moist Mixed-Conifer Ecosystem

The landscape ecology concepts of resilience and natural range of variation described in the previous sections of this report provide important tools for understanding animal habitat and population function within MMC forests of the Pacific Northwest. Native animals evolved in the context of historical disturbance regimes and resultant landscape patterns. Managing for the natural range of variability (NRV) provides a conceptual starting point for capturing the habitat needs of native wildlife. Landscape resilience is also important to animal populations because it represents the tendency of a landscape to return to conditions that the native animal community is adapted to. Landscapes that are not resilient may shift into novel environmental conditions that can contribute to substantial changes in the animal community and loss of biodiversity. However, it is important to note that simply managing for resilient landscape conditions that are within the NRV may not be sufficient for the conservation of all animals (Wiens et al. 2008).

Native animals evolved in the context of historical disturbance regimes and resultant landscape patterns.

Some native species have been affected by threats not related to habitat amount and distribution, including interactions with invasive species (e.g., northern spotted owls [NSO] [*Strix occidentalis caurina*] and barred owls [*Strix varia*] [Gutierrez et al. 2007]), exposure to exotic diseases (e.g., bighorn sheep [*Ovis canadensis*] [Schommer and Woolever 2008]), or sensitivity to effects of specific human activities (e.g., disturbance associated with roads or recreation [Gaines et al. 2003]). Conservation of these species often requires more specific strategies that address habitat in combination with the specific risks to which they are sensitive. Several recent assessments have used this conceptual approach to compare the current landscape to estimates of habitat patterns under historical disturbance regimes to provide a "coarse filter" for evaluating the amount and distribution of habitat conditions, in conjunction with "fine filter" assessments of conditions for selected individual species that are sensitive to specific risks (Gaines et al., in press; Suring et al. 2011; Wales, et al. 2011, Wisdom et al. 2000). Results of these assessments are summarized in "Effects of Altered Disturbance Regimes, Land Use, and Climate Change on Animal Populations and Habitats" on page 115. Our focus in this section is to provide an overview of important considerations for managing fish and wildlife habitat and animal populations in MMC forests.

As highlighted in previous sections, the MMC forest type is characterized by environmental conditions that are intermediate between warm/dry and cold/wet forest types that are often adjacent to or intermixed with the MMC. This pattern results in an animal community that is composed of an overlapping mix of species that are also found in the adjacent forest types. The composition of the animal community and abundance of individual species within MMC forests depends on many factors including landscape patterns, forest structure, and how wet or dry conditions are within an individual stand and the surrounding landscape.

Using the wildlife habitat relationships database of Johnson and O'Neal (2001), Lehmkuhl (2005) concluded that bird and mammal communities in eastside interior MMC forests were a mix of species typical of low-severity low-elevation ponderosa pine forest (84 percent species similarity) and high-elevation high-severity mixed-conifer forest (71 percent species similarity). About 40 percent of all species were shared in common among the three types. Mixed-conifer forest was more similar to ponderosa pine forest in supporting relatively more generalist or young forest species than higher elevation forests. Within eastside habitat types and disturbance regimes, the fire-prone ponderosa pine cover type supports the most species of amphibians, reptiles, and birds; whereas mammals are most species-rich in mixed-conifer types (Bunnell 1995; Kotliar et al. 2002; Sallabanks et al. 2001, 2002).

A key concept for understanding animal distribution and abundance in MMC forests is that animals need to acquire a variety of resources to meet their life-history needs and most animals use a variety of different habitats and structural features to acquire those resources. Morrison et al. (1998: 10) described wildlife habitat as "an area with a combination of resources (like food, cover, water) and environmental conditions (temperature, precipitation, presence or absence of predators and competitors) that promotes occupancy by individuals of a given species (or population) and allows those individuals to survive and reproduce." In MMC forests, these wildlife habitat components are emergent properties of the forest communities and their growth, disturbance, and stand dynamics (sensu Oliver and Larsen 1996) processes. How these processes work at a variety of scales is important in determining where habitat components occur and whether they are arranged in a manner that allows animals to survive and reproduce. Like landscapes, areas used by animals can be thought of as "habitats within habitats" (fig. 33).

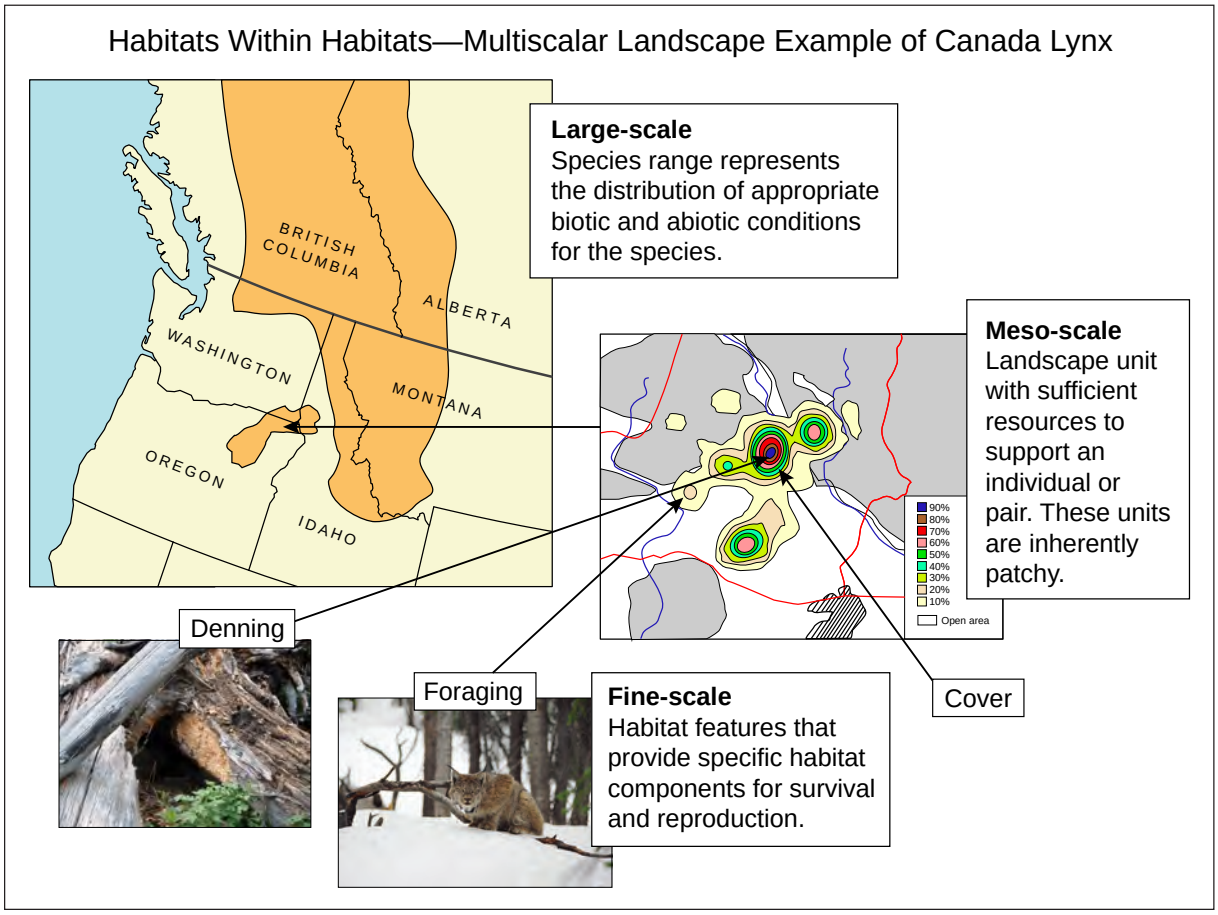


Figure 33—Wildlife habitat is represented at different scales. Individual animals are connected to key features of their environment over a confined spatial domain, small groups of a species interact regularly over a larger area, and populations of a species are distributed across large geographic areas. This multiscalar view illustrates the importance of considering habitat requirements of a species at different spatial scales.

At the finest scale, animals use habitat features associated with specific forest structure attributes (e.g., snags for foraging and nesting); at the meso-scale (sub-basin or watershed scale), they must find the appropriate configuration of those resources to meet their life-history requirements (e.g., the right combination of food availability and security from predators); and at the broadest scale, animals need to be able to move to find mates, disperse to new areas, prevent genetic isolation, and maintain broad-scale population function (meta-population dynamics). Selection of a finer-scale habitat feature is therefore constrained by habitat selection decisions made at broader scales (e.g., the forest stand an animal chooses to use is constrained by the variety of stands within the watershed where the animal is located [Johnson 1980]).

Landscape heterogeneity at a variety of scales plays an important role in determining the assortment of habitat conditions and resources available to the animal community in that landscape.

Landscape heterogeneity at a variety of scales plays an important role in determining the assortment of habitat conditions and resources available to the animal community in that landscape. At the broadest scale, the distribution of wildlife and fish species is determined by regional to subcontinental gradients in climate, topography, soils, and vegetation (Hansen et al. 2011). The tolerances of species to these biophysical gradients result in predictable patterns of community diversity. Across Oregon and Washington, species richness of birds, trees, and shrubs is highest in the Okanogan Highland and Siskiyou ecoregions (Hansen et al. 2006, Swenson and Waring 2006). The lower forest ecotones across the East Cascades, Okanogan Highlands, and Blue Mountains are also high in species diversity (Olson et al. 2001). These locations have intermediate precipitation, warm growing season temperatures, and intermediate primary productivity. These conditions provide diverse food resources, variable vegetation structure, and high levels of habitat diversity, with grassland/shrubland, dry forest, and moist forest habitats all in proximity. Amphibian diversity is low in the eastern Cascades compared to western Oregon and Washington, primarily because the dry climate in the eastern Cascades is less conducive to occupancy by amphibians (Olson et al. 2001).

The spatial patterning of habitats across Oregon and Washington is also important in influencing connectivity for wildlife and fish populations. Genetic diversity, metapopulation dynamics, and population viability for many species is dependent upon the ability of individuals to move across landscapes (Bennett 2003, Crooks and Sanjayan 2006, Hilty et al. 2006). Regional-scale landscape permeability patterns for forested landscapes in eastern Washington and Oregon (fig. 34) are important because these forests serve as important potential source areas for a variety of species in their own right, and they provide critical linkages between ecosystems in the Rocky Mountains, the Cascade Range, and into Canada (Singleton et al. 2002, Theobald et al. 2012, WHCWG 2010).

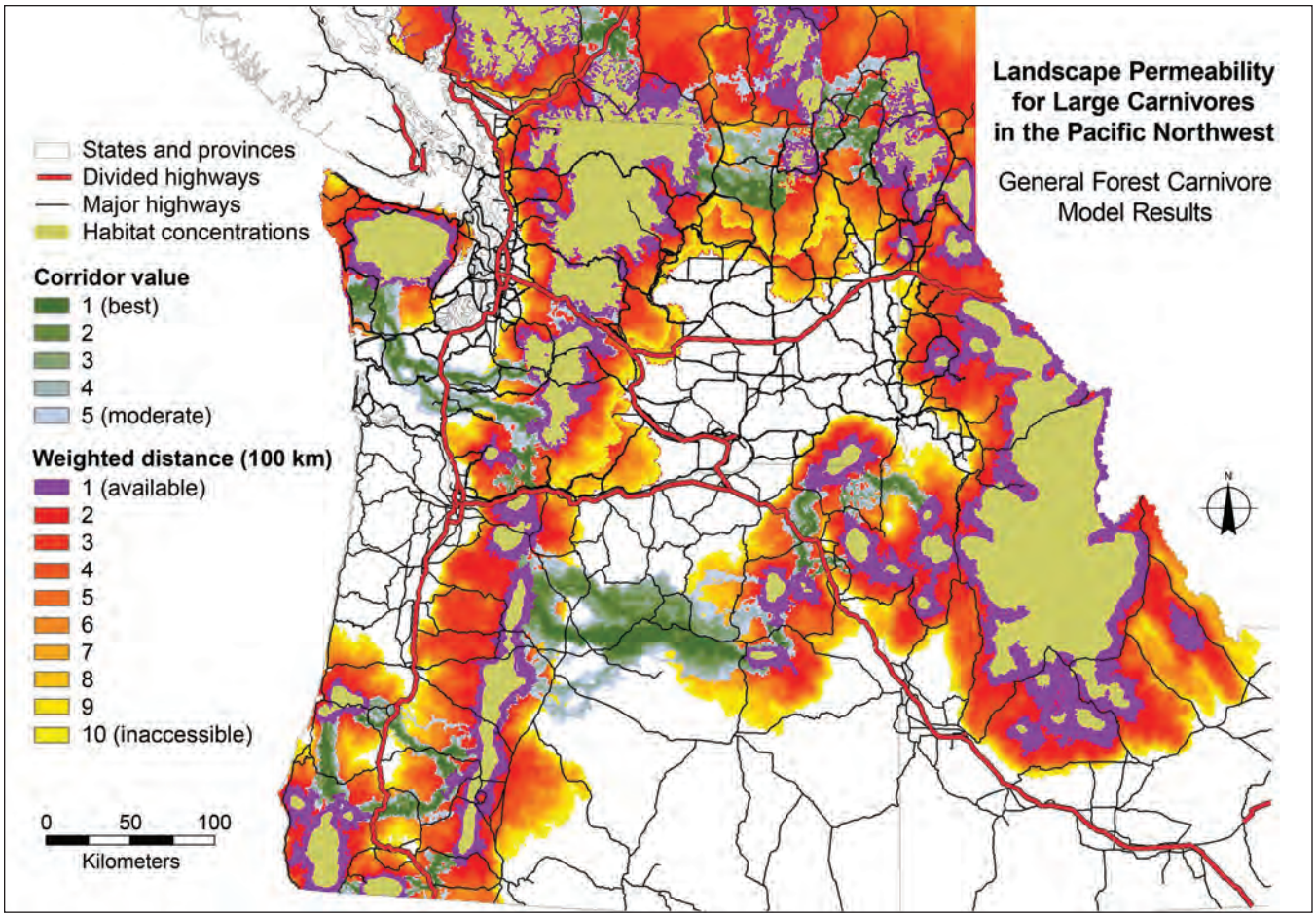


Figure 34—At a regional scale, habitat for large carnivores is more or less permeable to movement, depending on various vegetation and topographic conditions. This information is an important consideration when planning treatments for forests at a landscape scale.

Meso-scale landscape patchiness determines the arrangement of habitat resources for animals. A critical feature of wildlife habitat in mixed-conifer landscapes in eastern Washington and Oregon is the multiscale (landscape and stand) diversity and juxtaposition of patch types of differing composition and structure (Perry et al. 2011). Habitat heterogeneity on presettlement landscapes was largely a result of mixed-severity fire. As reviewed in previous sections of this report, the combination of extensive topographic variability, other intrinsic factors of the landscape (e.g., soils, accumulation of fuels, etc.), and the vagaries of weather interacted in each fire event to create complex mosaics of habitat with soft boundaries that distinguish the effects of varying fire severity. Forest patches in different stages of development typically have different habitat characteristics and provide different sorts of habitat features (Johnson and O'Neal 2001, Thomas 1979). These processes result in a variety of forest structure and composition patterns that can support different terrestrial wildlife communities (Smith 2000). Again, NRV provides a

conceptual guide for providing the mosaic of habitat conditions that native species evolved with, but species with specific habitat needs or sensitive to specific risks often require special consideration (e.g., Suring et al. 2011).

Fine-scale within-stand diversity of vegetation composition and structure provides specific wildlife habitat features required for denning, nesting, foraging, and security for individuals of many wildlife species. Different stand development stages provide different habitat structures and resources.

Recently disturbed patches tend to support high plant productivity, and often exhibit a particularly high diversity of plant and animal species, including many specialist species (Hagar 2007, Swanson et al. 2011) (fig. 35). Focal species for assessing early-seral and postfire habitats in interior MMC communities in the Pacific Northwest include fox sparrow (*Passerella iliaca*), white-headed woodpecker (*Picoides albolarvatus*), western bluebird (*Sialia mexicana*), and Lewis's woodpecker (*Melanerpes lewis*) (Gaines et al., in press; Wales et al. 2011).

Peter Singleton



Figure 35—Postfire and other recently disturbed forest sites provide productive habitat for many wildlife species. This recently burned area on the Okanogan-Wenatchee National Forest has shrub and herbaceous vegetation that provides habitat features generally not found in more mature forests.

Early successional habitats are also important for ungulate summer forage. Recent research has highlighted the importance of high-quality late-summer forage for elk survivorship and reproduction (Cook et al 2013). Early-seral openings within MMC forests can play a particularly important role by providing late-summer forage resources for ungulates (Lehmkuhl et al. 2013). Several species of migratory songbirds are also associated with deciduous shrub communities found in early-seral forest patches (Betts et al. 2010). Structural legacies (including live trees, snags, and logs) from predisturbance stands contribute important habitat components in recently disturbed areas by providing cavities, perches, escape cover, and protected microclimates (Bull et al. 1997, Franklin et al. 2000, Van Pelt 2008). The abundance of large snags and logs is a particularly important characteristic of post-fire habitats (Smith 2000).

Vertebrate communities within even-age young forest patches are generally less diverse and abundant than those found in other stand development stages, particularly for sites dominated by dense, closed-canopy conditions with little structural or understory diversity. Nevertheless, mid-seral stands can provide important ecological functions, depending on specific habitat conditions and landscape context. Dense even-age stands can provide security cover for prey species where conditions support the prey but prevent effective access for foraging predators. For example, avian predators like NSO and northern goshawks (*Accipiter gentilis*) select areas with structurally diverse forest canopies to facilitate foraging, even while their prey can often be relatively abundant in nearby dense stands (e.g., Greenwald et al. 2005). The presence of biological legacies (big old trees, snags, and logs) from predisturbance stands can provide important structural diversity in mid-seral stands by breaking up an otherwise continuous canopy, providing cavities for nesting and denning, and adding structure to the forest floor (Bull et al. 1997, Franklin et al. 2000). Mid-seral stands also serve an important role as "old growth in waiting." Late-successional forest conditions can be relatively transient in interior mixed-conifer forests compared to forests west of the Cascade Mountains owing to the variety of disturbance processes associated with this forest type (reviewed in this section and in "Natural Disturbance Factors" and "Aquatic Habitats"). Mid-seral forest stands can provide an important "conveyor belt" of forest stands that are developing structural characteristics of older forests that can serve as replacements when other older stands are affected by disturbance. Active management to facilitate the development of old forest characteristics including canopy structural diversity and small openings has become an important principle for management of mid-seral stands and is particularly important for the recruitment of old forest habitat conditions for wildlife (Franklin and Johnson 2012).

Older forests with a diversity of tree ages and sizes (including larger, older trees) provide many unique ecological functions. Across the variety of forest structural conditions found in MMC forests, animal abundance and species diversity are favored by structural complexity in the form of varied tree sizes, abundant snags, and coarse woody debris (McComb 2001). Big old trees, living and dead, standing and down, provide unique and important habitat structures within old forest stands (reviewed by Bull et al. 1997, Thomas et al. 1979, and Van Pelt 2008). For example, snags and down logs provide denning and resting sites for American marten (*Martes americana*) (Bull et al. 2005). Long-legged myotis bats (*Myotis volans*) roost in snags and bark crevices of large old trees (Ormsbee and McComb 1998). Stout lateral epicormic branches can provide nest sites for northern goshawks and other species (Daw and DeStefano 2001). Cavities (in snags or living trees) are particularly important keystone structures for wildlife communities. Such cavities are created by the interactions of pathogens, fire, strong winds, and primary cavity excavators, and are subsequently used by a variety of species (Bednarz et al. 2004, Parks et al. 1999).

The security, thermal, and moisture characteristics found beneath and within large down logs can be especially important for small mammals, amphibians, reptiles, and invertebrates.

The security, thermal, and moisture characteristics found beneath and within large down logs can be especially important for small mammals, amphibians, reptiles, and invertebrates (Bull et al. 1997). Large old trees, especially in dense mixed-conifer patches, have higher loads of epiphytic forage lichens, which are critical winter food for some species (Lehmkuhl 2005).

The multilayer canopies found in older stands contribute to unique thermal characteristics within stands and provide structural complexity important for arboreal mammals and their avian predators. Goshawks and NSO use multilayered canopies (often found in MMC forests subject to periodic fire) because such layering provides room to fly within forest stands. Canopy gaps allow for understory tree establishment and allow for sunlight to penetrate the canopy to the forest floor, contributing to understory productivity and diversity. Understory productivity is the foundation of food availability for many species. For example, northern flying squirrels (*Glacomys sabrinus*) are more abundant in stands with diverse understories with plants that provide critical fruit and mast foods (Lehmkuhl et al. 2006b); diverse understory vegetation can provide important forage resources for ungulates (Lehmkuhl et al. 2013); and fruit-bearing shrubs provide important food resources for black bears (*Ursus americanus*) and other species (Lyons et al. 2003).

Typical focal species for assessment of MMC old forest habitat conditions in Washington and Oregon are northern goshawk and pileated woodpecker (*Dryocopus pileatus*) (Gaines et al., in press; Wales et al. 2011; Wisdom et al. 2000). Northern goshawks are broadly distributed throughout the Interior West, and are

Impacts of Wildlife Herbivory

Herbivory (i.e., grazing and browsing) by wild ungulates, primarily elk, can significantly affect forested and grassland ecosystems and is worthy of consideration in any management plan (see Lehmkuhl et al. 2013 for a recent review). Elk and deer can account for a significant portion of the animal unit months (AUMs) on a range: e.g., elk and deer made up about 90 percent of the estimated 78,000 AUMs on the Yakima elk herd range in the eastern Washington Cascades. Utilization rates in grassland and forest are typically 40 to 60 percent of annual production, with herbivory concentrated in productive riparian areas and meadows but occurring in all forest types. Herbivory effects may intensify in some areas with a spring and summer forage base that has declined since the early 1900s with meadow contraction, development of dense forests due to fire suppression, regrowth of old burns and pre-1990 clearcuts, and infrequent forest clearcut harvesting as a result of regulatory changes during the last 20 years. Sustaining livestock and elk on a diminishing habitat base may have degraded habitat and enhanced establishment of exotic species in sensitive meadow and riparian areas.

The impact of wild ungulate herbivory has been well documented in the Blue Mountains from long-term exclosures and other research. In Douglas-fir and grand fir forests, Riggs et al. (2000) found that ungulate herbivory seriously depressed biomass of shrub genera *Acer, Linnaea, Amelanchier, Salix, Sorbus, Ceanothus, Physocarpus,* and *Rubus* outside of 25-year-old exclosures, within which understory biomass was two times greater than that outside exclosures. Johnson (2007) found that the shrubs *Rosa, Symphoricarpos,* and *Purshia* increased dramatically in the absence of long-term browsing in shrubland communities in the Blue Mountains. Tiedemann and Berndt (1972) reported five times more shrub cover, primarily snowbrush ceanothus (*Ceanothus velutinus*) with Saskatoon serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), and common snowberry (*Symphoricarpos albus*), inside versus outside a 30-year-old exclosure in a Douglas-fir/pinegrass (*Calamagrostis rubescens*) habitat type dominated by ponderosa pine with Douglas-fir. Likewise in the eastern Washington Cascades, Lehmkuhl et al. (2013) documented high long-term grazing impacts on some species of typical and atypical forage shrubs, such as common snowberry, oceanspray (*Holodiscus discolor*), and pinemat manzanita (*Arctostaphylos nevadensis*) in mid-elevation Douglas-fir and grand fir cover types, sticky currant (*Ribes viscosissimum*) in high-elevation subalpine fir cover types, and little sagebrush (*Artemisia arbuscula*), scabland sagebrush (*A. rigida*), and desert bitterbrush (*Purshia tridentate*) in low-elevation nonforest cover types. Impacts on ungulate herbivory on shrubs are likely underestimated because historically high levels of herbivory by both wild ungulates and livestock in the study area already may have suppressed or eliminated highly palatable shrubs.

Proposed forest restoration management in the Blue Mountains (mainly the Douglas-fir and dry grand fir types) to reduce uncharacteristic fuel loads and restore resilient stand structures and processes likely will increase the forage base for ungulates by reducing canopy cover to <40 percent and stimulating understory development (Hedrick et al. 1968, Long et al. 2008, Lyon and Christensen 2002, Skovlin et al. 1989, Vavra et al. 2005; but see Sutherland and Nelson 2010). Opening the canopy of long-closed stands with diminished seed banks of herbaceous species might increase invasive species cover (McGlone et al. 2009, Sabo et al. 2009; but see Wienk et al. 2004); however, responses of invasive species can vary considerably because of site conditions (Sutherland and Nelson 2010) and can be mitigated by management (e.g., weed control along roads). See Lehmkuhl et al. (2013) for a complete discussion of restoration impacts on ungulate habitat.

associated with structurally diverse old forest conditions that provide nest sites and foraging opportunities (reviewed by Greenwald et al. 2005, and Squires and Kennedy 2006). Pileated woodpeckers are also broadly distributed in wet to dry mixed-conifer forests throughout the Interior West. They are strongly associated with large snags and down logs for nesting and foraging (Bull and Holthausen 1993, Bull et al 1992). American marten are also included as a focal species for assessment of old forest conditions, but are more closely associated with forest types that are colder and wetter than the moist mixed-conifer forest (Gaines et al., in press; Munzing and Gaines 2005).

Conservation concerns about the NSO, a federally listed threatened species, have had a substantial impact on management of MMC forests in the eastern Cascade Range (USFWS 2011). We do not have the space for an exhaustive review of the substantial literature on NSO in the eastern Cascade Range, however we will highlight a few key aspects of spotted owl biology directly related to MMC forests. These highlights are important for understanding spotted owl management in MMC forests, but they also provide some useful insights for conservation of other old forest species associated with MMC forest outside of the range of the NSO (management considerations for old forest species are discussed in "Effects of Altered Disturbance Regimes, Land Use, and Climate Change on Animal Populations and Habitats" on page 115).

Spotted owls in the eastern Cascade Range have similar requirements for spatial and structural heterogeneity as in other parts of their range (reviewed by Courtney et al. 2004), but differences in disturbance processes (i.e., mixed-severity fire regimes, past selection harvest practices, and presence of mistletoe clumps) contribute to some differences in apparent habitat associations. The classic description of NSO nesting, roosting, and foraging habitat is "a multilayered, multispecies canopy dominated by large (>76.2 cm [30 in] diameter at breast height [d.b.h.]) conifer overstory trees, and an understory of shade-tolerant conifers or hardwoods; a moderate to high (60 to 80 percent) canopy closure; substantial decadence in the form of large, live coniferous trees with deformities—such as cavities, broken tops, and dwarf mistletoe infections; numerous large snags; ground-cover characterized by large accumulations of logs and other woody debris; and a canopy that is open enough to allow owls to fly within and beneath it" (Thomas et al. 1990: 164). Although NSOs in the eastern Cascade Range inhabit patches that meet this description (particularly in moist sites), they also use patches with smaller trees, where structural heterogeneity is enhanced by the presence of mistletoe brooms and biological legacies from previous, more open stand conditions (Buchanan et al. 1995, Everett et al. 1997, Sovern et al. 2011). These stand structure conditions are

often highly divergent from historical conditions (Everett et al. 1997, Hessburg et al. 2005, Lehmkuhl et al. 1994), and provide fuel characteristics and spatial patterns that are conducive to uncharacteristically high-intensity, widespread wildfire events (Agee 2003).

Spatial and structural heterogeneity is also important for spotted owl prey. Bushy-tailed woodrats (*Neotoma cinerea*) and northern flying squirrels compose more than 50 percent of NSO prey biomass in these areas (Forsman et al. 2001, 2004). Lehmkuhl et al. (2006a, 2006b) found that bushy-tailed woodrats and northern flying squirrels were associated with the presence of large snags, mistletoe brooms, and downed logs, with woodrats being found in both mixed-conifer and ponderosa pine types. Presence of diverse understory vegetation that provided a variety of food items was also important for flying squirrels (Lehmkuhl et al. 2006b).

Competitive interactions with barred owls are an important factor contributing to recent NSO population declines (Forsman et al. 2011). Spotted owl populations in Washington and northern Oregon declined by approximately 40 to 60 percent from 1989 to 2008 (Forsman et al. 2011). Many experts expect that NSO populations will continue to decline through much of their range as barred owl numbers increase (USFWS 2011). Barred owls in the eastern Cascade Range are most abundant in flatter valley bottom moist forest settings (Singleton et al. 2010). Interactions with barred owls may have contributed to the displacement of NSO pairs into drier midslope settings as early as the 1990s when most NSO activity centers were documented, resulting in relatively few historical NSO sites being documented in valley-bottom MMC settings that otherwise appear to be suitable NSO habitat (Singleton 2013). Persistence of the NSO population in mixed-conifer forest landscapes may depend on the ability of the local NSO population to adapt to the presence of barred owls (Gutteriez et al. 2007). Substantial habitat loss from natural or human-caused disturbances (e.g., fire or forest management activities) has the potential to exacerbate the negative impacts of interactions with barred owls by increasing competition for limited habitat resources (Dugger et al. 2011, Forsman et al. 2011).

Several other unique habitats also occur in landscapes that support MMC forests, including deciduous forest patches, meadows, riparian areas, rock piles, cliffs, and caves (reviewed in Johnson and O'Neil 2001 and Thomas et al. 1979). Deciduous tree patches provide important habitat characteristics for a variety of species (Hagar 2007), particularly migratory birds (Betts et al. 2010), and can provide abundant cavities for woodpeckers and other species (Martin et al. 2004). Aspen stands were an important component of the historical landscape in areas that support MMC forest, but the availability of aspen habitats has been reduced

substantially by altered disturbance regimes and herbivory impacts from both native and domestic animals (Shirley and Erickson 2001, Strong et al. 2010). Natural moist meadows are another particularly productive community within landscapes that support MMC forest. Meadows provide important ungulate forage resources (Lehmkuhl et al. 2013) and contribute to unique edge conditions that are important for a variety of wildlife including great grey owls (*Strix nebulosa*) (Bull and Henjum 1990) and long-eared owls (*Asio otus*) (Bull et al. 1989).

Area of meadows has been reduced by tree encroachment as a consequence of altered disturbance regimes (Haugo and Halpern 2007). Meadow communities have also been altered by domestic livestock grazing and intense use by native ungulates (Beebe et al. 2002). Large carnivores (particularly wolves) historically played an important role in limiting concentrations of native ungulates in these highly productive areas (Beschta and Ripple 2009). Ecological functions of streams and associated riparian areas are reviewed below, but it is worth emphasizing that in the context of animal habitat in disturbance-prone landscapes, riparian areas can provide unique linear landscape features that contribute to important ecological flows through the landscape, including animal movement. Rocks, cliffs, and caves also provide unique landscape elements that can be important for many species (Thomas 1979). Rocky talus and scree slopes can provide unique habitat features for amphibians including larch mountain salamander (*Plethodon larselli*) (Crisifulli 2005) and secure areas for rodents including bushy-tailed woodrats and pika (Simpson 2009). Cliffs provide nesting opportunities for raptors (including peregrine falcon [*Falco peregrinus*]), and caves can provide hibernacula for bats.

The literature on wildlife habitat associations within MMC forests in western North America is vast and beyond the scope of this document. However, two main themes emerge from our review of the information: (1) natural disturbance processes play a key role in the development of stand structure conditions and landscape patterns that determine habitat values for animals, and (2) biological legacies (big old trees, snags and logs) provide important habitat structures across all stages of stand development. Within-stand structure is influenced by disturbance processes that function at a variety of scales. Endemic levels of disturbance can contribute to stand and landscape heterogeneity, while large-scale, high-intensity disturbances can reduce stand and landscape heterogeneity. Within-stand structural diversity is generally much greater in stands with a variety of tree age and size classes, even if those stands are recently disturbed or dominated by younger trees. Big trees and logs are often a legacy of previous stand conditions that have been retained after some disturbance event, like fire or harvest (Franklin et al. 2000). The variety of extremely valuable habitat structures provided by these large old

trees include cavities, large branches, broken tops, brooms, and platforms (Bull et al. 1997). The presence of large old trees within a stand can make a big difference for wildlife habitat values in both old and young forests.

Aquatic Habitats

From the literature, two concepts emerge as foundational for managing linked terrestrial and aquatic ecosystems: (a) watersheds and their aquatic habitats and species are dynamic and adapted to insect, disease, weather, and wildfire disturbances, and (b) the climate will continue to have a profound influence on terrestrial and aquatic ecosystems, disturbance processes, and their interactions (Bisson et al. 2003; Luce et al. 2013, 2014; Tague and Grant 2009).

Disturbances play a vital role in structuring aquatic ecosystems.

Disturbances play a vital role in structuring aquatic ecosystems. Wildfires influence hydrological and physical processes, such as surface erosion, sedimentation, solar radiation, wood recruitment, and nutrient exchange in streams (Benda et al. 2003, Luce et al. 2009, Miller et al. 2003, Wondzell and King 2003). The timing and severity of erosion and sedimentation differ by the physical geography, geology, and geomorphic processes; precipitation; and fire regime. Erosion contributes to sedimentation and can depend on riparian vegetation density and the speed of vegetation recovery after disturbance. Chronic erosion delivers fine sediment for a fairly long time, usually in the absence of revegetation after disturbance, or it comes from road rights-of-way, trails, and bulldozer lines. Postfire riparian erosion results in larger pulsed sediment and wood delivery to streams, and in some circumstances, channels can be reorganized, affecting aquatic habitats (Benda et al. 2003, Miller et al. 2003, Minshall 2003, Reeves et al. 1995). Water retention properties of the soils and reduced evapotranspiration from vegetation loss in the surrounding landscape affect runoff dynamics. Over time, coarse wood and sediment are depleted. Fluvial action and rot tend to break down stream wood, which can then be transported downstream along with sediment and rock. These processes continue until the system is replenished by subsequent postfire erosional events (Benda et al. 2003, Miller et al. 2003).

In general, episodic large-scale disturbances (e.g., fire) to aquatic ecosystems are inevitable and often beneficial when spaced out over long periods, and this knowledge can form an important ecological foundation for fire and forest management. Anadromous and resident species in such landscapes evolved with these disturbances and the attendant shifts in habitat quantity and quality. These species are affected by habitat reorganization associated with wildfires, including addition of wood material and sediment deposition; thus, they are considered to be fire-adapted. The natural frequency, severity, and extent of historical fires governed the

pulse of erosional events that carried wood, rocks, and soil to streams and created variation in the level of stream shading and aquatic habitat available to fish provided by riparian vegetation. Fish populations have been shown to recover rapidly to the natural fire regime in burned reaches, depending on connectivity of stream networks (Burton 2005). Thus, restoration of conditions that promote a natural fire regime will benefit fish populations overall. Where fish populations are robust, recolonization of stream segments disturbed by fire is tenable (Burton 2005).

This dynamic view diverges from traditional frameworks that suggest that aquatic ecosystems should be managed as stable systems perpetually maintained for select species. Stable equilibrium and balance of nature views are equally intractable in terrestrial and aquatic ecosystems. The dynamic view of aquatic systems accepts patterns of disturbance and recovery across landscapes as necessary processes to interconnect mosaics of diverse and changing habitats and communities.

Streams draining burned areas of the Entiat Experimental Forest (EEF) on the east side of the Cascades crest in Washington had peak flows 120 percent higher than prefire conditions (Siebert et al. 2010). Additionally, there were deeper snowpacks and more rapid snowmelt as a result of the disturbance. However, only the upper elevations of the EEF consist of mixed-conifer forest with slightly higher moisture (mean annual precipitation at mid-elevation = 580 mm) (Seibert et al. 2010). Similar hydrologic issues could likely prevail following fire disturbance in moist forests. The primary lesson from Siebert et al. (2010) is that prefire hydrologic data are essential to quantifying the postfire response.

Climate change affects forest landscapes, wildfire regimes, aquatic habitats, management options, and their interactions. Climate variability can have important effects on stream hydrology (Jain and Lall 2001, Poff et al. 2002, Tague and Grant 2009) and related physical processes (Bull 1991, Meyer et al. 1992, Pederson et al. 2001, Schumm and Hadley 1957). Changes in hydrology can happen rather abruptly (i.e., 10 to 100 years), and decadal- to multidecadal-scale climate regime shifts can influence stream flows more than the management practices on which we focus most attention (Jain and Lall 2001). April 1 snowpack has declined in mountainous regions across the Western United States (Mote 2003, Mote et al. 2005). Changes are largely attributed to elevated winter and spring temperatures (Hamlet et al. 2007, Stewart et al. 2005). Snowpack decline is expected to continue as temperatures rise throughout the region. Changes in the timing and magnitude of precipitation are expected because of interactions between rising air temperatures, snowfall, and rainfall across complex local terrain. Warming will result in more precipitation falling as rain than snow, and earlier snowmelt timing (e.g., Hamlet et al. 2005).

Climate change profoundly affects processes that create and maintain aquatic habitats. Some effects are direct, particularly those involving stream temperature, water yield, peak flows, and timing of runoff (Luce et al. 2014). Other effects occur indirectly as climate change forces alteration of the structure and distribution of forest communities and the characteristics of wildfire. These processes will indirectly affect fish in relevant watersheds. Altered snowmelt run-off regimes in the mixed-conifer forests will affect downstream fish-bearing reaches. Discharge patterns affect water depth; thus, earlier low flows downstream may reduce habitat availability for fish dependent on deeper, slower flowing habitats. Changing precipitation and fire regimes are expected to compound the effects of warming trends by shifting hydrologic patterns and those of sediment transport and solar radiation (Dunham et al. 2007, Isaak et al. 2010). The structure and composition of riparian vegetation imparts important influences on temperature and soil moisture gradients immediately adjacent to streams (Anderson et al. 2007).

Fish and other aquatic biota are likely to be affected by wildfire and climate change in MMC forests. Aquatic ecosystems consist of interacting species at all trophic levels. Productivity in each level can depend on inputs and transfers across the terrestrial-aquatic ecotone. Movement of terrestrially derived production into streams can affect primary production with implications further up the food web, including aquatic insects and fish (e.g., Baxter et al. 2004, Nakano et al. 1999). Resources transported downstream and organic matter of terrestrial origin can alter downstream fish-bearing habitats according to spatial variation in the headwaters (Baxter et al. 2004, Binckley et al. 2010, Wipfli et al. 2007). Convergence of low-order streams that drain large landscapes at downstream habitats potentially results in productivity "hot-spots" (e.g., Kiffney et al. 2006). Efforts to establish transport distances and specific responses in fish have been limited in mixed-conifer areas (but see Polivka et al. [N.d.][1]). Nevertheless, some successional stages can have measurable influence on the standing crop of aquatic macroinvertebrates (Medhurst et al. 2010).

Streams in dry and MMC forests are not especially diverse in terms of fish species, but they do consist of species that are sensitive to temperature increases in spawning and rearing streams and that respond to disturbances such as wildfire. Less is known about how fire will affect macroinvertebrate communities that serve

[1] Polivka, K.M.; Dwyer, G.; Mehmel, C.J.; Sirianni, K.M.; Novak, J.L. [N.d]. Effects of temperature and virus persistence time on wild and pesticide strains of the nucleopolyhedrovirus (NPV) pathogen of larval Douglas-fir tussock moth (*Orgyia pseudotsugata*). Manuscript in preparation. On file with: Karl Polivka, Pacific Northwest Research Station, Forestry Sciences Laboratory, 1133 N. Western Ave., Wenatchee, WA 98801.

as food resources for fish. Successional patterns following disturbance can affect macroinvertebrate communities, but it is unclear whether changes at one trophic level will be detectable at levels above (i.e., fish) (Medhurst et al. 2010).

In fish-bearing streams of Idaho, the intensity of fire determined the density and age structure of rainbow trout (*Oncorhynchus mykiss*) (Dunham et al. 2007). Relative to controls, streams adjacent to habitats that burned showed relatively more rapid growth of age 1+ rainbow trout, an effect that was augmented in streams that were physically re-organized by erosion and sedimentation following the fire (Rosenberger et al. [N.d.]). This study ranged from lower elevation dry forest to elevations containing MMC and subalpine forest in the Boise River basin. Fish recovery following riparian fire can be fairly rapid in streams where there is a robust local population to recolonize disturbed habitat, and management of fire severity might be most important in areas where local populations are weak and isolated (Burton 2005). Management of roads might also be necessary, given that fragmentation of stream habitat might not only affect the ability of a fish population to recolonize stream segments affected by fire, but might also affect patterns of genetic diversity in resident trout species (Neville et al. 2009).

Cutthroat trout (*Onchorhynchus clarki*) and bull trout (*Salvelinus confluentus*) are the most temperature-sensitive species likely to be present in mixed-conifer zones. Bull trout occupy the coldest freshwater habitats of all salmon and trout species and these habitats are predicted to be severely affected by climate change in coming decades (Isaak et al. 2010, Rieman et al. 2007, Wenger et al. 2011). Bull trout life histories include migratory forms that spawn and rear in cold streams close to headwaters, then migrate downstream to larger rivers where they live as adults prior to spawning ("migratory") or migrate to lakes following rearing ("adfluvial"). Fragmentation of cold water habitats by stream warming can increase physiological stress to bull trout and decrease interconnectivity of adequate spawning and rearing aggregations. In the "resident" life history form, bull trout remain in cold headwater streams for spawning and rearing, and as adults. Thus, they are subject to these physiological stressors at all life stages. Cutthroat trout are also common to upland streams in mixed-conifer forests of the eastern Cascades. Management for the persistence of these and other coldwater fish species in the face of climate change should again focus on maintaining strong, genetically diverse populations in well-connected stream networks. This may mean road management as a means of addressing climate change, by increasing passage and opening stream networks. In small streams within mixed-conifer watersheds of the Wenatchee River sub-basin, cutthroat trout density and total biomass are limited

by higher flows (fig. 36).[2] Thus, changing flow regimes as a result of precipitation and snowmelt-timing shifts can potentially have consequences for the persistence of populations of this species.

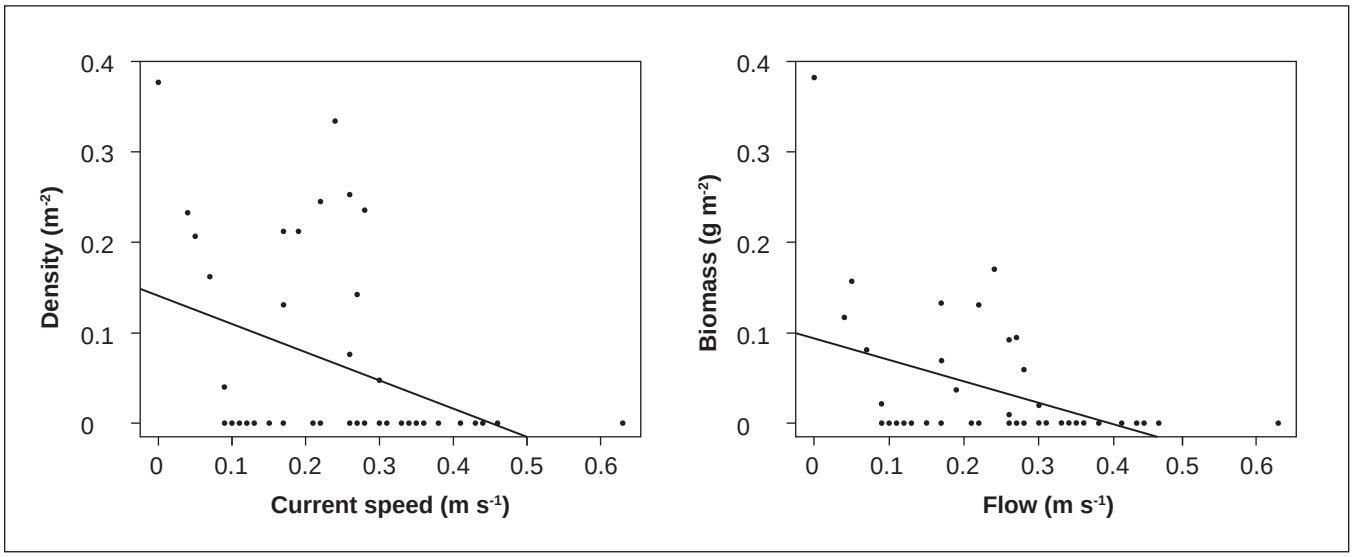


Figure 36—(Left) Cutthroat trout (*Oncorhynchus clarki*) density as a function of current velocity in habitat units (usually pools) distributed among six first-order streams in moist mixed-conifer forests in the Wenatchee River Basin (Washington, USA). Decreasing linear relationship was significant with much unexplained variation ($F_{1,43} = 7.75$, $p = 0.008$, $r^2 = 0.133$). (Right) Cutthroat trout biomass as a function of current velocity in habitat units (usually pools) distributed among six first-order streams in moist mixed-conifer forests in the Wenatchee River Basin (Washington, USA). Decreasing linear relationship was significant with much unexplained variation ($F_{1,43} = 8.34$, $p = 0.006$, $r^2 = 0.143$) (see footnote 2).

Active management can restore a full spectrum of ecological patterns and processes. Long-term restoration and maintenance of the physical, biotic, and ecological processes that are important to maintaining diverse terrestrial and aquatic systems requires strategies that go beyond simply treating fuel accumulations, attempting to prevent high-severity fires, or attempting to maintain existing fish strongholds. The most effective means to minimize negative consequences of expected climate change, and related effects on aquatic systems, is to protect the evolutionary capacity of these systems to respond to disturbance. In this light, management would focus on protecting relatively undisturbed aquatic habitat, and, where necessary, restoring habitat structure, the processes that support it, and the life history complexity of native species, to the best practical extent (Gresswell 1999). Restoring degraded aquatic ecosystems requires a similar perspective. To conserve or promote resiliency in aquatic (as in terrestrial) systems,

[2] Bennett, R.L.; Polivka, K.M. [N.d]. Factors important to monitoring of headwater fish populations and possible effects of landscape features. Manuscript in preparation. On file with: Karl Polivka, Pacific Northwest Research Station, Forestry Sciences Laboratory, 1133 N. Western Ave., Wenatchee, WA 98801.

land managers can turn their focus to conserving and restoring the physical and biological processes and patterns that create and maintain diverse networks of habitats and populations, rather than engineering the condition of the habitats themselves (Benda et al. 2003, Ebersole et al. 1997, Frissell et al. 1997, Gresswell 1999, Minshall 2003, Naiman et al. 2000, Rieman et al. 2003). This means that management is capable of restoring (1) natural patterns in the timing and amount of stream flows (Poff et al. 1997); (2) natural production and delivery of coarse sediment and large wood to streams (Beechie and Bolton 1999, Meyer and Pierce 2003, Reeves et al. 1995); (3) riparian communities that function as sources of organic material, shade, and stream buffering (Gregory et al. 1991); (4) streams, flood plains, and hyporheic zones that are reconnected (Naiman et al. 2000); and (5) habitats that are required for the full expression of native life history strategies, gene flow and variability, and demographic support among populations (Dunham et al. 2003, Gresswell et al. 1994, Healey and Prince 1995, Poole et al. 2001, Rieman and Dunham 2000; Rieman et al. 2003, Roghair et al. 2002). Management maintains forests and streams that can respond to and benefit from disturbances across a broad range of event sizes and intensities, rather than minimizing the threat of the disturbance.

Logical priorities for restoration activities emerge from an evaluation of the changes and constraints imposed by these changes (e.g., Beechie and Bolton 1999, Luce et al. 2001, Pess et al. 2002). Habitat loss and fragmentation, channelization, chronic sediment inputs, accelerated erosion, and changes in hydrologic regime (Lee et al. 1997, NRC 1996) are all problems that merit attention. However, restoring physical connections among aquatic habitats may be one of the most effective first steps to restoring productivity and resilience of many native fish populations (Rieman and Dunham 2000, Roni et al. 2002), given that network connectivity is a key component of the adaptive response by fish to disturbances (Burton 2005). Eliminating the threat of large and severe disturbance may be insufficient to prevent local fish population extinctions in many streams (Dunham et al. 2003, Rieman et al. 2003).

The geographic location and sensitivity of watersheds can be used to guide priority setting for management actions (Rieman et al. 2000, 2010). From an aquatic conservation and restoration perspective, priorities for active vegetation and fuels management occur as follows:

Priority 1. Watersheds in which the threat of extensive, high-severity fire is high and local populations of sensitive aquatic species are at risk because they are isolated, small or vulnerable to invasion of exotic fish species (Dunham et al. 2003, Kruse et al. 2001). In these instances, the first priority for management is to restore connectivity among patches of favorable fish habitat (Dunham et al. 2003,

Rieman et al. 2003). Where this is impractical, active forest management to reduce the severity and impact of potential fires could be an important short-term strategy (Brown et al. 2001, Rieman et al. 2003).

Priority 2. Watersheds in which there is little to lose, but much to gain. In some watersheds, habitat degradation is extensive and remaining native fish populations are depressed or locally extinct. Watersheds that are heavily roaded and influenced by past intensive management often contain forests vulnerable to severe fires (Hessburg and Agee 2003, Rieman et al. 2000). Existing road systems can initially facilitate understory vegetation treatments and fuel reduction, and can subsequently be removed, moved, or improved to reestablish hydrologic and biological connectivity (e.g., Roni et al. 2002). Here, short-term risk of ground-disturbing activities may be offset by the potential long-term benefit of reconnecting and expanding habitats and populations. In many of these locations, ongoing treatment with fire will likely be needed.

Priority 3. Watersheds in which sensitive aquatic species are of limited significance. Given that the vulnerability of dry and MMC forests to high-severity fire is associated with lands that have been intensively managed (and absent any subsequent composition or stocking management following treatment), the need for active fire and fuels management now may be greatest in areas where aquatic ecosystems and related physical processes have been most significantly altered (Rieman et al. 2000). In some locations, complete restoration of all native plants and animals may be impractical. These are logical places to experiment with active management, where learning can proceed without taking unacceptable risks (Ludwig et al. 1993; see Rieman et al. 2010 for an example).

Management for climate change requires consideration of dynamic hydrologic simulations that are used to represent climate change scenarios (e.g., see Hamlet et al. 2005, Miller et al. 2003). These must relate sensitivity of models and inferences to the main assumptions about climate change, and the low-frequency climate variability that is assumed (e.g., decadal and longer scale fluctuations). Additionally, dialogue between landscape ecologists and hydrologists will be necessary to integrate the effects of climate change on watersheds in MMC forests and how these will be transmitted across the terrestrial-aquatic ecotone to stream habitats. In other words, climate will affect fire frequency and intensity, and management options for aquatic habitats will require consideration of processes discussed above and how the ecological outcome is related to them (Bisson et al. 2003). Landscape heterogeneity will contribute to the issues faced on the ground by managers in MMC ecosystems throughout the interior northwest (Rieman et al. 2003).

There will be key uncertainties to consider in the management of aquatic habitat in MMC landscapes as well. Variable incidences of fire, variable need for fuels treatment, variable current quality of aquatic habitat, and management tradeoffs between human well-being (property, resources) and conservation all increase the complexity of management decisions (Bisson et al. 2003). Establishment of an effective adaptive management program will incorporate all of these considerations, as well as the spatial and temporal scale. Specific areas might require a more explicit management approach, whereas across the entire MMC forest ecosystem, a more generalized approach based on existing research might be effective (Bisson et al. 2003). Success will depend on continued dialogue between landscape ecologists, aquatic ecologists, and forest managers. Also stakeholders in the public should be asked to consider the scientific recommendations and to participate in further development of management and research objectives.

Riparian habitats—
There are relatively few studies that focus specifically on the historical disturbance regimes and structure and composition of riparian zones of mixed-conifer forests. The little that we do know comes from what can be gleaned from the studies of Agee (1988, 1994), Camp (1999), Camp et al. (1997), Everett et al. (2003), Fetherston et al. (1995), Garza (1995), Gregory et al. (1991), Gresswell (1999), Naiman and Decamps (1997), Naiman et al. (1993, 1998), Olson (2000), Olson and Agee (2005), Skinner (1997), Taylor and Skinner (1998, 2003), and Wright and Agee (2008). With the exception of low-gradient stream reaches (e.g., ≤5 degrees of in-stream slope angle), the fire regimes of riparian zones track fairly well with those of the adjacent upslopes. In contrast, the disturbance regime of low-gradient and often fish-bearing reaches tracks with the hydrologic regime. Low-gradient reaches were often depositional zones during flood events, with intact flood plains, and often supported hardwood tree and shrub vegetation cover. Disturbance in these environments was typically driven by flooding and ice flows, and their spatial and temporal variability, rather than wildfires, although wildfires do burn through these areas.

Riparian areas are key wildlife habitats in interior dry forests because of the presence of free water, cool moist microclimates, and soil moisture that supports diverse vegetation.

Gaining a better understanding of the historical disturbance regimes and vegetation patterns of riparian zones is a fertile area of research. The existing datasets of the Interior Columbia River Basin mid-scale assessment (Hessburg et al. 1999a, 2000a) provide extensive reconstructions of now nearly 400 subwatersheds whose riparian zones could be reevaluated to provide further insights on successional patterns and historical fire severity.

We also know that riparian areas are key wildlife habitats in interior dry forests because of the presence of free water, cool moist microclimates, and soil moisture

that supports diverse vegetation (Lehmkuhl et al. 2007b, 2008). Small mammals are more diverse in dry forest riparian areas compared to adjacent uplands. Several species, such as the water shrew (*Sorex palustris*), are associated with free water, whereas species typical of wet or mesic forests become obligate riparian species as the surrounding upland vegetation becomes dryer (Lehmkuhl et al. 2008). Forest birds are no more diverse in riparian areas than in adjacent uplands, but the composition of birds differs with the addition of many riparian obligate species associated with deciduous trees, dense shrubs, and herbaceous vegetation (Lehmkuhl et al. 2007b).

Postfire riparian conditions can have long-term effects on aquatic biota owing to changes in temperature and sedimentation according to local geomorphology and burn severity. In fish-bearing streams of Idaho, the intensity of fire determined the density and age structure of rainbow trout (Dunham et al. 2007). Relative to controls, streams adjacent to habitats that burned showed relatively more rapid growth of age 1+ rainbow trout, an effect that was augmented in streams that were physically reorganized by erosion and sedimentation following the fire (Rosenberger et al. [N.d.]). This study ranged from lower-elevation dry forest, to elevations containing MMC and subalpine forest in the Boise River basin. These observations are thus relevant to management strategies in mixed-conifer forests at higher elevations.

Human Impacts to Moist Mixed-Conifer Systems: Influences of the Last 100 to 150 Years

Humans have inhabited parts of eastern Oregon and Washington for more than 10,000 years. Native American communities developed many land management practices to serve their needs for sustenance and used fire extensively in woodland environments east of the Cascades (Agee 1993; Langston 1995; Robbins 1997, 1999; Robbins and Wolf 1994; White 1983, 1991, 1992, 1999). However, there is limited knowledge of the impacts of their management on MMC forests (Whitlock and Knox 2002).

With the arrival and settlement of Euro-Americans in the early 1800s came another wave of human impacts. Key change agents included initial widespread timber harvests, highly effective fire prevention and suppression (largely since the 1930s), extensive sheep and cattle grazing and livestock fencing, development of extensive road and railroad networks, subdivision of regional landscapes by ownership, widespread and repeated timber harvest entry via selection cutting and clearcut logging, conversion of native grasslands and shrublands to agricultural uses, and urban development. As a result, today these forests neither resemble nor function as they once did 100 or 200 years ago.

Changes to the landscape that naturally flowed from these impacts include:

- A highly fragmented range of forest patch sizes, stemming from 4, 8, and 16 ha (10, 20, and 40 acre) treatment areas and from other land uses near urban areas. The resulting patchiness differed greatly from the original spatial pattern of the landscape. In some places, patches created by repeated harvesting entries created homogenous forest with a skewed species composition and more uniform age and size classes. The original mosaic, more of a gradient of seral stages created by the complex patterns of fire and other tree mortality factors, included an array of different sized patches and a full complement of seral or successional stages.
- After regeneration harvests, a more homogenized forest structure emerged, in which treatments drove stand structure and composition toward a single cohort and commercially desired species. After selection cutting, stand structure moved toward multiple cohorts because of continuous regeneration and release (some stands were entered several times), and species composition moved toward domination by shade-tolerant species in dense multilayered arrangements.
- A simplified vegetation mosaic was created by removal of large, fire-tolerant trees over repeated harvest entries, which typically left many smaller and fewer large trees. The result was ever increasing density and a surplus (in comparison with the native disturbance regimes) of young and mid-aged forests.
- A shift from fire-tolerant to intolerant tree species composition (timber harvest removed large ponderosa pine, Douglas-fir, western larch, western white and sugar pine [*Pinus lambertiana* Dougl.], and regenerated grand fir, white fir, Douglas-fir, and subalpine fir dominated stands).
- An increased vulnerability to large and severe fires, insect outbreaks, and disease pandemics.
- Fewer grasslands and shrublands.

Management activities have also had a profound effect on the spread of nonnative species, especially in the dry rangeland and forest ecosystems. As the climate continues to change, conditions for spread of some nonnative invasive (e.g., cheatgrass [*Bromus tectorum*]) and native invasive (e.g., barred owl) species will improve. Despite substantial efforts to control invasive species in the United States, the threat will remain high in coming years unless significant steps are taken to slow the advance of invasive plants and animals.

Timber Harvest and Associated Activities

Timber harvest and road development over the last 100 years have had a significant impact on the landscape patterns of MMC forests in eastern Oregon and Washington (fig. 37). Harvest activity was quite intense for nearly five decades beginning at the start of World War II. Clearcutting, selective harvesting, and subsequent planting for reforestation created substantial areas of structurally simple early- to mid-aged stands. Present-day stand structure of these previously harvested areas is

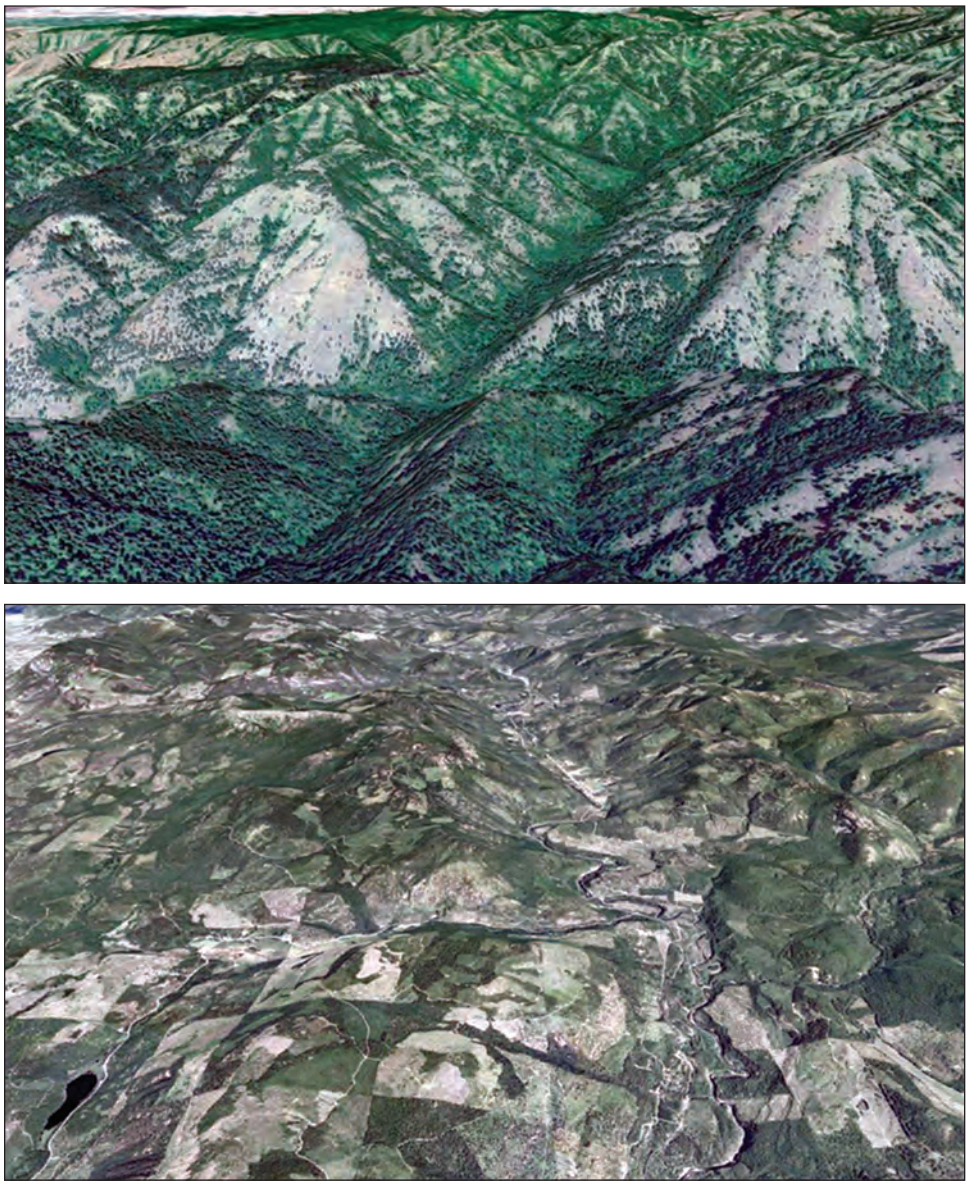


Figure 37—Timber harvest and road development over the last 100 years have had an impact on the spatial configuration of mixed-conifer forests in eastern Oregon and Washington. The upper image shows a portion of the Umatilla National Forest without stand management, fragmentation with land ownership, and roads. The lower image shows the effects of land ownership, roads, and harvest units on forest pattern. Images are from Google Earth™.

predominantly even-aged where regeneration harvesting was practiced and uneven-aged where selection cutting was more common, with tree species and genetic compositions that are often not particularly well-adapted to the environment. Large and old live and dead trees (snags) are conspicuously absent from many forests (Churchill et al. 2013; Franklin and Johnson 2012; Hessburg et al. 2003, 2005; Larsen and Churchill 2008, 2012; Merschel 2012).

Historical replanting at many sites used maladapted seedling stock from distant seed sources, and frequently with species compositions that were not ecologically appropriate for the site conditions (e.g., overly high proportions of economically important ponderosa pine and Douglas-fir). Seed collection zones were not yet established and there was only rudimentary understanding of the relationships linking seed provenance adaptation to particular site conditions. Prior to replanting, broadcast burning treatments were often employed. If omitted, significant surface fuel accumulations were often left behind (Agee 1998, Hann et al. 1997, Hessburg et al. 1999a, Huff et al. 1995). These and others factors have limited the function of some present-day MMC forests and the ecosystem services that can be obtained from them. Some of the post-harvest stands across this region contain large (more than about 53 cm [21 in] d.b.h.) young trees with species compositions and stand structures that may succumb to bark beetles or fire, and may benefit directly from manipulation of tree species composition and density.

Since the early 1990s, when certain management constraints (e.g., the "eastside screens") were adopted, timber harvest has been scaled back by about 90 percent. Currently, the scale and scope of active management focuses on a limited number of cautiously selected locations, primarily for the purposes of restoring ecological processes and reducing fuel loads.

Fire Exclusion and Natural Fire Dynamics

In the absence of fire, forest density increased, the role of shade-tolerant tree species expanded, and fuel loads have increased.

Fire frequency in the region declined because of land-use changes in limited areas as early as 1880 or 1890. By 1900, fire frequency in dry forest types was in sharp decline (Everett et al. 2000; Haugo et al. 2010; Hessburg et al. 1999a, 1999c, 2000a, 2005, 2007; Hessl et al. 2004; Heyerdahl et al. 2001, 2008; Wright and Agee 2004), resulting in further changes to forest structure and composition. In the absence of fire, forest density increased, the role of shade-tolerant tree species expanded, and fuel loads have increased (Baker 2012; Everett et al. 1994; Hessburg et al. 2000b, 2003, 2005; Huff et al. 1995; Lehmkuhl et al. 1994; Merschel 2012; Perry et al. 2011). Not coincidentally, human population densities have increased rapidly as many people prefer to live at the lower forest ecotone. The amount of area classified as wildland-urban interface (WUI) has increased dramatically in recent decades (Gude et al. 2008, Radeloff et al. 2005).

Departure from historical fire regimes—
Land use activities and fire-suppression efforts from the early 20th to early 21st centuries have been effective at controlling small fires, eliminating the landscape patchiness that was historically important for interrupting fire flow at large spatial scales (Moritz et al. 2011, Perry et al. 2011). Large wildfires today typically result from rare or extreme weather or climatic events (Littell et al. 2009, Moritz et al. 2011). That was also the case historically. The significant difference associated with 20th century vegetation and climate change is the increase in frequency of very large (>10,000 ha) wildfires in many ecoregions of the West as a result of both more flammable landscapes and changing weather conditions. Owing to their increasing frequency and size, some large wildfires may synchronize large areas of the mixed-conifer landscape, setting the stage for more large and severe fires in the future. This happens because large fires, especially those dominated by crown-fire effects, can simplify and homogenize landscape patterns of species composition, tree size, age, density, and layering.

However, this is not always the case. A recent study in California found that some wildfires can achieve ecological and management goals by reducing landscape-scale fire hazard and increasing forest heterogeneity (Miller et al. 2012). This is likely to be true when the pattern and dispersion of fire severity and fire event patches are more or less consistent with the native fire and climatic regimes. We note here that despite referenced changes in fire regimes, many contemporary fires are still substantially dominated by mixed-severity fire, and the building blocks for landscape restoration are readily apparent. One can still observe the interactions of bottom-up, local (e.g., stand and landscape structure, topography), and top-down spatial controls on fire extent and fire severity (Perry et al. 2011).

Grazing

Sheep and cattle entered the region with the first settlers, but the earliest of them focused on agriculture, and their herds were typically small, including just enough livestock to work and support their family farms. Cattlemen initially believed that their stock could survive the harsh winters, and by 1860 there were at least 200,000 head of cattle in the region. A severe winter in 1861–1862 killed many cattle (Galbraith and Anderson 1991). Severe winters occurred again in 1880–1881 and in 1889–1890, after which most cattlemen recognized that shelter and feed were required for a sustainable operation.

By the late 1880s, severe grazing by cattle left the rangelands stressed (overgrazed). Large cattle herds also grazed adjacent dry forests and nearby grassy riparian zones. Because cattle require a lot of water, they preferred to graze the riparian zones, creek bottoms, and wet meadows that supported lush grasses through the dry

summers, and provided a ready supply of water. Riparian zones constitute 1 to 4 percent of the land area of eastern Oregon and Washington national forests (Kauffman 1988), yet supply more than 80 percent of the grasses and herbs consumed by livestock (Roath and Krueger 1982).

Introductions of sheep, which require less water and are capable of using varying rangeland conditions, boomed in the mid- to late 1880s coincident with the decline in cattle. Eventually sheep numbers outstripped cattle, and violent conflicts often arose between Basque and Mormon sheepherders and resident cattlemen. The battles were the fiercest in Crook, Lake, Wheeler, and Deschutes Counties in south-central Oregon, where 8,000 to 10,000 sheep were killed per year for several years (Galbraith and Anderson 1991). Extensive grazing by sheep left native bunchgrasses and forbs in worse condition than was caused by cattle grazing. By the late 19th century, numerous exotic plants such as the bull and Canada thistles (*Cirsium vulgare* and *C. arvense*), cheatgrass, Dalmation and yellow toadflax (*Linaria dalmatica* and *L. vulgaris*), diffuse and spotted knapweeds (*Centaurea diffusa* and *C. maculosa*), and leafy spurge (*Euphorbia esula*) had become established in the region (Hann et al. 1997; Langston 1995; Wissmar et al. 1994a, 1994b).

Grazing permits and fees were required on national forest lands beginning in 1906, although grazing intensity increased until the 1920s (Wilkinson 1992). Congress approved the Taylor Grazing Act of 1934, which regulated grazing on the public domain (later, Bureau of Land Management lands) through the use of permits; subsequently, cattle and sheep numbers declined. Recent assessments of grassland condition suggest that grasslands are slowly recovering from some of the impacts of historical grazing, and current conditions are perhaps the best they have been in 100 years (e.g., see Harvey et al. 1994, Johnson et al. 1994, Skovlin and Thomas 1995). However, because of countless nonnative plant species introductions, some changes in native plant community structure and productivity are likely permanent (Lehmkuhl et al. 2013). There is ongoing public debate over whether livestock grazing on public lands should be continued under the Taylor Grazing Act (e.g., see Belsky et al. 1999, Beschta et al. 2012). Although public land managers have made steady progress in reducing cattle impacts to riparian vegetation and sediment load in small streams and creek bottoms, this is likely an area for continued improvement.

Land Development

The national forests of eastern Oregon and Washington are largely surrounded by private lands. Throughout most of the 1900s, these lands were used for natural resource extraction or agriculture. In recent decades, rural home development has

expanded. The rapid increase of these exurban homes adjacent to wildlands poses a major threat to ecological functioning, fire management, and native biodiversity. Exurban development can fragment habitats, create barriers to animal movement and other ecological processes, alter natural disturbance, extirpate top predators, increase weeds, increase mesocarnivores (medium-sized predators) and diseases, and ultimately, cause local extirpation of some native species (Hansen et al. 2005, McKinney 2002, Pickett et al. 2001). The presence of homes in the WUI also strongly affects fire management options in adjacent national forests, increasing the need to suppress fire to protect property and lives, requiring identification and mitigation of hazard trees, and increasing firefighting costs.

Theobald et al. (2011) evaluated changes in abundance and connectivity of "high-quality" forest patches resulting from land use changes in the Western United States. They estimated that land uses associated with residential development, roads, and highways have caused roughly a 4.5-percent loss in area (20 000 km^2 [7,722 mi^2]) of large, unmanaged forested patches, and continued expansion of residential land will likely reduce forested area by another 1.2 percent by 2030. Projected losses for 2000–2030 were particularly high in Oregon and Washington (fig. 38). When considering both patch size and overall landscape connectivity for forests across the West in 2000, the most important forested areas were found in the Cascades Ecoregion and the Canadian/Middle Rockies Ecoregion, which includes the Okanogan Highlands and the Blue Mountains (Theobald et al. 2011). This

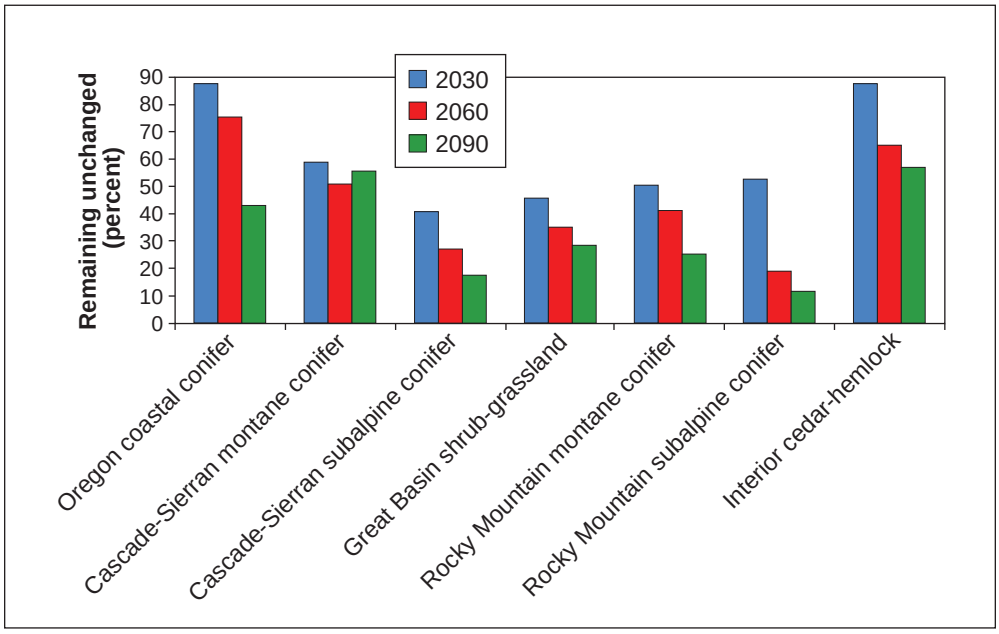


Figure 38—For biomes in Oregon and Washington, the model results among scenarios indicate that Rocky Mountain subalpine conifer in the Blue Mountains and Cascade Range will undergo the greatest loss in area. Data from Rehfeldt et al. (2012).

analysis illustrates the high contribution to subcontinental forest connectivity made by forests in Oregon and Washington, and the vulnerability of this connectivity to future land use changes.

Climate Change

Climate change is affecting MMC forests in eastern Oregon and Washington through changes that include warmer temperatures (Mote and Salathé 2010) and snowpack declines (fig. 39; Mote 2003, Mote et al. 2005). Over the next 100 years, because CO_2 concentrations are projected to rise, these impacts will likely increase in magnitude and extent over the region (Littell et al. 2010). Impacts to terrestrial ecosystems include increased fire frequency and severity, increased susceptibility to some insects and diseases (Fettig et al. 2013, Preisler et al. 2012), and increases in the presence of some invasive species (CIG 2009). Regionally, increased summer temperature and decreased summer precipitation and snowpack (Cayan et al. 2001) are projected to result in a doubling of the area burned by fire by the 2040s and a tripling by the 2080s (CIG 2009). Changes in the length and timing of seasons, especially the growing season, the timing of bud break (phenology), and the seasonal availability of soil moisture are expected to produce large positive and negative shifts in forest growth, with a net effect of increased forest mortality in the eastern Cascades (Choat et al. 2012, Grant et al. 2013, Williams et al. 2012).

In addition to general regional changes in temperature and precipitation predicted by models is the likelihood that change at the local scale could be quite variable owing to high variability in physiographic environments where moist mixed-conifer forests are found.

In addition to the general regional changes in temperature and precipitation predicted by various regional models there is the likelihood that change at the local scale could be quite variable owing to high variability in physiographic environments where MMC forests are found (Daly et al. 2007). While most areas may become warmer, some may become moister and others drier, particularly during certain seasons of the year. Canyon bottoms may remain cool due to accentuated cold air drainage.

For wildlife, changes in climate and vegetation will impact habitat characteristics, reproductive success, and food and water availability. These changes will alter species assemblages and distributions, migration routes, interactions with competitors and predators, and may impact population viability for many species (Staudinger et al. 2013). Impacts may be particularly severe for currently rare or endemic species with restricted distributions (Parmesan 2006). Anticipated changes to wildlife include (1) the susceptibility of high-elevation habitats and species dependent on snowpack (e.g., wolverine [*Gulo gulo*] for the Blue Mountains), (2) impacts on wetlands and associated species, especially those sensitive to water temperature (e.g., tailed frog [*Ascaphus montanus*]), and (3) phenological mismatches for migratory birds and other species (Parmesan 2006). Changes are expected to happen more quickly than species' potential to adapt (Staudinger et al. 2013).

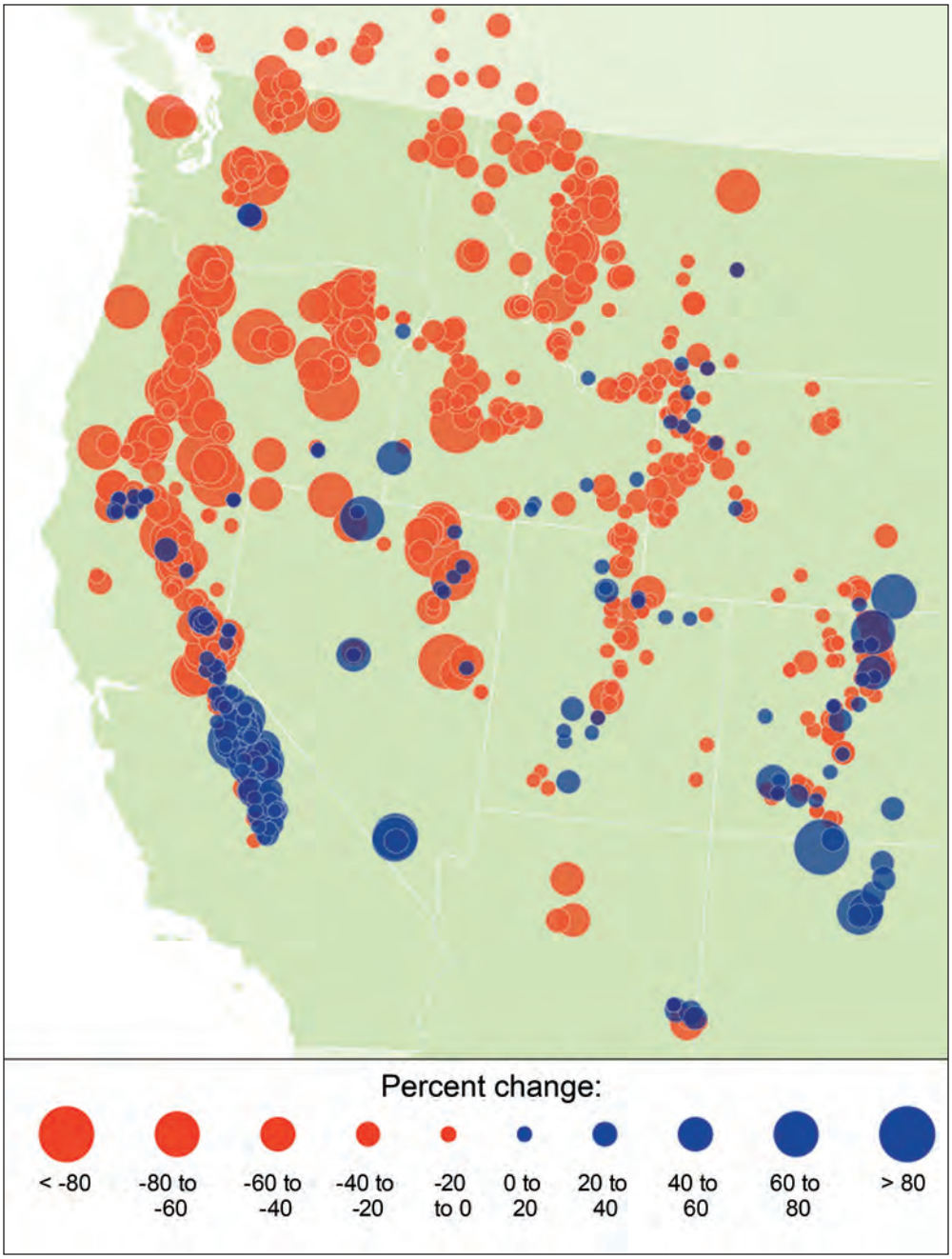


Figure 39—Historical snowpack decline in the Pacific Northwest region 1950–2000 (Mote 2009).

Maintaining landscape patterns that allow species to move in response to changes in climatic and habitat conditions may be particularly important for conservation of sensitive species (Heller and Zavaleta 2009, Nuñez et al. 2013).

Change in climate and disturbance: 1950 to present—
El Niño/Southern Oscillation (ENSO) remains the most important coupled ocean-atmosphere phenomenon to cause climate variability on seasonal to interannual

time scales in the Pacific Northwest. Across decadal timescales, longer-term oscillations such as the Pacific Decadal Oscillation (PDO) come into play. The PDO was in an extended cool phase from about 1945 to 1976 and in a warm phase from 1977 to 1998 (Mantua and Hare 2002, Mantua et al. 1997, Mote et al. 2003, Waring et al. 2011). Minimum temperatures have increased most rapidly in the semi-arid Columbia River basin and the Great Basin, and in semi-arid portions of the Okanogan Highlands, but have changed relatively little west of the Cascade Crest and in the Blue Mountains (fig. 40). Mean average temperature has been observed to have increased by 0.8 °C (1.50 °F) since 1900 (Mote and Salathé 2010). Climate

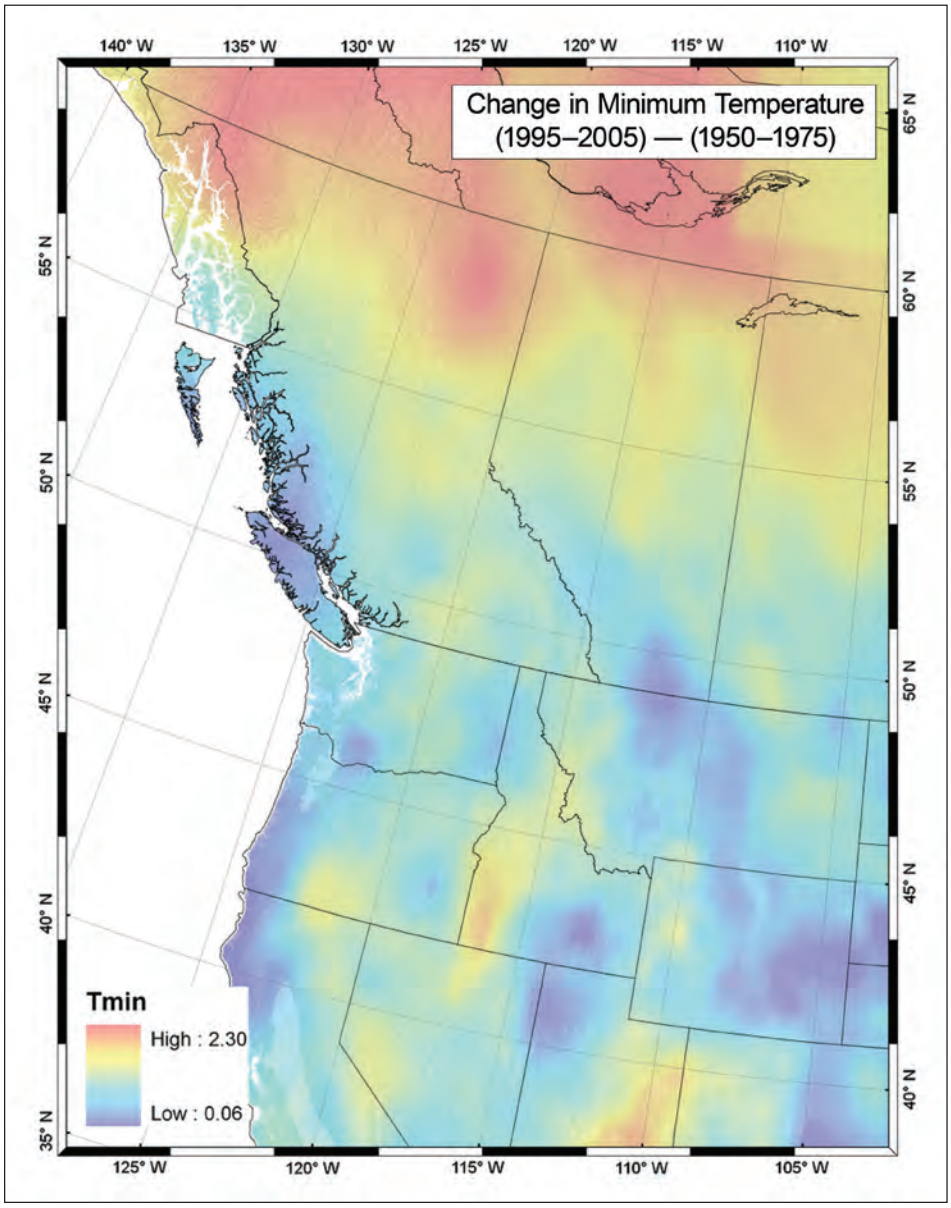


Figure 40—Changes in minimum temperature throughout the Pacific Northwest. Source: Waring et al. 2011.

forecasting models, when averaged, project increases in annual temperature of 1.1 °C (2.0 °F) by the 2020s, 1.8 °C (3.2 °F) by the 2040s, and 3.0 °C (5.3 °F) by the 2080s, compared with the average temperature from 1970 to 1999.

Trends in historical and projected future changes in precipitation in the Pacific Northwest are less clear than for temperature (Stephens et al. 2010). For example, precipitation in the Pacific Northwest has increased by 13 to 38 percent since 1900, but has shown substantial interannual and interdecadal variability during the 20th century (Mote et al. 2003), which current climate models are unable to simulate under future warming scenarios (Ault et al. 2012). Some, but not all models predict slight future increases in annual precipitation (1 to 2 percent in 2030 to 2059, and 2 to 4 percent in 2070 to 2099; Littell et al. 2009).

The ecoregions of eastern Oregon and Washington (notably the eastern Cascades and the Blue Mountains) have a Mediterranean type of climate characterized by warm dry summers and cool moist winters. The lack of summer precipitation coupled with earlier springs and later winters suggest increased vulnerability of forests and forest associates to climate change. Anticipated changes in fire regimes in the Northwest United States is a direct result of these changes in climate (Westerling et al. 2006). The following summarizes the key climate change projections and impacts to moist mixed conifer forests in the Pacific Northwest region (CIG 2009, IPCC 2013, Mote et al. 2005).

Projected outcomes:

- Reduced snowpack amounts (up to 50 percent projected decline)
- Increased rain on snow
- Warmer air temperatures (up to 3 °C by 2080)
- Change in the timing of snowmelt (earlier)
- More climate extremes

Projected impacts to moist mixed-conifer forests:

- Reduced soil moisture
- Increased drought stress
    - Increased fire intensity, severity, and frequency
    - Increased susceptibility to insect attack
- Phenologic shifts (earlier onset of budbreak, longer growing season)

Climate change impacts on forest ecosystems—
Climate change influences on forest tree species are a function of the ecophysiological tolerances unique to each species. Waring et al. (2011) used a process-based forest model to estimate changes in tree species competitiveness (influenced by a variety of ecological factors) between 1950–1975 and 1995–2005 based on climate

effects on simulated leaf area index (LAI). Although LAI may not be the prime indicator of a conifer tree's capacity to respond to changing climates, it provides an index of potential response. Across their western North America study area, they found a significant decrease in the competitiveness of over 50 percent of the evergreen species in ecoregions in the northern and southern portions of the study area. Within Oregon and Washington, competitiveness changed little in the West Cascades and was moderately reduced in the East Cascades, the Okanogan Highlands, and the Blue Mountains (fig. 41). Furthermore, regions exhibiting reduced competitiveness under climate change scenarios were predicted to experience higher rates of disturbance by insects, fire, and other factors (Waring et al. 2011).

These changes in climate are also projected to influence the area of suitable climate for vegetation types differently and shift vegetation assemblages over the landscape. Rehfeldt et al. (2012) developed climate envelope models for biomes of North America and projected change in area and distribution under six climate change scenarios. However, there is still debate about whether this approach realistically captures physiological tolerances of forest species (Loehle 2011).

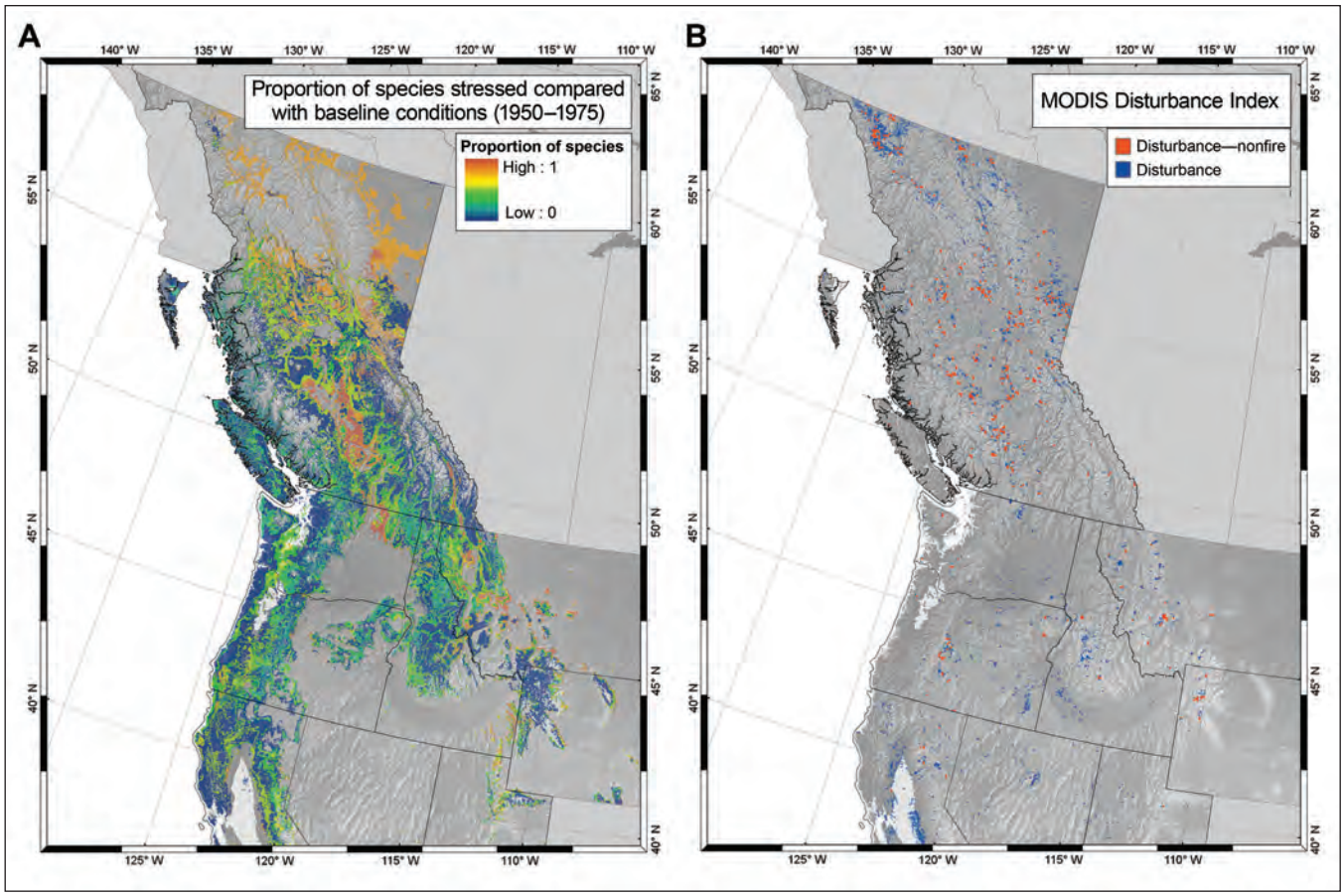


Figure 41—Map presenting the proportion of 15 coniferous species predicted as no longer well-adapted in the years 1995–2005 compared with baseline conditions (1950–1975). From Waring et al. (2011).

We acknowledge that limitations to the use of climate envelope approaches for modeling potential species distribution changes are well known (Fettig et al. 2013). Nonetheless, modeling approaches provide some insight into the possible magnitude and geography of projected changes in species distribution in the coming decades.

For biomes in Oregon and Washington, model results among scenarios estimate that all Oregon Coastal Conifer and Interior Cedar-Hemlock types will undergo the least reduction in the areas they currently occupy. Subalpine biomes in the Cascades and the Rockies are projected to eventually undergo substantial reduction in currently occupied areas, with only 27 percent and 19 percent of these biome types remaining. Drier conifer forest area is also forecasted to decline substantially: 41 percent of Rocky Mountain Montane Conifer, which currently occurs in the Okanogan Highlands and the Blue Mountains, is forecasted to remain in 2060. Importantly, by 2090, only 12 to 57 percent of the current area is forecasted to have climates suitable to the biomes occurring there today, although the rate of decline is uncertain. Of course we do not know how extensive the geographic shift in biomes will eventually be, because there are many complex ecological interactions that will play out over time, and ecophysiological modeling is in its infancy. Current models give us an indication of how dramatic the changes could be. Nonetheless, some areas currently occupied by subalpine forest in the Cascades, for example, will likely become suitable as mixed-conifer forests now found at mid elevations. Climate in the Northeast Cascades of Washington becomes suitable for the Coastal Hemlock Biome type. Forest areas in the Okanogan Highlands and Blue Mountains are largely replaced by climates suitable for the Great Basin Shrub-Grassland type.

Forest productivity is also projected to change under future climates. Productivity is forecasted to increase in what are currently subalpine and alpine zones across the region and to decline in the drier forests, which are largely at the lower forest ecotone in the East Cascades, Okanogan Highlands, and Blue Mountains (Latta et al. 2010). Concomitantly with warmer temperatures, forests may respond to increased atmospheric CO_2 concentrations through increased water use efficiency. However, forest growth response to rising CO_2 is less clear than it appears it will be for temperature, perhaps because soil moisture availability is expected to decline (Peñuelas et al. 2011). Warming may allow some insect species (e.g., some bark beetles) to complete extra generations per year, and adult emergence and flight activity could occur earlier and last longer. Cold-induced mortality of insects during winter may also decrease. For example, model simulations indicate that the climatic suitability for mountain pine beetle will increase during the next several decades in eastern Oregon and Washington (Bentz et al. 2010, Preisler et al. 2012),

and when combined with current forest conditions (Fettig et al. 2007, Hicke and Jenkins 2008), higher levels of tree mortality are expected.

Conversely, there could be some reductions in insect-induced tree mortality when warming increases susceptibility to predators, parasitoids, or pathogens. Preliminary evidence suggests that warmer conditions might shorten the incubation period (time between infection and mortality) of the baculovirus that limits Douglas-fir tussock moth populations (see footnote 2). Given projected warming in winter and decreases in precipitation in summer, the impact of western spruce budworm will likely decrease in the future relative to the current distributions of susceptible forest types in this region (Williams and Liebhold 1995). The insect hibernates in winter, and elevated temperatures during this period reduce survival. Warming may also change the timing and synchrony of bud break in Douglas-fir, which in turn may influence outbreak frequency and severity. Projected climate change impacts to MMC forests in the region are likely to be manifest through ENSO and other oscillations such as the PDO. Moreover, the multiscale (broad-scale and fine topographic) nature by which climate change is likely to manifest across the landscape necessitates a multiscale hierarchy such as the one we have outlined in previous sections of this synthesis (CIG 2009, IPCC 2013, Mote et al. 2005):

- El Niño/Southern Oscillation remains the most important coupled ocean-atmosphere phenomenon to cause climate variability on seasonal to interannual time scales in the Pacific Northwest.
- Projected changes in climate will be manifest at both highly localized and broad regional scales for moist mixed-conifer forests.
- Necessitating the need for multiscale, hierarchical approach to address future climate change impacts.

Changes in Vegetation

Changes in the structure and composition of forests since Euro-American settlement are well documented (Hessburg and Agee 2003). For example, forests are now typically several times denser in most locations than under native fire regimes (Camp 1999, Hagmann et al. 2013, Merschel 2012, Perry et al. 2004) (table 5). However, one recent study (Baker 2012) has indicated that these forests were "generally dense" (100 trees per acre [275 trees per hectare]) in the late 1800s and suggested that the amount of change in the structure of these forests and the need for density reduction has been overstated. It is unclear how density estimates from the Baker study apply to MMC forests, which are a subset of the ponderosa, dry mixed-conifer, and lodgepole pine stands that he sampled, as less than 1 percent of the trees were identified as white or grand fir. This suggests that either his records

Table 5—Historical and current tree density (trees per hectare, TPH) estimates in dry and moist mixed-conifer forests

Region	Forest description	Historical density	Current density	Source	Notes
		Mean ± standard deviation (range) and time period			
Eastern slope of the Cascade Range, southern Oregon	Mixed-dry	64 ± 22 (14–156) 1914–1922	286 ± 130 (109–572) 1997–2006	Hagmann et al. 2013	Historical density is reported for trees >15.2 cm diameter at breast height (d.b.h.) based on timber inventory transects that covered 10 to 20 percent (6646 ha) of a 38 641 ha study area of ponderosa pine and dry and moist mixed-conifer forest. Current density is reported for trees >15 cm d.b.h. and is based on 24 current vegetation survey plots within the sample area. Inventory plots were assigned to habitat types using mapped potential vegetation types (ILAP).
	Mixed-moist	78 ± 37 (0–296) 1914–1922	233 ± 90 (104–378) 1997–2006		
Warm Springs Indian Reservation, eastern slope of the Cascade Range, Oregon	Mixed-dry	65 ± 25 (6–188) 1922–1925	NA	Hagmann, unpublished data, 2013[a]	Historical density is reported for trees >15.2 cm d.b.h. based on timber inventory transects that covered 20 percent (32 293 ha) of a 158 354 ha study area of dry and moist mixed-conifer forest. Inventory plots were assigned to habitat types using mapped potential vegetation types (ILAP).
	Mixed-moist	70 ± 32 (0–289) 1922–1925	NA		
Austin-Whitney Tract in the Blue Mountains of northeast Oregon	Mixed-dry	120 1910	NA	Munger 1912 (summarized by David Powell)	Density is reported for trees >10 cm d.b.h. Munger specifically inventoried "well stocked" stands.
Crawford Creek Tract in the Blue Mountains near Unity, Oregon	Mixed-dry	126 1912	NA		
Lookinglass Creek Tract in the Wallowa Mountains of northeast Oregon	Mixed-moist	162 1910	NA		
Eastern slope of the Cascade Range, central Oregon	Mixed-dry	136 1912	NA	Munger 1917	Density is reported for trees >10 cm d.b.h. Munger specifically inventoried "well stocked" stands.
Eastern slope of the Cascade Range, central Oregon	Mixed-conifer	275 Late 1800s	NA	Baker 2012	General land office survey records were used to estimate stand density. Estimates for a 398 346 ha area are based on 11 856 trees marking section and quarter-section corners. Four trees were used to estimate density at section corners, and two were used at quarter corners. This inventory area included lodgepole pine forests, which can have high stand densities.

Table 5—Historical and current tree density (trees per hectare, TPH) estimates in dry and moist mixed-conifer forests (continued)

Region	Forest description	Historical density	Current density	Source	Notes
		Mean ± standard deviation (range) and time period			
Eastern slope of the Cascade Range, central Oregon	Mixed-dry (Douglas-fir)	447 ± 186.8 (227–778) 14 sample sites 2009–2010	NA	Merschel et al. [N.d.]	Density is reported for trees >10 cm d.b.h. Sample sites (1.0 ha) were widely distributed in mature forest mapped in any of the mixed-conifer dry or mixed-conifer dry plant association groups. The number of sample sites used in each estimate is reported following the reported density.
	Mixed-dry (grand fir)	NA	536 ± 185 (113–825) 16 sample sites 2009–2010		
	Mixed-moist	NA	429 ± 200 (52–900) 24 sample sites 2009–2010		
Ochoco Mountains, central Oregon	Mixed-dry (Douglas-fir)	NA	274 ± 132 (95–533) 26 sample sites 2009–2010		
	Mixed-dry (grand fir)	NA	203 ± 102 (76–430) 19 sample sites 2009–2010		
	Mixed-moist	NA	312 ± 211 (67–799) 26 sample sites 2009–2010		
Eastern slope of the Cascade Range, central Oregon	Dry and moist mixed-conifer	40–80 in 8 stands,<30 in 5 stands. Refers to trees >150 years old.	868 (335–1415) ~2004	Perry et al. 2004	Age and size were sampled for live trees at thirteen 0.2-ha sites. Historical density refers to the number of trees per hectare >150 years in age. Current density refers to all trees >5 cm d.b.h.
Eastern slope of the Cascade Range, northern Washington	Mixed-conifer-dry	HDSG[b] —119 WDSH—168 WDTS—315 CDG—311 WMSH—113 1899	HDSG—218 WDSH—326 WDTS—293 CDG—376 WMSH—556 1999	Ohlson and Schellhaas 1999	Historical density was estimated using 52 one-tenth-acre plots. Authors suggest that changes in fire regime and associated changes in structure began in the 1860s and that maximum density was reached in the mid-20th century. Historical reconstructed densities and current densities are reported for all trees >12.7 cm d.b.h., and are stratified by different Douglas-fir potential vegetation types ranked from most xeric to most mesic. WMSH would correspond to moist mixed-conifer potential vegetation types. It had a fire return interval of <19 years. The relatively high historical density in WDTS, a type related to a mixed severity fire that occurred in 1886.

Table 5—Historical and current tree density (trees per hectare, TPH) estimates in dry and moist mixed-conifer forests (continued)

Region	Forest description	Historical density	Current density	Source	Notes
		Mean ± standard deviation (range) and time period			
Eastern slope of the Cascades Range and foothills, Oregon and Washington	Mixed-dry	NA	470 ± 267 (n = 512) 1994–2004	M. Reilly, unpublished data[c]	Density is reported for trees >10 cm d.b.h. Density is based on forest current vegetation survey (CVS) plots distributed on a 2.5 by 2.5 km grid (5 km in wilderness areas) throughout national forests of Oregon and Washington. Sample sites include developmental stages ranging from early seral in recently disturbed areas (logging, wildfire, etc.) to mature old-growth forest. The number of CVS plots used to calculate density is reported in parentheses. CVS plots were assigned to PVTs based on ILAP map.

Note: Dry mixed-conifer forests are included because several studies indicate that historical and current disturbance regimes and stand densities of the two sites overlap to a large degree (see table 2). Diameter thresholds, methods of estimation, and spatial coverage used to develop estimates varies among authors.

[a] On file with: Keala Hagmann, School of Environmental and Forest Sciences, University of Washington, Box 352100, Seattle, WA 98195.

[b] Plant association groups with respective plant associations:

HDSG (Hot/Dry/Shrub/Grass):
Pinus ponderosa/Agropyron spicatum
Pseudotsuga menziesii/Agropyron spicatum
Pinus ponderosa/Purshia tridentata/Agropyron spicatum
Pseudotsuga menziesii/Purshia tridentata/Agropyron spicatum
Pseudotsuga menziesii/Symphoricarpos albus/Agropyron spicatum

WDSH (Warm/Dry/Shrub/Herb):
Pseudotsuga menziesii/Arctostaphylos uva-ursi
Pseudotsuga menziesii/Arctostaphylos uva-ursi/Purshia tridentata
Pseudotsuga menziesii/Spirea betulifolia var. *lucida*

WDTS (Warm/Dry/Tall Shrub):
Pseudotsuga menziesii/Physocarpus malvaceus
Pseudotsuga menziesii/Physocarpus malvaceus/Linaea borealis var. *longiflora*

WMSH (Warm/Mesic/Shrub/Herb):
Pseudotsuga menziesii/Symphoricarpos albus
Pseudotsuga menziesii/Symphoricarpos albus/Calamagrostis rubescens

CDG (Cool/Dry/Grass)
Pseudotsuga menziesii/Arctostaphylos uva-ursi/Calamagrostis rubescens
Pseudotsuga menziesii/Purshia tridentata/Calamagrostis rubescens
Pseudotsuga menziesii/Spirea betulifolia var. *lucida/Calamagrostis rubescens*

[c] On file with: Matthew Reilly, Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331.

did not sample much MMC forest or that there were few individuals of these *Abies* species present in the late 1800s. Hagmann et al. (2013) examined stand inventory records from the 1920s in landscapes that overlap areas sampled by Baker (2012) and found much lower tree densities for the same areas. Munger (1917) reported a density of 55 large trees per acre for ponderosa pine forest, and 61 in dry mixed-conifer forests in the eastern Cascades in the early 20th century. That study characterized dry mixed-conifer stands as open with widely spaced trees, but noted that the forests consisted of open stands of mature trees interrupted by treeless areas and denser patches of young trees.

Although total stand densities have increased several fold, the densities of large trees (>50 cm [~20 in]) have declined in many areas within older mixed-conifer forest areas (excluding clearcut areas) by as much as 50 percent based on a few studies (table 3). The decline has been observed in both Oregon and Washington and is likely a result of selective logging of large pines and Douglas-firs during the 20th century. One study from Washington reported increases in the density of large trees.[3]

Heyerdahl showed that fire occurrence in several pine and mixed-conifer forest patches in central Oregon strongly declined after 1880, and grand fir establishment started to increase in the 1880s and 1890s (Heyerdahl et al. 2001 and unpublished data; Merschel 2012). If we assume that the presettlement density of trees in mixed-conifer patches was 50 to 100 trees per hectare (20 to 40 trees per acre), then current densities for mixed-conifer forests may be two to six times the historical densities of some patches. For example, several recent studies have estimated current mixed conifer densities at about 200 to more than 300 trees per hectare (80 to more than 120 trees per acre) (Camp 1999, Merschel 2012, Perry et al. 2004). Under the recent disturbance regime of fire suppression and logging of old trees, MMC forests often consist of scattered remnants of medium- to large-sized shade-intolerant dominant trees, with medium-sized shade-tolerant co-dominant trees, and often several dense layers of intermediate and overtopped or suppressed shade-tolerant trees (Oliver and Larsen 1996). Thus, land use and fire regime changes have shifted successional pathways from dynamic fine scale mosaics driven by low- to mixed-severity fire to coarser grained, more homogenous patch types driven by high-severity fire.

Seed availability, either the absence of seeds of a species or the presence of nearby seed sources (e.g., a kind of "mass effects" in which a high rate of

[3] Ohlson, P.; Schellhaas, R. 1999. Historical and current stand structure in Douglas-fir and ponderosa pine forests. Unpublished report. Portland, OR: U.S. Department of Agriculture, Forest Service, Okanogan and Wenatchee National Forests.

propagule input maintains species on sites that are not well suited for reproduction or long-term survival) (Shmida and Wilson 1985), can have a strong influence on community development, and is often overlooked as a factor in succession. For example, fire suppression has led to an increase of grand or white fir in many forest environments, which has converted many acres of open ponderosa pine forests to dense mixed-conifer forests (Everett et al. 1994, 1997; Hann et al. 1997; Hessburg et al. 1999a, 2000a). In many cases, the true firs and Douglas-fir may be establishing on sites that are less optimal for their growth only because there are massive amounts of seeds in the local landscape (these species dominate the seed rain) that swamp out some of the environmental and ecological controls over species distributions within a community. The densification of these stands could inhibit regeneration of early-seral species such as ponderosa pine and western larch, which are an important component of the overstory, and require relatively open conditions and frequent disturbance for establishment. In many areas, high-grade logging over the 20th century has reduced the densities of these large young forest dominants (Harrod et al. 1999), and they will not return to these sites without disturbances that open the canopy, reduce the overall seed rain of the shade-tolerant species, and reduce stem densities.

Old-growth forests are one of the most ecologically and socially valuable successional stages in the Pacific Northwest (Spies and Duncan 2009), but they are also quite variable in structure and dynamics, especially between the west and east sides of the Cascade Range. The classic old-growth forests of the coastal portion of the Pacific Northwest—fire-infrequent forests that contain large, emergent, long-lived conifers (e.g., Douglas-fir) and dense multilayered mid- and understories of shade-tolerant trees (e.g., western hemlock)—have analogs on the east side of the Cascades. Fire-infrequent old growth on the east side establishes through different pathways and exists under differing conditions. Much of what developed prior to the onset of the timber utilization era, beginning in the later part of the 1800s, consisted of large old ponderosa pine and Douglas-fir in the upper canopy, with occasional western larch and shade-tolerant white/grand fir in the upper canopy and white/grand fir filling lower canopy layers (Merschel 2012). However, this old-forest type would have been uncommon in the drier, fire-prone landscapes, occupying moist, less fire-prone sites. For example, Agee (2003) estimated that only 10 to 17 percent of MMC forest sites would have supported dense old forests under the native fire regime, although some individual watersheds may have had as much as 20 to 35 percent (Hessburg et al. 1999a, 2000a).

The composition of patches of old-growth trees on the east side also depended very much on topographic position. Solar insolation and soil moisture retention,

The composition of patches of old-growth trees on the east side depends very much on topographic position. Solar insolation and soil moisture retention, key factors in determining growing potential and relative drought stress, are considerably different depending on slope aspect and slope position.

key factors in determining growing potential and relative drought stress, are considerably different depending on slope aspect and slope position. Thus the species composition and structure of patches of old forest are quite different at the bottom of a drainage, where soil moisture and shade enable the growth of mixed species of denser, multilayered patches compared with patches on a south-facing midslope, which tend to be single layers of more sparse groups of predominantly large pines.

Another important difference between older, structurally diverse, interior MMC forest stands is that they do not persist for long periods as westside old growth does. It is important to continually recruit forest stands into this older, structurally diverse condition because forests on the east side do not stay in that condition. The transience of old forest conditions in interior MMC forest is a consequence of the unique assemblage of primary disturbances (e.g., fire, insects, and diseases) found in these drier landscapes. The dense, multilayered old forests that have developed under extended periods of fire exclusion are vulnerable to a host of disturbance factors and are unlikely to persist except where local topography, soils, and microclimate are suitable (e.g., sufficient soil moisture). By contrast, the sparser, single-layered old forests, dominated by large pines, are capable of persisting for as long as 500 years.

Historically, the most common expression of old growth would have been a "fire climax" (Perry et al. 2008) or old single-story, park-like forest (sensu O'Hara 1996), where various combinations of large, old, fire-resistant ponderosa pine, Douglas-fir, and western larch would occur in the canopy over a relatively open but variable and ephemeral understory of pines or shade-tolerant tree species depending on the fire frequency at the site. On sites with longer fire return intervals (>25 years) dominated by mixed-severity fire regimes, the canopies of the fire-dependent old growth would include patches (fractions of an acre to several acres) formed by small mixed-severity disturbances from fire or insects and disease. In many landscapes, streamside environments would have longer fire return intervals (>50 years), and support old growth stands with larger components of fir in the understories and sometimes in the overstories.

Young forest communities may have been altered as well, but we have less information about the amounts and patterns of open plant communities maintained by high-severity fire, which was a variable component within the mixed-severity regime of the mixed-conifer forest. Of special interest, clonal aspen patches, often imbedded within mixed-conifer forests, have been heavily affected by fire exclusion owing to their relatively short life expectancy (stands begin to deteriorate at 55 to 60 years of age and are pathologically old and decadent at 90 to 110 years; Bartos

2000). Wildfires normally revitalized aspen clones, with some patches sprouting 10,000 to 20,000 stems per hectare (24,710 to 49,421 stems per acre) in early life stages after fires. Ungulate browsing, both wild and domestic, and a host of stem cankers, foliar diseases, and insect defoliators naturally thin aspen clones to a few hundred stems per hectare after several decades.

Changes in Disturbance Factors: Insects and Disease

The frequency, severity, and scale of insect outbreaks in MMC forests of eastern Oregon and Washington vary considerably (table 5), even by species. In short, effects on vegetation range from short-term reductions in crown cover (e.g., larch casebearer), to modest increases in background levels of tree mortality (e.g., balsam wooly adelgid [*Adelges piceae*]), to regional-scale outbreaks resulting in extensive amounts of tree mortality under some circumstances (e.g., Douglas-fir tussock moth and western spruce budworm). Of more recent concern is the impact of mountain pine beetle outbreaks in the region (see "Animals of the Moist Mixed-Conifer Ecosystem"). Wickman (1992) noted that historically the impacts of insects on mixed-conifer forests were typically of shorter duration and lower severity than was observed in recent decades. A heterogeneous landscape is thought to be more resilient to insect- and disease-caused disturbances (Fettig et al. 2007, Filip et al. 2010). Although it is difficult to isolate the confounding effects of recent management practices and climatic changes, a more heterogeneous landscape likely ensured that most disturbances in MMC forests were more brief and spatially confined in the past (Hessburg et al. 1994). This has been well documented for dry mixed-conifer forests in the region, and it is likely a similar trend existed for MMC forests as they are interconnected with dry mixed-conifer forests that are now substantially modified by fire exclusion and selective harvesting (Hessburg et al. 1994, Lehmkuhl et al. 1994).

Outbreaks of forest diseases caused by native and introduced pathogens are generally thought to become more frequent and severe as a result of climate change (Sturrock et al. 2011). However, diseases caused by pathogens directly affected by climate (e.g., needle blights) are predicted to have a reduced impact under warmer and drier conditions. For thorough reviews on the expected effects of climatic change on forest pathogens, see Dale et al. (2001) and Sturrock et al. (2011).

Effects of Altered Disturbance Regimes, Land Use, and Climate Change on Animal Populations and Habitats

There have been significant changes to fish and wildlife populations associated with MMC forests during the last 150 years. The effects of human land uses and altered disturbance regimes discussed in previous sections of this report have

had a significant impact on fish and wildlife populations across this entire area. Additionally, climate change has already produced observable changes in animal communities in the Pacific Northwest (Hixon et al. 2010), and those changes are likely to intensify in the future (Dalton et al. 2013).

Regional landscape assessments over the past 20 years have documented the profound effects of historical human use and forest management on mixed-conifer and other wildlife habitats of eastern Oregon and Washington (Everett et al. 1994; Hann et al. 1997; Hessburg et al. 1999a, 2000a; Lehmkuhl et al. 1994; USDA FS 1996). The area and condition of grasslands, shrublands, and old forest multistory and late-seral single-story forests, and the forest backbone of large residual trees, have declined markedly (Hessburg and Agee 2003, Hessburg et al. 2005) (fig. 42). At the same time, the area occupied by invasive species, roads, intermediate-aged forest, and insect, disease, and fire susceptibility (as indicated by changes in forest structure, fuel loading, and crown fire potential) have increased. Habitat trends reported in recent wildlife habitat assessments reflect a widespread reduction in habitat values relative to historical conditions for wildlife associated with early-seral, open forest, and postfire habitats (Gaines et al., in press; Suring et al. 2011; Wales et al. 2011; Wisdom et al. 2000). Old forest habitat conditions show less decline at a regional scale, but patterns are variable across sub-basins.

For example, Wisdom et al. (2000) found that habitat for species associated with low-elevation old forest, which includes single-story ponderosa pine forest and single- and multistory mixed-conifer forest, has declined in most of eastern Oregon and Washington (table 6). The habitat trend for species associated with old forest (i.e., forests with multistory stands and large old trees), which spans the elevation gradient from low to high, varies across the region from markedly declining in the northeastern Cascade Range, to neutral in the southeastern Cascades and Blue Mountains, to increasing in the Klamath province. The habitat trend for generalist forest mosaic species, which use a broad range of forest cover types and structural stages, has been neutral or positive. The habitat trend for young forest species varies from highly or moderately negative in the Klamath and Blue Mountain provinces, respectively, to positive to neutral in the Cascade Range province (Wisdom et al. 2000).

Habitat assessments in support of national forest plan revision activities in eastern Washington and Oregon have produced results similar to those of Wisdom et al. (2000). In their assessment of wildlife habitat and population viability in national forests of eastern Washington (the Okanogan-Wenatchee and Colville National Forests), Gaines et al. (in press) found that the species whose viability had declined most relative to historical conditions were those species sensitive to

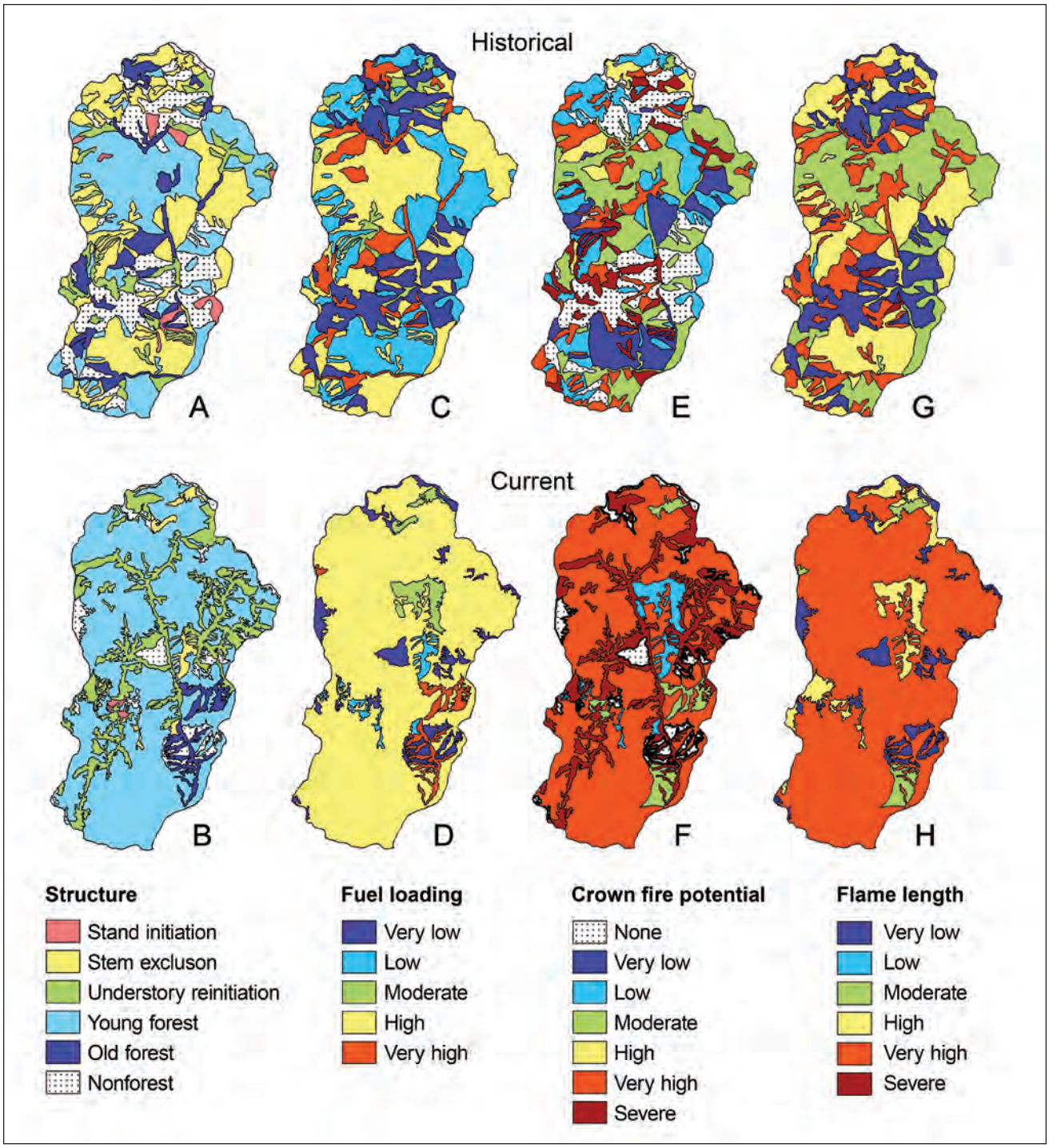


Figure 42—Comparison of an example watershed from the early (ca. 1900, historical) and late (1990s, current) 20th century. Note how spatial patterns of fuel loading, crown fire potential, and flame length closely track forest structural conditions: i.e., process followed pattern. Maps are of the Peavine Creek drainage, a dry forest subwatershed of Lower Grande Ronde subbasin in the Blue Mountains Province displaying historical and current structural classes (A and B), fuel loading (C and D), crown fire potential (E and F), and flame length during wildfire (G and H). Fuel loading classes are very low <22.5 Mg/ha; low = 22.5 to 44.9 Mg/ha; moderate = 45 to 56.1 Mg/ha; high = 56.2 to 67.3 Mg/ha; very high >67.3 Mg/ha. Crown fire potential classes were a relativized index. Flame length classes were very low <0.6 m; low = 0.7 to 1.2 m; moderate = 1.3 to 1.8 m; high = 1.9 to 2.4 m; very high = 2.5 to 3.4 m; severe >3.4 m (Hessburg and Agee 2003, Hessburg et al. 2005).

Table 6—Source forest-habitat trends (1800s to 1995) for families of focal wildlife species in 6th hydrologic unit code (HUC) subwatersheds of the interior Columbia River basin in eastern Oregon and Washington

		Percentage of 6th-code watersheds			
Province	**Family name**	**Decreasing**	**Neutral**	**Increasing**	**Trend**
Blue Mountains	Low-elevation old forest	67	20	13	–
	Broad-elevation old forest	47	17	36	0
	Forest mosaic	7	15	78	+
	Early-seral montane and lower montane forest	53	4	42	–
	Average	43.5	14.0	42.3	0
Northern Cascades	Low-elevation old forest	69	24	7	–
	Broad-elevation old forest	74	13	13	–
	Forest mosaic	17	45	37	0
	Early-seral montane and lower montane forest	30	8	63	+
	Average	47.5	22.5	30.0	0
Southern Cascades	Low-elevation old forest	56	22	22	–
	Broad-elevation old forest	37	15	47	0
	Forest mosaic	0	20	80	+
	Early-seral montane and lower montane forest	45	13	42	0
	Average	34.5	17.5	47.8	0
Upper Klamath	Low-elevation old forest	33	19	48	0
	Broad-elevation old forest	7	5	88	+
	Forest mosaic	5	7	88	+
	Early-seral montane and lower montane forest	98	0	2	–
	Average	35.75	7.75	56.50	0

Note: Trend was determined by >50 percent of subwatersheds decreasing (–) or increasing (+); otherwise, trend was neutral.
Source: Wisdom et al. (2000).

human disturbances or grazing, and associated with shrub-steppe, early-seral, or postfire habitats (e.g., fox sparrow, white-headed woodpecker, western bluebird, and sage thrasher [*Oreoscoptes montanus*]). Species associated with older forest conditions (including northern goshawk, pileated woodpecker, and American marten) also experienced declines in viability relative to historical conditions, but those declines were not as substantial as experienced by the shrub-steppe, early seral, or postfire species.

In their assessment of wildlife habitat values in three national forests in northeastern Oregon (the Umatilla, Wallowa Whitman, and Malheur National Forests), Wales et al. (2011) found that focal species representative of old forest conditions (including goshawk and pileated woodpecker) had current habitat values that were generally consistent with historical conditions at a regional scale, while species associated with open, large tree forests and early-seral or postfire habitats (including Cassin's finch [*Carpodacus cassinii*], white-headed woodpecker, western bluebird, fox sparrow, black-backed woodpecker [*Picoides arcticus*], and Lewis's

woodpecker) generally had experienced declines in habitat values relative to historical conditions. Species sensitive to human disturbances (including wolverine and American marten) also experienced declines in habitat values relative to historical conditions. Both Gaines et al. (in press) and Wales et al. (2011) noted that the area of postfire habitat in eastern Washington and Oregon has increased since 1980, but most of it is concentrated in a few watersheds that have experienced large-scale, high-intensity wildfire, producing patterns that did not contribute to population viability for postfire species at a regional scale as effectively as the patterns produced by historical mixed-severity fire regimes.

Two broad factors contributing to reductions in wildlife population viability were highlighted in these assessments: (1) changes in amount and distribution of old forest, deciduous, early-seral, shrub-steppe, and postfire habitats, and (2) impacts of human activities associated with grazing, roads, and recreation. These habitat trends give a general sense of the regional and provincial status of those habitats, but there is much variability in the trends among subwatersheds within provinces. As with stand and landscape management, the variability in conditions is perhaps more important to understand and manage for than the average. Hence, managers need to assess the trends in their local subwatersheds for an accurate assessment of habitat trends and management needs. For example, the trend in broad-elevation old forest habitat was neutral in two of the four provinces; but within those neutral provinces old forest habitat decreased in 47 percent of the subwatersheds in the Blue Mountains and 37 percent of the subwatersheds in the southeastern Cascades (Wisdom et al. 2000).

Human land uses have important effects on animal populations at several scales. At the broadest regional scale, residential, agricultural, and transportation network development has resulted in habitat loss and fragmentation throughout western North America (Theobald et al. 2011). In eastern Oregon and Washington, broad-scale habitat connectivity patterns for species associated with MMC forests are determined by major landform features and associated ecotonal boundaries, in combination with human development patterns (Singleton et al. 2002, WHCWG 2010). Major natural barriers for species associated with MMC forest habitats in the Pacific Northwest include the shrub-steppe landscapes of central Washington and Oregon, and dramatic landforms like the Columbia Gorge, Lake Chelan, the Okanogan Valley (U.S.), and Hells Canyon (Singleton et al. 2002, WHCWG 2010). Major anthropogenic barriers include high-volume highways (e.g., Interstate 90, Interstate 84, portions of U.S. Highway 97, and Canada Highway 3), as well as areas of agricultural, residential, and industrial development. One area of dramatic recent rapid development has been in southern British Columbia, through the Okanogan

Valley and portions of the Highway 3 corridor between Osoyoos and Castelgar (Singleton et al. 2002, WHCWG 2010). These linkage patterns are particularly important for species associated with MMC forests in Washington because populations in Washington are often southern extensions of populations centered in Canada (Singleton et al. 2002, WHCWG 2010).

At a finer scale, forest roads and trails and associated recreational activities can have substantial impacts on wildlife populations associated with MMC habitats (reviewed by Gaines et al. 2003). Common responses of animals to roads and trails include displacement and avoidance, which can contribute to disruption of nesting, breeding, or wintering areas and reduced population density (Benitez-Lopez et al. 2010, Gaines et al. 2003). For example, Naylor et al. (2009) quantified elk behavioral responses to off-road recreational activities including ATVs, mountain biking, hiking, and horseback riding in the Blue Mountains. They found that feeding time decreased and travel time increased in response to these activities. Road access for firewood gatherers can also contribute to loss of large snags and logs in many areas (Hollenbeck et al. 2013). Ecological effects of domestic livestock grazing are reviewed in "Grazing" on page 99.

Altered disturbance regimes and historical land management practices have contributed to substantial changes in the amount and distribution of forest habitats relative to historical conditions, but management activities focused on restoration of historical habitat patterns and stand structure conditions can also have a variety of effects on wildlife populations. These effects can differ substantially across species (reviewed by Kennedy and Fontaine 2009, and Pilliod et al. 2006). At a stand scale, restoration treatments tend to favor those species associated with more open conditions and increased understory vegetation diversity, and have the potential to reduce abundance of species associated with closed canopy, old forest conditions (e.g., Converse et al. 2006, Gaines et al. 2010). However, responses can be quite variable depending on the intensity of the treatment, and although the abundance of individual species can change, restoration treatments generally do not cause substantial changes in species diversity (e.g., Gaines et al. 2010, Lyons et al. 2008, Russell et al. 2009).

Retention of large, old trees, snags, and logs can help maintain the old forest functions of many stands when smaller trees are removed for fuel reduction or forest restoration objectives.

Retention of large, old trees, snags, and logs can help maintain the old forest functions of many stands when smaller trees are removed for fuel reduction or forest restoration objectives. For example, Bull et al. (1995) found that a MMC stand in the Blue Mountains continued to function as old growth for pileated woodpecker and Vaux's swift (*Chaetura vauxi*) when large trees and logs were retained after treatment to remove small trees killed by western spruce budworm. Most research

on the effects of forest restoration or fuel reduction treatments on wildlife have focused on responses soon after treatment (<5 years post-treatment; Kennedy and Fontaine 2009). Longer-term (>10 year post-treatment) effects of forest restoration treatments on animal populations have yet to be well documented. This will be a fertile area for future research as recently treated areas mature and provide opportunities for monitoring the effects of those restoration-oriented treatments.

Old forest habitats are of particular conservation concern because they provide a variety of ecological and social values (reviewed in Spies and Duncan 2009), and old forest characteristics take a long time to regenerate when they are lost as a consequence of high-intensity disturbance or intensive management. In the following section we present information on habitat dynamics and conservation of the NSO. We recognize that much of the area being addressed by this document is outside of the range of the NSO, but we present this information to highlight the lessons from spotted owl conservation that are also important for conservation of other old forest species associated with MMC forests across eastern Washington and Oregon.

The old growth forests of the east Cascades are diverse, dynamic, and shaped by the complex behavior of multiple disturbance factors including fire. The historical structure and function of these forests have been extensively altered by fire exclusion, logging, and other activities (Buchanan et al. 1995, Spies et al. 2006, USFWS 2011). The implications of these changes and the current and future conditions of east Cascades forests for NSO recovery are complex. Habitat conditions for spotted owls in this region are significantly different today than 150 years ago. Although much habitat has been degraded, particularly with the chronic loss of suitable structures for nesting and roosting sites (i.e., selective removal of large trees, removal of snags and damaged live trees) there has also been an increase in dense forest across portions of the landscape (Everett et al. 1997, Hessburg et al. 2005). These changes present multiple challenges for land managers. Where and how much of these dense stands should managers strive to retain? How is retention of dense forest reconciled with meeting restoration goals that necessarily consider the resiliency of a forest in light of impending disturbance factors and climate change?

The recent recovery plan for the NSO (USFWS 2011) stated that the recovery strategy requires action in the face of uncertainty. The plan cites Carey (2007) in advocating "active management for ecological values that will trade short-term negative effects for long-term gains. Collaborative management must be willing to accept short-term impacts and short-term risks to achieve long-term benefits and long-term risk reduction." The recovery plan described the difficulties in defining conservation objectives for habitat of NSO in these drier forests of the east side:

> Changing climate conditions, dynamic ecological processes, and a variety of past and current management practices render broad management generalizations impractical. Recommendations for spotted owl recovery in this area also need to be considered alongside other land management goals—sometimes competing, sometimes complementary—such as fuels management and invasive species control. In some cases, failure to intervene or restore forest conditions may lead to dense stands heavy with fuels and in danger of stand-replacing fires and insect and disease outbreaks (USFWS 2011: III-20).

In general, dynamic, disturbance-prone forests of the eastern Cascades, California Cascades, and Klamath Provinces could be actively managed in a way that reconciles the overlapping goals of spotted owl conservation, responding to climate change, and restoring dry forest ecological structure, composition and processes, including wildfire and other disturbances

As stewards of NSO habitat, land managers are endeavoring to provide the full complement of habitat requirements. Strong evidence exists suggesting that nesting and roosting habitat, the array of structures in trees that provide a platform, cover, or both, have been largely removed from many areas through decades of selective cutting and sanitation treatments (USFWS 2011). Managers are advised to pay special attention to this habitat management issue when assessing and planning projects, and to make special efforts to retain and restore these habitat elements to the landscape. However, less certainty exists regarding the relationship between owls and habitat used for foraging across the broader landscape. Evidence suggests that owls tend to forage in the moderate- to higher canopy-closure forests and by the same token tend to avoid open stands (reviewed by Courtney et al. 2004).

Northern spotted owl numbers may continue to decline as a consequence of competition with barred owls, but retention and recruitment of habitat continues to be important because reductions in habitat availability are likely to increase competition between the species and will limit opportunities for spotted owls to adapt to the presence of barred owls (Dugger et al. 2011, Forsman et al. 2011, Singleton 2013). Risk and uncertainty are inescapable with management of these forests. Employing a landscape view of assessment and management can help us understand these risks and uncertainties more clearly.

Spotted owls are different from other old forest species associated with MMC forest. For example, northern goshawks and pileated woodpeckers have a broader distribution throughout the Interior West and are associated with a broader range of forest conditions including drier, more open mixed-conifer stands than those used by NSOs, but there are some lessons from spotted owl management that are worth

considering for conservation of these other old forest species. In particular, loss of old forest structures to large-scale, high-intensity wildfire is a concern for all old forest species. Landscape conditions that provide for mixed-severity fire patterns and that are resilient to intermittent disturbances will be most likely to provide a shifting mosaic of old forest habitat conditions for all old forest species over time. Managing for patterns that continually bring stands into old forest conditions is also important because we cannot rely on existing old forest stands to remain in that condition over long time periods. This approach of maintaining a shifting mosaic of old forest conditions is likely to be an increasingly important concept for old forest wildlife conservation under future disturbance regimes that are anticipated under many climate change scenarios.

Conservation of unique forest structures (particularly big old trees) is important, but it will be most effective if it is done in the context of sustainable landscape patterns. Big old trees, both vertical and horizontal, living and dead, are important across all stages of stand development (Bull et al. 1997). Where big old trees are absent from a landscape, retaining the largest trees, even of undesirable species, may be appropriate for retaining and developing stand structure. Retaining legacy structures can also provide conditions that facilitate more rapid development of multistory canopy conditions in younger forests.

Another fundamental challenge is that overly aggressive stand sanitization can contribute to a loss of structural diversity. This is a key issue in balancing silvicultural and wildlife habitat objectives at the stand scale. For example, past forest management practices often focused on reducing pathogens like mistletoe and root-rot to enhance fiber production through vigorous tree growth. At moderate levels, these pathogens can enhance spatial and structural complexity within forest stands. Mistletoe can contribute to tree mortality, but it also provides important structures for forest wildlife, particularly in harvested or young stands devoid of snags where mistletoe can create large clumps that function much like cavities to provide nesting and roosting opportunities for a variety of bird and mammal species, including spotted owls and their prey (Parks et al. 1999, Sovern et al. 2011, Watson 2001) (fig. 43). Endemic levels of insects and disease can contribute to stand and spatial heterogeneity important to wildlife, but epidemic levels can be detrimental. We acknowledge that retention of these endemic insect and disease processes involves a delicate balance between tree growth and wildlife habitat objectives, and it entails a certain degree of risk.

Climate change has the potential to strongly influence wildlife populations and habitats (Dalton et al. 2013, Hixon et al. 2013). At the broadest level, changes in the area and location of major habitat types influence wildlife. The habitat types

Peter Singleton



Figure 43—Fine-scale structural diversity associated with dwarf mistletoe clumps and other tree defects provide important habitat components for many wildlife species. This Douglas-fir tree is severely infested with dwarf mistletoe.

that are projected to change in the near future may be of highest concern. Within Oregon and Washington, Rocky Mountain and Cascade subalpine systems are forecast to decline most rapidly (Rehfeldt et al. 2012). Several Forest Service-designated sensitive species are associated with subalpine habitats including wolverine, grizzly bear (*Ursus arctos*), lynx (*Lynx canadensis*), and American marten (Gaines et al. 2000). The wolverine, for example, is thought to be restricted to places with late spring snow pack (Aubry et al. 2010). McKelvey et al. (2011) modeled change in the distribution of such areas in the Western United States under projected future climates. Based on a downscaled ensemble model, they projected that 67 percent of

predicted spring snow cover will persist within the study area through 2030–2059, and 37 percent through 2070–2099. Areas with spring snow are currently relatively limited in eastern Oregon and Washington.

Nearly all of these areas except the Eagle Cap Wilderness are projected to entirely lose spring snow by mid-century, which will likely substantially reduce viability of the wolverine populations in those areas (McKelvey et al. 2011). Substantial reductions in the Rocky Mountain montane conifer habitats that cover much of the Okanogan Highland and Blue Mountains are of concern for lynx and the old-forest specialists mentioned above (Aubry et al. 2000). There are many other wildlife species that are likely to be affected by phenological changes resulting from climate change. We are already observing earlier onset of spring and longer, dry summer periods that will increase drought stress (Hixon et al. 2011). These changes will have significant ramifications for the entire biological community (Rosenzweig at al. 2008, Walther et al. 2002).

Maintaining broad-scale landscape patterns that allow species to move in response to changes in climatic and habitat conditions may be particularly important for conservation of sensitive species (Heller and Zavaleta 2009, Nuñez et al. 2013). Climate change also has the potential to alter connectivity for some species. Initial studies have estimated reductions in habitat connectivity under future climate change for wolverine (McKelvey et al. 2011) and American marten (Wasserman et al. 2012). However, we are not aware of studies that have estimated the combined effects of climate and land use change on connectivity in the Northwestern United States.

The effects of climate change are also manifest within the landscape and stand scales most familiar to forest managers. Many wildlife species require access to two or more habitat types in close proximity, such as use of grasslands and forest by elk. Over the past century, ecotones between habitat types have shifted within landscapes owing to changes in climate, livestock grazing, and fire exclusion. In many portions of eastern Oregon and Washington, conifer forests have encroached into grasslands and shrublands (e.g., Hessburg and Agee 2003; Hessburg et al. 2000b, 2005). In the last decade, the frequency of severe fire in the lower forest ecotone has increased (Perry et al. 2011), sometimes leading to a retraction of the forest ecotone. Under future climate and land use, habitat mosaics across landscapes are likely to be even more dynamic. Within forest stands, structural complexity also varies with climate, land use, and disturbance. Fire exclusion can lead to increased density of stems and higher canopy closure; insect outbreaks can result in losses of live large trees and major increases in snags and coarse woody debris. In sum, interactions among climate, land use, and disturbance are expected to bring wide swings in

habitat composition within landscape, developmental stage distribution, and within-stand structure. These conditions will challenge forest managers to maintain the stand, landscape, and regional habitat components required by many native species.

Altered snowmelt run-off regimes in the mixed-conifer forests will affect downstream fish-bearing reaches. Discharge patterns affect water depth; thus, earlier low flows downstream may reduce habitat availability for fish dependent on deeper, slower flowing habitats (Luce et al. 2013, Tague and Grant 2009). Cutthroat trout and bull trout are the most sensitive species likely to be present in mixed-conifer zones. Bull trout occupy the coldest freshwater habitats of all salmon and trout species and these habitats are predicted to be severely affected by climate change in coming decades (Isaak et al. 2010, Rieman et al. 2007, Wenger et al.

Sensitive Species of Moist Mixed-Conifer Forests

A variety of terrestrial wildlife species is associated with the moist mixed-conifer (MMC) forests and surrounding landscapes in the Pacific Northwest, including one endangered species (gray wolf [*Canis lupus*], recently delisted in part of its range), three federally listed threatened species (NSO, grizzly bear, and lynx), and three federal candidate species (Oregon spotted frog [*Rana pretiosa*], fisher [*Martes pennanti*], and wolverine). In addition, several other wildlife species of concern recognized by state or federal agencies inhabit these forests (table 7). Many of the species that are at risk in the region are associated with particular stand structure conditions, vegetation community types, and landscape configurations. For example, NSOs are found in MMC forests on the east slope of the Cascades from the Canadian border into northern California (USFWS 2011). They are associated with structurally diverse, large tree, moderate- to closed-canopy conditions generally found in older forests that do not have a recent history of fire, much of which has been altered by both logging and more recently large fires in the last 50 to 100 years. A small population of grizzly bears inhabits MMC forest in the Pacific Northwest. Distribution of this population is limited to a few areas along the Canadian border in the North Cascades and Kettle Mountain/Wedge areas of northeast Washington (Gaines et al. 2010, USFWS 1997). Grizzly bear habitat associations in the Cascades and northeast Washington include moist forests, particularly areas of those forests that are interspersed with moist meadows or avalanche chutes where food plants are abundant (Gaines et al. 2000). Oregon spotted frogs were once found near moving water through much of the Cascades in Oregon and Washington (Cushman and Pearl 2007, McAllister and Leonard 1997). More recently, populations have been documented in Washington's southeast Cascades (near Trout Lake and Conboy in Klickitat County) and in Oregon's south-central Cascades. The historical range of fishers encompasses mesic interior forests in the Oregon and Washington Cascades, northeast Washington, and Blue Mountains (Lewis and Stinson 1998). Fishers were extirpated from most of that range as a result of fur trapping. A small population is present in Oregon's southern Cascades but at present they are largely absent from interior forests in Oregon and Washington.

Table 7—Sensitive wildlife species found in interior mesic forests, including species broadly associated with interior moist forest and ecotones; many of these species are associated with specific forest structure or seral stages found within the interior mesic forest zone

Common name	Scientific name	Class	Status[a]	Comments
Western toad	*Anaxyrus boreas*	Amphibian	FCo	
Rocky Mountain tailed frog	*Ascaphus montanus*	Amphibian	FCo	
Oregon slender salamander	*Batrachoseps wrighti*	Amphibian	FCo	Eastern Oregon Cascade Range
Larch mountain salamander	*Plethodon larselli*	Amphibian	FCo	Southeast Washington Cascade Range
Columbia spotted frog	*Rana luteiventris*	Amphibian	SC	
Northern leopard frog	*Rana pipiens*	Amphibian	FCo	
Oregon spotted frog	*Rana pretiosa*	Amphibian	FC	
Northern goshawk	*Accipiter gentilis*	Bird	FCo	
Upland sandpiper	*Bartramia longicauda*	Bird	SE	
Vaux's swift	*Chaetura vauxi*	Bird	SC	
Olive-sided flycatcher	*Contopus cooperi*	Bird	FCo	
Black swift	*Cypseloides niger*	Bird	FCo	Associated with waterfalls and wet cliffs
Pileated woodpecker	*Dryocopus pileatus*	Bird	SC	
Peregrine falcon	*Falco peregrinus*	Bird	FCo	
Harlequin duck	*Histrionicus histrionicus*	Bird	FCo	
Lewis' woodpecker	*Melanerpes lewis*	Bird	SC	
Flammulated owl	*Otus flammeolus*	Bird	SC	Associated more with dry forest
White-headed woodpecker	*Picoides albolarvatus*	Bird	FCo	Associated more with dry forest
Black-backed woodpecker	*Picoides arcticus*	Bird	SC	
Northern spotted owl	*Strix occidentalis*	Bird	FT	
Silver-bordered fritillary	*Boloria selene atrocostalis*	Insect	SC	
Manns mollusk-eating ground beetle	*Scaphinotus mannii*	Insect	SC	
Gray wolf	*Canis lupus*	Mammal	FE[b]	
Townsend's big-eared bat	*Corynorhinus townsendii*	Mammal	FCo	
Spotted bat	*Euderma maculatum*	Mammal	FCo	
Wolverine	*Gulo gulo*	Mammal	FC	
Silver-haired bat	*Lasionycteris noctivagans*	Mammal	FCo	
Lynx	*Lynx canadensis*	Mammal	FT	
Fisher	*Martes pennanti*	Mammal	FC	Northeast Washington, east of Okanogan River
Long-eared myotis bat	*Myotis evotis*	Mammal	FCo	
Long-legged myotis bat	*Myotis volans*	Mammal	FCo	
Woodland caribou	*Rangifer tarandus caribou*	Mammal	FE	Selkirk Mountain population in northeast Washington
Preble's shrew	*Sorex preblei*	Mammal	FCo	
Grizzly bear	*Ursus arctos*	Mammal	FT	
Poplar Oregonian	*Cryptomastix populi*	Mollusk	SC	
Dalle's sideband	*Monadenia fidelis minor*	Mollusk	SC	
Western pond turtle	*Actinemys marmorata*	Reptile	SC	
Sharptail snake	*Contia tenuis*	Reptile	FCo	Local in eastern slope of the Cascade Range

[a] Status codes are FE = federal endangered, FT = federal threatened, FC = federal candidate, FCo = federal species of concern, SE = state endangered, SC = state species of concern.

[b] Recently delisted east of U.S. Highway 97.

Data sources: Oregon or Washington federal status from http://www.fws.gov/oregonfwo/species/Lists/Documents/OregonStateSpeciesList.pdf and http://www.fws.gov/wafwo/pdf/specieslist120613.pdf. Washington state status from http://wdfw.wa.gov/conservation/endangered/All/. Oregon state status from http://www.dfw.state.or.us/wildlife/diversity/species/sensitive_species.asp.

2011). Changing precipitation and fire regimes are expected to compound the effects of warming trends by shifting hydrologic patterns and those of sediment transport and solar radiation (Dunham et al. 2007, Isaak et al. 2010).

Bull trout life histories include migratory forms that spawn and rear in cold streams close to headwaters, then migrate downstream to larger rivers where they live as adults prior to spawning ("migratory") or migrate to lakes following rearing ("adfluvial"). Fragmentation of cold water habitats by stream warming can increase physiological stress to bull trout and decrease interconnectivity of adequate spawning and rearing aggregations. In the "resident" life history form, bull trout remain in cold headwater streams for spawning, rearing, and as adults. Thus, they are subject to these physiological stressors at all life stages.

Cutthroat trout are also common to upland streams in mixed-conifer forests of the eastern Cascades. In small streams within mixed-conifer watersheds of the Wenatchee River sub-basin, cutthroat trout density and total biomass are limited by higher flows (fig. 36) (see footnote 1). Thus, changing flow regimes as a result of precipitation and snowmelt-timing shifts can potentially have consequences for the persistence of populations of this species.

Current Socioeconomic Context

When this science synthesis was initiated, the decision was made to focus on the biophysical science associated with managing MMC forests. However, management of these forests takes place within the broader socioeconomic context of eastern Oregon and Washington, which both influences and is influenced by forest management.[4] In addition, some concepts of resilience include interactions between social and ecological subsystems (see "The Concept of Resilience" on page 18). Thus, some important socioeconomic issues relevant to forest management in the region are briefly reviewed here, recognizing that the topics covered are not all-inclusive. We focus on issues most relevant to accomplishing forest restoration on eastside forests by creating a more enabling social and economic environment. Two such topics—collaboration and the social acceptability of forest restoration treatments—are addressed in chapter 6. The key issues of focus in this section are wood products infrastructure and business capacity to support forest restoration, opportunities for biomass utilization, and some of the tribal concerns associated with forest restoration in the region. Also highlighted are the potential impacts of restoration treatments on recreation. Germane management implications are included in each sub-section. It is important to note that the literature addressing

[4] For purposes of this section, eastern Oregon and Washington refer to all of the counties that lie east of the Cascade crest in Oregon and Washington.

the socioeconomic context of forest management in eastern Oregon and Washington is rarely specific to the MMC forest type; is more extensive for eastern Oregon than for eastern Washington; is largely gray literature (as opposed to peer-reviewed literature); and consists mainly of assessment work rather than scholarly research.

The region is dominated by rural counties where natural resources have historically played an important role in contributing to local economies through agriculture, ranching, forestry, and more recently, recreation.

The region is dominated by rural counties where natural resources have historically played an important role in contributing to local economies through agriculture, ranching, forestry, and more recently, recreation. Many of eastern Oregon's counties exhibit high levels of poverty and unemployment however (Davis et al. 2010), and many eastern Washington counties have been characterized as having relatively low socioeconomic resilience (Daniels 2004). Social and economic assessments of interior Columbia River basin communities carried out as part of the Interior Columbia Basin Ecosystem Management Project (Harris et al. 2000, Reyna 1998) found that small population size, geographic isolation, low economic diversity, heavy dependence on one or a few employment sectors, low level of money coming in from the outside, poorly developed infrastructure, and less active leadership all contribute to low community resilience in the region.[5] Conducting forest restoration can potentially increase community resilience by sustaining existing and creating new and future job opportunities, diversifying the local employment base, retaining existing jobs and stimulating new infrastructure development, and spurring innovations and investments to create new business and employment opportunities—all of which contribute to community resilience (Berkes and Ross 2013, Davidson 2010, Magis 2010, Walker and Salt 2006).

The Forest Service 2012 Planning Rule provides direction to contribute to social and economic sustainability through forest management to help support vibrant communities and rural job opportunities. In addition to employment, other economic benefits resulting from fire hazard reduction through forest restoration may include reduced fire suppression costs over the longer term, increased production of wood products, higher state tax revenues, reduced unemployment payments, and lower expenditures on social services (State of Oregon 2012). Forest restoration to improve forest health can also benefit other ecosystem services associated with national forest lands, including clean water, fish and wildlife habitat, and recreation activities (State of Oregon 2012). Frameworks for identifying the ecosystem services from national forests that are important to stakeholders, and for evaluating the social and ecological tradeoffs between services that are associated with different forest management actions, have been developed by Asah et al. (2012), Kline (2004), Kline and Mazotta (2012), and Smith et al. (2011).

[5] Community resilience is defined here as the ability of a community to successfully cope with, adapt to, and shape change and still retain its basic function and structure.

Forest restoration to reduce hazardous fuels also reduces the risk of wildland fire to communities located in the wildland-urban interface.

Wood Processing Infrastructure and Business Capacity for Forest Restoration

Decreased timber harvesting on federal lands in Oregon and Washington (and elsewhere in the West) since the late 1980s, together with changing technology and markets, industry restructuring, and the recession of 2007–2009 have led to dramatic declines in the production of wood products and mill infrastructure throughout these states (Charnley et al. 2008, Keegan et al. 2006, OFRI 2012). In Oregon and Washington, most of the remaining mills are on the west side of the Cascades (Keegan et al. 2006, Nielsen-Pincus et al. 2012). The increase in severe, large-scale fires that has occurred during the 2000s points to the need for hazardous fuels reduction, in which treatments to remove trees of different sizes play an important role (Keegan et al. 2006). Such removals may include trees having commercial value, as well as trees with smaller diameters than what have traditionally been considered merchantable. Important questions are how to retain what remains of the wood processing infrastructure, whether existing mills can process trees of different size classes (Keegan et al. 2006), and how to develop a new and more diversified infrastructure.

In eastern Oregon, the primary wood processing infrastructure that exists today represents about 20 percent of what it was in the 1980s (Swan et al. 2012). Associated milling capacity has also declined (OFRI 2012). In 2012, there were 45 major primary wood processing facilities and operations in eastern Oregon, including 11 open and three closed sawmills, two open plywood plants, and a number of chipping facilities and operations, post and pole mills, species-specific specialty mills, firewood processors, and whole log shaving operations (Swan et al. 2012). Together, these wood processing facilities employed an estimated 1,730 people (at minimum). Although this diversified mill infrastructure provides opportunities for producing a range of products from logs of different sizes and types, existing mills are not operating at full capacity. Sawmills and chip mills currently operate at about 50 percent of capacity, and whole log mills at 40 percent. Increasing the capacity of their operations could potentially increase employment at eastern Oregon's wood processing facilities by 35 percent (Swan et al. 2012). Doing so would require an increased and sustained supply of logs and fiber of the appropriate sizes and species, favorable market conditions, adequate financing, and a reliable, experienced workforce (OFRI 2012, Swan et al. 2012).

With regard to production from MMC forests to help meet supply needs, eastern Oregon mills that produce lumber graded for strength prefer interior Douglas-fir

and white fir, but also use Engelmann spruce, lodgepole pine, and subalpine fir (Swan et al. 2012). Mills that produce lumber graded for appearance prefer ponderosa pine but also use high-quality white fir. Pulp and paper mills that consume wood products from eastern Oregon, located mainly along the Columbia and Snake Rivers, prefer lodgepole pine and white fir, but accept other tree species. Size preferences typically range from 31 to 41 cm (12 to 16 in) diameter for large logs (though some mills take up to 56 cm [22 in] logs), and 10 to 15 cm (4 to 6 in) to 25 to 30 cm (10 to 12 in) for small logs (Swan et al. 2012).

Ownership of eastern Oregon's timberlands is 67 percent Forest Service and 29.2 percent private (OFRI 2012). However, 75 percent of the current supply of wood products for industry in eastern Oregon comes from nonfederal lands, and 25 percent from federal lands (nearly all Forest Service) (Swan et al. 2012). Eastern Oregon sawmills obtain an average of 63 percent of their supply from nonfederal (almost all private) lands (Swan et al. 2012).

Assessments have found that in eastern Oregon, private lands will not be able to support pre-economic recession (2007) harvest levels in a sustainable way, implying that increased wood supplies will need to come largely from federal lands (OFRI 2012). Harvests from federal lands in eastern Oregon are currently estimated at 7 percent of annual growth (OFRI 2012).

The nature of the supply from Forest Service lands has also shifted significantly since the 1980s from predominantly sawlogs greater than 31 cm (12 in) in diameter, to mostly non-saw logs (biomass). Thus, to significantly increase forest restoration treatments in eastside forests, new investment in mill facilities designed to process smaller-diameter material will likely be needed, which in turn will hinge on public support and a reliable supply of raw material over a 10-year time horizon at a minimum (OFRI 2012). The State of Oregon (2012) provided a number of recommendations for how to increase the scale of restoration on Forest Service lands in eastern Oregon.

There is also a need in eastern Oregon to recruit more people into the logging workforce and to increase access to capital to support investments in new equipment (OFRI 2012). One consequence of the loss of forest products industry infrastructure has been a loss of people having the skills and knowledge to work in eastern Oregon's forestry sector (OFRI 2012). The business capacity to engage in forestry support work (e.g., activities in support of timber production, firefighting, and reforestation) has been growing in eastern Oregon over the past decade (Davis et al. 2010). Retaining and increasing the local infrastructure, workforce, equipment, and businesses needed to engage in forest management is critical for carrying out landscape-scale forest restoration to improve the ecological integrity and resilience of forest ecosystems (Kelly and Bliss 2009, State of Oregon 2012).

Another consequence of reduced forestry infrastructure has been that the average distance between mills is often greater than 161 km (100 mi) in eastern Oregon, increasing log haul distances and associated transportation costs (Swan et al. 2012). This leads to reduced competition for logs—driving down stumpage prices—and higher transportation costs to get logs to more distant mills, which together can result in uneconomical timber sales, making it more difficult and costly to engage in forest restoration and hazardous fuels reduction. Nielsen-Pincus et al. (2012) found that national forest ranger districts that are close to sawmills and biomass facilities treated more overall hectares for hazardous fuels reduction, and more hectares in the WUI, than those farther away, and that there was a threshold distance (hauling time) for this effect in Oregon and Washington of 40 minutes. A lack of local wood processing infrastructure constrains the management options available to forest managers and, in turn, affects managers' capacity to address declining forest health and increasing fire risk (Eastin et al. 2009).

In Washington state, there was a steady decline in the number of wood processing facilities between 1991 and the 2000s, with several mills closing along the east side of the Cascades, and the remaining industry shifting from rural to urban areas to be nearer to major transportation corridors (WA DNR 2007). In 2010, there were 14 mills in central and eastern Washington, half of them sawmills (Smith 2012). Three pulp mills, one veneer and plywood mill, and three roundwood chipping mills comprise the remainder of the infrastructure. Few new mills have replaced the mills that closed, though the remaining mills tend to be larger and more efficient (Smith 2012). The distance between mills is greater than 322 km (200 mi) in some parts of eastern Washington however, meaning high transportation costs for what are often low-value, small-diameter logs, and less competitive prices (WA DNR 2007).

The dominant log species consumed by eastern Washington mills in 2010 were Douglas-fir (38 percent), ponderosa pine (25 percent), true firs (18 percent), and lodgepole pine (9 percent) (Smith 2012). Of these logs, 48 percent came from private lands, 21 percent from tribal lands, 17 percent from state lands, and 11 percent from national forest lands. The dominant size classes harvested were 13 to 25 cm (5 to 10 in) (40 percent) and 25 to 51 cm (10 to 20 in) (36 percent) (Smith 2012).

Studies have found that in order to achieve forest restoration goals in eastern Washington, new investments in wood processing infrastructure will be needed (WA DNR 2007). Again, having a stable and adequate supply of wood is critical for stimulating such investments. Increasing harvests from state and private lands to meet supply needs is unlikely to be sustainable however, implying an important role for federal land harvests. Other factors that would help would be government

incentives for investing in wood processing facilities, diversification of processing infrastructure (as has occurred in eastern Oregon), establishing markets for carbon and biodiversity, and reducing local regulatory constraints to mill construction and forest products manufacturing (WA DNR 2007).

Ensuring a reliable supply of wood of all size classes from federal lands in eastern Oregon and Washington is critical for maintaining existing and establishing new wood processing infrastructure (Keegan et al. 2006). To stay in business, mills also need to remain competitive by investing in improvements such as increasing the efficiency of log conversion, producing higher value products and a more diverse product mix, or constructing drying kilns on site (Dramm 1999). Stewardship contracting, where appropriate, is one tool that can help in this regard because it allows the Forest Service to enter into contracts of up to 10 years in duration and to provide a reliable supply of wood. The Collaborative Forest Landscape Restoration Program is another mechanism that should encourage a more reliable supply of small-diameter wood to support industry investments in infrastructure in participating landscapes (which currently include four areas of eastern Oregon and Washington, plus one affiliate in Washington). This program aims not only to encourage national forests to commit to carrying out restoration projects by providing a source of funding for up to 10 years, but to incentivize restoration treatments on other ownerships within the same landscapes by leveraging funding from other sources (Schultz et al. 2012). Doing so may help increase the supply from other ownerships. The program also requires projects to make use of existing or proposed processing infrastructure to support jobs and local economies (Schultz et al. 2012).

Ensuring a reliable supply of wood of all size classes from federal lands in eastern Oregon and Washington is critical for maintaining existing and establishing new wood processing infrastructure.

Developing biomass utilization opportunities is also important for retaining and increasing the number of sawmills. Sawmills produce a large volume of residual material associated with log processing that can be used for many biomass utilization applications, as well as for producing pulp and paper and other wood products (Davis et al. 2010). Unless they can market these residuals, sawmills may not be able to operate economically (Swan et al. 2012). The next section addresses this topic.

Biomass Utilization

The development of woody biomass utilization opportunities has received much attention over the past decade because (1) biomass is a domestic source of renewable energy; (2) biomass utilization can help to partially offset the cost of needed hazardous fuels reduction treatments on public lands and contribute to economic development opportunities in forest communities (Aguilar and Garrett 2009, Morgan et al. 2011, Nechodom et al. 2008); and (3) biomass utilization reduces the need for onsite burning of piled material produced by fuels treatments, and associated

environmental effects (Daugherty and Fried 2007, Springsteen et al. 2011). To date, biomass utilization infrastructure remains underdeveloped in eastern Oregon and Washington. As of 2012, there was only one stand-alone biomass energy cogeneration plant in eastern Oregon, which was temporarily closed because it could not obtain a favorable power sales agreement (Swan et al. 2012). When market conditions are good, biomass from eastern Oregon may be transported to western Oregon or to mills along the Columbia and Snake Rivers for use, but markets are highly variable. There were no stand-alone biomass energy facilities in eastern Washington in 2010 (Smith 2012), posing a challenge for forest restoration there (WA DNR 2007). Davis et al. (2010) provide an overview of status and trends in woody biomass utilization, including challenges and opportunities, across many eastern Oregon counties.

A number of economic issues constrain the development of viable biomass utilization facilities. To attract investors, there must be an adequate and predictable supply of biomass, a concern in places where federal land is the main potential source of supply (Becker et al. 2011, Hjerpe et al. 2009). The supply problem could be addressed by diversifying sources of raw material, through the use of stewardship contracts, or by addressing internal institutional barriers to biomass utilization within the Forest Service (Becker et al. 2011, Hjerpe et al. 2009, Morgan et al. 2011). Supporting remaining wood products industry infrastructure to prevent its further loss can also help provide opportunities for biomass removal and utilization. For a number of reasons, the presence of wood products industry infrastructure has been found to enhance the development or expansion of biomass utilization, which is difficult to develop as a stand-alone enterprise (Becker et al. 2011).

The cost of harvesting and transporting biomass is another key constraint (Aguilar and Garrett 2009, Becker et al. 2009, Pan et al. 2008). Becker et al. (2009) found that the cost of transporting biomass from the harvest site to the market outlet is the single greatest cost associated with biomass utilization, and that decreasing the travel distance between markets and harvest sites is the only strategy that offsets this cost in a meaningful way. Strategies for addressing the cost issue include establishing a network of decentralized processing facilities of an appropriate size and type closer to the source where biomass is removed (Aguilar and Garrett 2009, Nielsen-Pincus et al. 2012); developing utilization options that focus on higher value products; bundling biomass removal with the removal of larger trees that produce higher value products (e.g., lumber) (Barbour et al. 2008); developing transportation subsidies, which Oregon has done (though these can be problematic) (Becker et al. 2011, Nicholls et al. 2008); and implementing financial incentives such as cost sharing and grant programs for facility development and equipment purchases, and

tax incentives for facility development and harvesting and transporting biomass (Sundstrom et al. 2012).

Because biomass produced as a byproduct of forest restoration tends to be of low value, strategies associated with national forest management are likely to focus on establishing smaller processing facilities closer to public lands (Becker et al. 2011). Small and mid-sized facilities that focus on electricity generation, firewood, animal bedding, commercial heating, or combined heat and power systems are likely to be more feasible than large processing facilities because they tend to be less controversial and require a smaller supply of biomass to operate (making it easier to obtain in a reliable manner) (Becker et al. 2011).

Markets are another major constraint on increasing biomass utilization. Key to increasing biomass utilization east of the Cascades is stimulating market demand and opportunities. The abundance of hydropower in the Pacific Northwest limits market opportunities for biomass electricity (Stidham and Simon-Brown 2011). Although low natural gas prices may also threaten the viability of biomass energy projects (OFRI 2012), eastern Oregon has large areas that lack access to natural gas, and woody biomass is more economical for heating than propane or heating oil (Swan et al. 2012).

The main constraints on developing stand-alone, industrial-scale biomass energy plants in eastern Oregon currently are low prices for electricity under power purchase agreements, and uncertain pricing in the California market, making construction of such plants unlikely in the near future (Swan et al. 2012).

Although the supply of biomass for manufacturing value-added products is greater than market demand (Stidham and Simon-Brown 2011), promising opportunities for biomass utilization lie in developing a broader range of products and applications such as pellets, bricks, small-scale institutional thermal applications (such as space and water heating), onsite electricity generation, transportation fuels, and bio-char (Davis et al. 2010, OFRI 2012, Swan et al. 2012). More diversified and integrated biomass utilization projects have been developing in eastern Oregon in recent years (Davis et al. 2010), signaling progress that may enhance forest restoration efforts there.

Tribal Concerns

Tribal concerns associated with the management of MMC forests on federal lands in eastern Oregon and Washington include protecting tribal lands from fire, insects, and disease; creating job opportunities for tribe members in forest restoration; management to address the potential impacts of climate change on forest resources that are important to tribes; and incorporating tribe members and their traditional ecological knowledge into forest restoration decisionmaking and implementation.

The 2004 Tribal Forest Protection Act (TFPA) was passed to protect tribal lands, resources, and rights from fire, insects, disease, and other threats (ITC 2013). The Act allows tribes to propose fire mitigation and environmental restoration activities on Forest Service and Bureau of Land Management lands adjacent to or bordering tribal trust lands and resources. The agencies may enter into contracts or agreements with tribes for this purpose. Despite the potential that TFPA authorities offer for fulfilling federal trust responsibilities, enhancing forest restoration activities, and creating job opportunities for tribe members in fuels reduction and postfire rehabilitation, only a handful of projects have been implemented. Reasons for this lack are described in ITC 2013. Ways that federal forest managers in eastern Oregon and Washington can take greater advantage of the opportunities provided by the Act include strengthening partnerships with tribes through formal agreements, promoting the use of the TPFA authorities internally, and conducting training and outreach to increase understanding and utilization of the TPFA (ITC 2013).

Regarding job opportunities, a survey of 31 of the 42 federally recognized tribes in Oregon, Washington, and Idaho found that tribes had a strong interest in obtaining jobs in fire management, such as work on wildland fire suppression crews and hazardous fuels reduction work (Rasmussen et al. 2007). A number of strategies for promoting tribal economic development through fire management can be found in the Tribal Wildfire Resource Guide (Intertribal Timber Council and Resource Innovations 2006). Obstacles that limit the capacity of tribes to engage in this work include the seasonality of the work, the training required for employees and contractors, the cost of investing in equipment, a lack of financial capital with which to start businesses, and supportive tribal leadership to help form partnerships with public agencies (Rasmussen et al. 2007). Different communication and operating styles and Forest Service bureaucratic processes can also create barriers (Charnley et al. 2007). To the extent that the Forest Service can assist tribes in addressing some of these obstacles, it can help build the capacity of tribal communities to engage in fire management and forest restoration activities.

The environmental impacts of climate change are expected to be disproportionately felt by American Indian and Alaska Native tribes relative to nonnative communities because of their unique rights, economies, and cultures that are linked to the natural environment.

The environmental impacts of climate change are expected to be disproportionately felt by American Indian and Alaska Native tribes relative to nonnative communities because of their unique rights, economies, and cultures that are linked to the natural environment (Lynn et al. 2011). In eastern Oregon and Washington, climate change impacts on forests that may affect tribes include the potential for increased frequency and intensity of wildland fire; increases in invasive species, insects, and disease; and shifts in the quantity, quality, and distribution of culturally important forest resources (plants, animals, fungi, water, and minerals) (Voggesser et al. 2013). As a result, climate impacts on forests may threaten tribal subsistence,

culture, and economies. The traditional ecological knowledge held by tribe members can play an important role in helping federal forest managers identify species having social, cultural, and economic importance to tribes in the MMC zone, and in helping to inform management strategies for these species in the context of climate change. Strong federal-tribal relationships around forest management may also help to mitigate climate change impacts on species important to tribes, and assist tribes in developing adaptation strategies (Voggesser et al. 2013). Resources and research to support federal forest management in a manner that is responsive to the climate change-related concerns of tribes in the Pacific Northwest can be found at http://tribalclimate.uoregon.edu/.

The relationship that exists between federally recognized tribes and the United States means that federal agencies are required to consult with tribes when they engage in policy making or undertake actions that affect tribal interests and resources. Consultation processes also promote collaboration between tribes and federal agencies in protecting and managing tribal resources on and off reservation lands (Whyte 2013). Working toward effective consultation processes will help ensure that restoration activities on national forests east of the Cascades address tribal concerns. Traditional ecological knowledge may also make an important contribution to forest restoration on national forest lands and can be fostered through federal-tribal consultation and partnerships and by directly engaging traditional knowledge holders in planning and implementing restoration activities (Vinyeta and Lynn 2013). A number of models for doing this are reviewed in Charnley et al. (2007), Donoghue et al. (2010), Vinyeta and Lynn (2013), and Voggesser et al. (2013).

Recreation

Moist mixed-conifer forests have high recreation value. The status of and trends in recreation activities on national forests in eastern Oregon and Washington can be found in the National Visitor Use Monitoring survey reports for these forests (http://www.fs.fed.us/recreation/programs/nvum/). Assessment information about recreation activities, trends, and issues in eastern Oregon and Washington can also be found in the Statewide Comprehensive Outdoor Recreation Plan (SCORP) reports for these states (http://www.oregon.gov/oprd/PLANS/pages/scrop08_12.aspx; http://www.rco.wa.gov/documents/rec_trends/SCORP_2008.pdf), and in Hall et al. (2009). National forest recreation in MMC forests is likely to be affected by forest restoration treatments, which could be a source of contention. Exactly how recreation values may be affected by restoration treatments is difficult to predict, however, in the absence of site-specific research.

A number of studies have been carried out in the Intermountain West to evaluate the effects of prescribed fire treatments and crown fires on recreation visitation and associated economic benefits. These studies have found that crown fires generally have a negative effect on recreation visitation and economic values over time, although there may be an initial, short-term positive response by some types of visitors (Englin et al. 2001; Hesseln et al. 2003, 2004; Loomis et al. 2001). Hikers, for example, may be drawn to see wildfire effects and wildflower blooms following a crown fire (Englin et al. 2001, Loomis et al. 2001). Longer term declines in recreation visitation may result from the negative aesthetic effects of the fire, reduced access for certain activities, or damage to recreation facilities and infrastructure (Kline 2004). Areas that have substantially recovered from a crown fire may experience a rebound in visitation, however (Englin et al. 2001). In contrast, a study from Oregon's Mount Jefferson Wilderness found that the B&B Fires of 2003 did not dramatically affect recreation in the first few years following the fire (Brown et al. 2008).

Prescribed fires have been found to have either no effect or a positive effect on recreation visitation and associated economic benefits over time in some places (Hesseln et al. 2004, Loomis et al. 2001). These effects can vary by recreation activity (e.g., hiking versus mountain biking) (Loomis et al. 2001). Elsewhere, prescribed fires have been found to have a negative effect on recreation visitation by hikers and mountain bikers and associated economic values, with visitation decreasing as the percent of a burn visible from the trail increased (Hesseln et al. 2003).

These findings have a number of management implications. Because crown fires can be detrimental to recreation visitation and values, fuels reduction treatments may be one way of mitigating the negative social and economic impacts of crown fires on recreation (Hesseln et al. 2004). In some places, mechanical treatments may be more effective at mitigating these impacts than prescribed fire, and have fewer overall social and economic costs, because prescribed fire may also have a negative impact on recreation visitation and values (Hesseln et al. 2003). If prescribed fire is used, minimizing the area of the prescribed burn visible from popular recreation trails may reduce its negative effects. It is important to note, however, that some wildfires, such as fires that take place in areas dominated by shrubs, may have positive effects on recreation by creating more open forest conditions (Kline 2004). The ways in which wildfire and fuels treatments affect recreation vary by recreation activity, geographic location, type of wildfire and fuels treatment, forest characteristics, and over time (Kline 2004). Thus, the best way forward for identifying how different types of recreation activities may be affected by restoration treatments, and the most appropriate approach to forest restoration in

places where recreation values are high, is likely to be through place-based research and collaborative processes (Hesseln et al. 2003, Kline 2004).

This brief overview of socioeconomic issues associated with forest restoration in eastern Oregon and Washington is not intended to be all-inclusive. Important issues not addressed include community wildfire protection, the effects of restoration treatments on other ecosystem services provided by national forests, the challenge of forest restoration at the landscape scale across ownership boundaries, and institutional barriers to forest restoration within federal agencies. This overview aims to touch on some of the key socioeconomic issues managers may face in trying to restore MMC forests, and provides some guidance about how to address these issues so that managers can evaluate both ecological and socioeconomic considerations when making decisions about forest restoration. Remaining research gaps with regard to the socioeconomic dimensions of managing MMC forests make it difficult to develop a robust framework for evaluating the social and economic tradeoffs entailed in management decisionmaking.

Summary of Key Scientific Findings and Concepts

The previous sections synthesize scientific findings most relevant to forest managers. We encourage the reader to investigate more thoroughly any of the topics discussed using the extensive reference section (about 400 citations) provided.

Our key scientific findings and concepts are as follows:

Landscapes

- **Broad-scale (top-down), meso-scale (within landscape), and fine-scale (bottom-up) spatial controls (aka, drivers or forcing factors) combine to control ecosystem behavior and ecological outcomes.** Examples of top-down drivers are broad-scale patterns of the regional climate, geology, land surface forms, and broad patterns of biota—lifeforms and land cover types. Meso-scale or within landscape spatial controls are natural and human disturbances, topography, patterns of structure, composition, fuelbeds, and patch size distributions. Examples of fine-scale drivers are patterns of local topography, microsite, soils, plant communities and plant life history and life cycle differences, patterns of micro-climate, and the like. Some patterns at each of the three scales are not likely to be stationary in time or space, while others (geology, topography, geomorphic processes) are relatively more stationary. Any given landscape today is on a trajectory to a future condition that will be a result of these combined forces.

- **Regional landscapes can be viewed as a multi-level hierarchy of mosaics** for landscape planning and management purposes; patches exist within local landscapes, which provide the patchiness and variability of the regional landscape. Patchiness also exists within patches (clumped tree distributions and gaps of various sizes) and this forms the variability of the local landscape.
- **Steep, topographically driven precipitation and temperature gradients have a significant influence** on the vegetation east of the Cascade Range divide; the most significant effect is the rain shadow created by the high divide.
- **Forest productivity and disturbance regimes are highly influenced by these gradients.** Position on the landscape combined with local weather conditions (precipitation and temperature), surface lithologies (parent materials and the soils that are derived from them), and land surface forms contribute to a complex mosaic of patches supporting a diverse array of vegetation. **On any given landscape, dry, moist, and wet mixed-conifer forests occur within a large ecological gradient.** As a consequence it is difficult to neatly disentangle these forest types for management purposes.
- **Landscapes exhibit varying degrees of inertia.** The degree of change over the 20th century in forest structure, tree species composition, and disturbance regimes has given landscapes an inertia (which can be thought of also as ecological momentum or resistance to change) that will be difficult to alter through restoration-based management. For example, field observations suggest that after recent wildfires, instead of regenerating to ponderosa pine or western larch, some areas now quickly regenerate to Douglas-fir and white, grand, or subalpine fir, or lodgepole pine, despite intentional efforts (which often fail unless done well) to reestablish ponderosa pine or larch. The presence of abundant seed from shade-tolerant tree species (e.g., firs) provides this inertia. Likewise, high contagion of surface and canopy fuels creates large homogeneous patches that reinforce the occurrence of a higher than normal number of large and very large fires, and higher than normal fire severity.
- **The historical range of variability (HRV) that created pre-Euro-American forest landscapes has been changing and returning to it is no longer feasible or practical** in some places. The pattern and processes of forest ecosystems in a landscape are functions of the range of variability in disturbances, climate, and species movements that has occurred over a long period of time. The range of variability in these processes in the future

will determine how the current patterns and processes of ecosystems and species will develop. Managers can influence the future range of variability to achieve desired future ecosystem conditions for a landscape. The HRV can serve as a guide but not a target.

- **Depending upon the biogeoclimatic setting and physiographic region, historical and future ranges of conditions may be either strongly or weakly overlapping.** Future climate projections suggest that large differences between the past and the future tend to be associated with the extreme ends of ecological gradients, and ecotones may be particularly sensitive areas. For example, at forest and shrubland ecotone margins, and at subalpine-alpine ecotones, digital global vegetation models suggest significant changes, where life forms and plant community composition may suddenly shift after disturbances. Within the MMC forest, which falls within mid-montane and valley bottom environments, there may be only small differences in environments when comparing past and future range of variability, but the degree of difference will vary with topography and ecoregion.

Disturbances

- **Significantly altered disturbance regimes exist as a result of 150 years of Euro-American land use, altering the manner in which systems behave.** In general, mixed-conifer forests are on a trajectory leading to further divergence from a resilient condition.
- **Wildfires, along with insect, pathogen, and weather disturbances, historically did the bulk of the work to continuously restructure and recompose the historical landscape,** providing sustainable patterns of terrestrial and aquatic habitats, and supporting processes. Several forest insects (e.g., bark beetles and defoliators) and pathogens (e.g., dwarf mistletoe and root diseases) are notable disturbances in this region today and they are imparting influences at uncharacteristically high levels.
- **The disturbance ecology and resulting vegetation of the mixed-conifer type is influenced by the dominant disturbance regimes of the local landscape.** Historical fire regimes in dry and MMC forests differed across a broad range of spatial and temporal scales in response to local and regional variation in climate and weather, topography, soils, and fuels. Where dry mixed-conifer forests are a dominant feature within a landscape, the MMC forest often is influenced by more frequent fire. The converse is also true.

- **Small and medium sized fires (<1000 ha in size [2,471 ac]) were most numerous,** comprising 85 to 95 percent of the fires, but representing no more than 5 to 15 percent of the total area burned. **Larger fires (>2000 ha in size [4,942 ac]) were least abundant, but accounted for the majority of area burned.**
- **Low-, mixed-, and high-severity fires all occurred in dry and MMC forest but the relative portion of these fires varied across ecoregions.** Surface fire effects coming from low- and mixed-severity fires tended to dominate in dry forests, and local topography was especially influential during common events. Patches of high-severity fire resulted from rare or extreme weather and climatic events. Low-severity fires within MMC forest may have been more common in drier warmer ecoregions with less topographic relief. High-severity fires within MMC forests appear to be more common in cooler and wetter ecoregions and areas with stronger topographic relief. Low-severity fires occurred commonly in moist forests where they were intermixed with dry forests; high-severity fires in moist forests may have been more common where moist forests were intermixed with wet and subalpine forests.
- **We are in the early stages of anthropogenically induced climate warming in eastern Oregon and Washington, and we anticipate significant vegetation and disturbance impacts to dry and MMC forests during this century.** Over the 21st century, climate change impacts will increase in magnitude and extent, transforming some forests. Impacts to terrestrial ecosystems will include increased fire frequency, severity, and burned area, increased susceptibility to insects and diseases, and increased presence of invasive plant and animal species. Climate change will likely reduce or eliminate some subalpine habitats and snow cover that are essential to the survival of some wildlife species.

Vegetation

- **Fire exclusion, silvicultural practices, agriculture, livestock grazing, intensive road and rail development, and introductions of alien plant species** have significantly influenced the structure, composition, and disturbance regimes of many forests.
- **Dry and MMC forests represent a broad range of potential vegetation types** and include the grand fir, white fir, and Douglas-fir series. MMC forest falls within a gradient between the dry ponderosa pine and dry mixed-conifer forest and woodland types at the lowest end of the moisture gradient and subalpine and wet conifer forests at the upper end of the gradient. MMC forests are

often intermixed with dry mixed-conifer forests on the lower end and wet (e.g., western hemlock, western redcedar [*Thuja plicata* Donn ex D. Don], Pacific silver fir), or subalpine forests at the upper end of the gradient. The neighborhood a forest type lives in can influence the nature and extent of processes that are influential. We do not provide a precise definition of the mixed-conifer plant associations for different ecoregions or national forests. Agency ecologists are best suited to make the final decisions on MMC types occurring on each national forest.

- **A large number of successional pathways and old forest conditions historically existed** in the MMC forests of eastern Oregon and Washington as a result of the environmental complexity and disturbances that shaped them. Some old forests were the result of repeated low-intensity fire that maintained multicohort single-stratum condition of fire-tolerant species, while others developed to complex, multiple-strata structures that occasionally experienced mixed- or high-severity disturbances. Managers have options to shape the trajectories of vegetation patches and landscapes along these different pathways. However, targeting a single developmental stage as a management objective does not fit with variability of the mixed-conifer forest.
- **Fire- and drought-tolerant trees of medium diameter (about 41 to 64 cm [16 to 24.9 in]) and large diameter (more than about 64 cm [25 in]) are the backbone of wildfire- and climate-tolerant landscapes, and are an essential component of wildlife habitat.** The occurrence of older trees and older forests currently is far below the historical range of variability, despite their ecological importance.
- **Areas of ecologically diverse, early-seral grass, shrub, and seedling- or sapling-dominated forest patches are in short supply in some landscapes.** Historically, these areas would have been created and often maintained by mixed- and high-severity fires, complete with fire-killed snags and down logs. The largest fire-killed snags and down logs would have lasted a long time and provided needed plant and animal habitat. Grassland and shrubland patches were historically quite abundant on forested PVT settings, owing to variability in wildfire regimes and frequently reburned areas. It is likely, according to climate change projections, that grassland and shrubland conditions will be more common in forested PVT settings.
- **The assumption that plant association groups** (e.g., moist and dry mixed conifer) **can be used to infer historical disturbance regimes is only moderately true.** Limited studies suggest considerable variability in

Fire- and drought-tolerant trees of medium and large diameter are the backbone of wildfire- and climate-tolerant landscapes, and are an essential component of wildlife habitat.

disturbance regimes within and between moist and dry mixed-conifer types. They both contain components of the mixed-severity regime, which is a highly variable disturbance regime. Managers need a variety of information sources (e.g., known history, landscape context) in addition to plant association types when assessing the historical and future range of variability for a landscape.

- **In many areas of the mixed-conifer type, the density of large fire-tolerant trees has declined from historical levels largely because of past logging and recent high-severity fire.** The density of mid-sized trees may have increased; most of these are shade-tolerant species that reduce resiliency of the MMC forest.

Wildlife and Fish

- **The diversity and juxtaposition of patch types of differing composition and structure that were produced by historical mixed-severity fire regimes provided a variety of habitat resources to resident wildlife.** A key concept for understanding animal distribution and abundance in MMC forests is that animals need to acquire a variety of resources to meet their life-history needs, and most animals use a variety of different habitats and structural features to acquire those resources. The mosaic of conditions provided under historical mixed-severity fire regimes provided a rich variety of habitat features for native wildlife.
- **Different stand development stages provide different habitat structures and resources for wildlife:** Recently disturbed patches tend to support high plant productivity, and often exhibit a particularly high diversity of plant and animal species, including many specialist species.

  Even-age young forest patches generally support less diverse and abundant animal communities than are found in other stand development stages, but can provide important ecological functions, depending on specific habitat conditions and landscape context.

  Older forests with a diversity of tree ages and sizes (including large old trees) provide many unique ecological functions. Big old trees, living and dead, standing and down, provide unique and important habitat structures within old forest stands. The multilayer canopies found in older stands contribute to unique thermal characteristics within stands and provide structural complexity important many species.
- **Natural disturbance processes play a key role in the development of stand structure conditions and landscape patterns that determine habitat values for animals.** Endemic levels of disturbance and pathogens (including

dwarf mistletoe) can contribute to stand and landscape heterogeneity, while large-scale, high-intensity disturbances can reduce stand and landscape heterogeneity. Balancing the risk of long-term loss of stand structure and landscape heterogeneity with the retention of current ecological values often associated with the presence of forest pathogens and local high fuel loads is a fundamental challenge for land managers.

- **Biological legacies (including big old trees, snags, and logs) provide important habitat structures across all stages of stand development.** Within-stand structural diversity is generally much greater in stands with a variety of tree age and size classes, even if those stands are recently disturbed or dominated by younger trees. Big trees and logs are often a legacy of previous stand conditions that have been retained after some disturbance event, like fire or harvest. The variety of extremely valuable habitat structures provided by these large old trees include cavities, large branches, broken tops, brooms, and platforms.
- **Recent wildlife habitat assessments have reported a widespread reduction in habitat values relative to historical conditions for wildlife associated with early-seral, open forest, and postfire habitats.** Old forest habitat conditions show less decline at a regional scale, but patterns are variable across sub-basins. Owing to the variation in habitat trends across the interior Pacific Northwest, managers need to assess the trends in their local subwatersheds for appropriate guidance on wildlife habitat management needs.
- **Management activities focused on restoration of historical habitat patterns and stand structure conditions can have a variety of effects on wildlife populations.** At a stand scale, restoration treatments tend to favor those species associated with more open conditions and increased understory vegetation diversity, and have the potential to reduce abundance of species associated with closed-canopy, old-forest conditions. However, responses can be quite variable depending on the intensity of the treatment, and although the abundance of individual species can change, restoration treatments have generally not been shown to cause substantial changes in species diversity.
- **Loss of old-forest structures to large-scale, high-intensity wildfire is a concern for all old-forest species, including northern spotted owls.** Landscape conditions that are resilient to intermittent disturbances will be most likely to provide a shifting mosaic of old forest habitat conditions for all old forest species over time. Managing for patterns that continually bring stands into old forest conditions is also important because we cannot rely on existing old forest stands to remain in that condition over long time periods. This approach

of maintaining a shifting mosaic of old forest conditions is likely to be an increasingly important concept for old-forest wildlife conservation under future disturbance regimes that are anticipated under many climate change scenarios. Conservation of unique forest structures (particularly big old trees) is important, but it will be most effective if it is done in the context of sustainable landscape patterns.

Management Applications in the Field

- Ecological restoration has become a principle objective that drives current management on national forest system lands in the Western United States. It is defined as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed. Ecological restoration focuses on **re-establishing the composition, structure, pattern, and ecological processes necessary to facilitate terrestrial and aquatic ecosystem sustainability, resilience, and health under current and future conditions.**" The scientific thinking on restoration has evolved as we learn more about land use change effects, climate change, paleoecology, and socioecological interactions (Hobbs et al. 2011). In using the term "restoration," our intended meaning is that restoration involves restoring degraded ecosystems to a desired state considering historical and future ranges of conditions. Where the historical conditions strongly resemble the predicted future range of variability, they will be quite relevant. Where they do not, the focus will be on the future ranges. For example, the concept of socioecological resilience focuses on the adaptive capacity of species, ecosystems, and institutions rather than restoring or recovering a condition. In this report, we define restoration as the applied practice of renewing degraded and damaged landscapes, habitats and ecosystems with active human intervention.
- Rates of environmental change vary across eastern Oregon and Washington, and as a consequence some ecosystems have attributes that may still be similar to their HRV. In other ecosystems, however, **attributes and entire ecosystems are clearly out of their HRV**. For purposes of understanding and prioritization, it is important to assess the degree of landscape departure from the HRV. However, there is obvious importance for considering the future range of variability (FRV) and how that will influence vegetation. It is important to consider the dynamics of ecosystems that are possible as a result of climate change, changing land uses, and evolving social values. Projections or scenarios of FRV recognize the important implications of climate change on forests (Fettig et al. 2013).

Chapter 5—Management Considerations

In the midst of complicated social and political forces, forest managers make decisions that require the application of complex scientific concepts to case-specific project conditions. Decisions often must balance risks (e.g., elimination of fuels hazards vs. preservation of old-forest conditions) while acknowledging and allowing for uncertainties. Decisionmakers also must weigh tradeoffs associated with alternative courses of action to obtain multiple-use policy and land management objectives. We acknowledge this difficult task and the concurrent need to have and thoughtfully apply thoroughly the body of available scientific information.

It is not the role of the research community to direct management decisions, but it is appropriate to synthesize research and its core findings, and underscore key management implications of that research in specific management contexts. It is also the role of researchers to work alongside managers and seek to learn from their successes and failures. Here we provide considerations for management and emphasize that their application to local and regional landscapes requires the skill and knowledge of local practitioners to determine how best to apply them to each local situation they encounter, and its particular management history. Legacy effects matter and one size does not fit all.

One of the roles of researchers is to work alongside managers and seek to learn from their successes and failures.

In the following section we synthesize the principle scientific findings that have been gleaned from the body of scientific literature (summarized in chapter 4) as it pertains to management of moist mixed-conifer (MMC) forests. These constitute the "take home" messages that are intended to assist land managers.

Key Concepts to Consider in Management of MMC Forests

- **Resilience at regional scales is fostered by heterogeneity in patterns of local landscapes**, but not just any heterogeneity will do. Heterogeneity that is useful to maintaining resilience is that which is supported by the inherent variability of the local climate, geology, and disturbance regimes of each subregional locale. The variability of the regional landscape mosaic should be represented in unique patterns of local landscapes. Management for resilience at broad scales can promote this variability.

Resilience at regional scales is fostered by heterogeneity in patterns of local landscapes.

- **Overlap in the historical range of variability (HRV) and future range of variability (FRV) may be useful to defining desired local landscape patterns** (fig. 44). If landscapes reflect these overlapping envelopes of an eco-region, they are likely to be more resilient and conserve more future options for management. If all local landscapes look the same, the regional landscape will have been simplified. We make this suggestion because of high uncertainty about the use of the FRV alone.

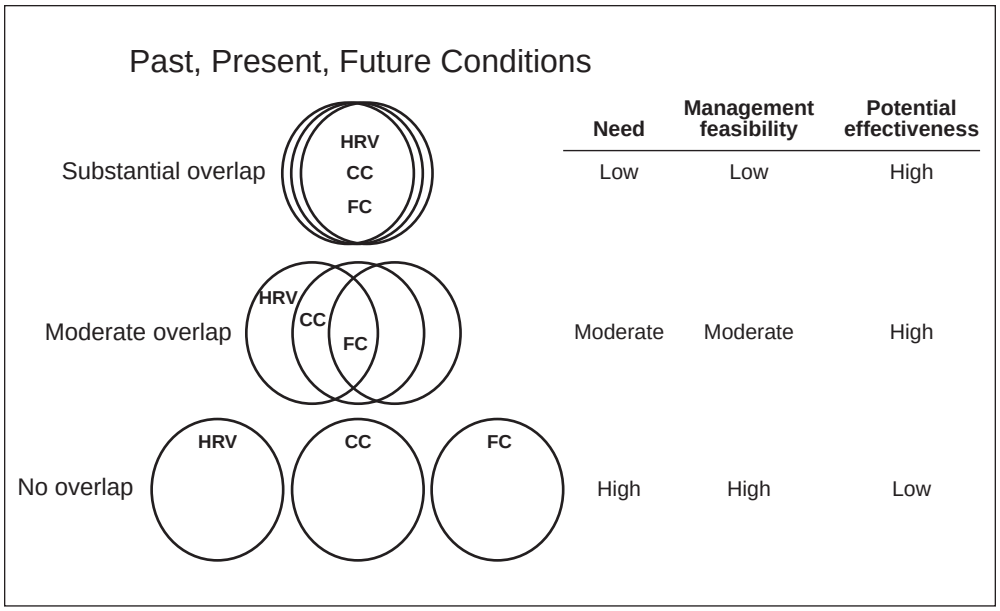


Figure 44—Conceptual illustration of the extent to which current ecosystem conditions (CC) in a place differ from the historical range of variability (HRV) in conditions and from projected future conditions (FC).

- **Managing for resilient landscapes that have patterns consistent with the range of variation under current and expected future disturbance regimes provides a conceptual starting point for capturing the habitat needs of native wildlife.** Native animals evolved in the context of historical disturbance regimes and resultant landscape patterns. Landscape resilience is also important to animal populations because it represents the tendency of a post-disturbance landscape to return to conditions to which the native animal community is adapted. Landscapes that are not resilient may shift into novel environmental conditions that can contribute to substantial changes in the animal community and loss of or change in biodiversity.
- **Some native wildlife species have been affected by threats not related to habitat amount and distribution,** including ecological interactions with invasive species and sensitivity to effects of specific human activities (e.g., livestock grazing or residential, highway, or forest road development). Conservation of these species often requires specific strategies that address habitat in combination with the specific risks to which they are sensitive.
- **Well-connected patterns of habitats across regional landscapes are important to sustaining diversity of native species.** A regional goal is to maintain interconnected networks of habitats that link ecoregions and subregions that would normally provide suitable habitats. Understanding how patterns on the

natural landscape (including vegetation communities and landforms) interact with human-created features (e.g., major highways and residential developments) to influence animal movement and population functions is also important for maintaining landscapes that can sustain populations of wide-ranging species over time.

- **When restoring within-patch heterogeneity, consider varying the tree clump and gap size distribution among patches.** If patches within local landscapes have the same structural characteristics, patch heterogeneity will have been simplified. Consider adapting methods like those developed by Larson and Churchill (2012) and Churchill et al. (2013) to the management of MMC forests. To do that, additional ecoregion-specific datasets will be helpful in fine-tuning innovative silvicultural and forest management strategies.
- **Second-growth 60- to 100-year-old forests offer substantial opportunities for restorative management.** Consider an emphasis on restoring patterns of successional stages that better match the variability of the inherent disturbance regimes. A large acreage of highly productive MMC forest, managed via regeneration and partial harvests during the 20th century, is in this general age class. Resulting forests are intermediate-aged and contribute to simplified landscape patterns.
- **Consider restructuring large areas of the dry and MMC forest on the landscape to return to more resilient forest conditions.** After more than a century of forest and fire management, the current mixed-conifer landscape has developed more than a century's worth of successional inertia (compositional and structural change) and fuel accumulation. Wildfires and insect outbreaks are resetting conditions on the landscape; spatial allocation is driven by ignitions, fire weather, and fuels; changes are occurring suddenly; and the window of treatment opportunity for restoration is growing shorter. Consider identifying patches in key geographic, topographic, and edaphic locations that because of soils, aspect, elevation, and site climate are not likely to sustain these dense, drought- and disturbance-intolerant conditions. Likewise consider reestablishing the inherent landscape heterogeneity, using topography as the underlying template. Where early-seral species would naturally dominate (ponderosa pine [*Pinus ponderosa* Lawson & C. Lawson], western larch [*Larix occidentalis* Nutt.], and western white pine [*Pinus monticola* Douglas ex D. Don]) and natural regeneration is improbable (i.e., grand fir [*Abies grandis* (Douglas ex D. Don) Lindl.], white fir [*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.)],

Second-growth 60- to 100-year-old forests offer substantial opportunities for restorative management.

and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] will likely dominate for a long time), consider regenerating these areas, as is appropriate to the topo-edaphic conditions.

- **To the extent practicable, consider reestablishing the inherent resilience capacities of ecological systems.** This can be done by restoring ecological processes as the foundation of ecosystem resilience. A keystone priority may be to reestablish the central role of the natural or inherent fire regime as the source of reinitiation, development, and maintenance of a heterogeneous landscape mosaic. Where feasible and socially acceptable, create management conditions that enable natural processes to do important work on the ground that is otherwise expensive and less effective to emulate with direct management. Doing this will be economically beneficial, contribute to fire and climate resiliency, and improve diversity of wildlife habitat conditions. Repeated treatments over time will be required to achieve such goals given the century's worth of successional inertia and fuel accumulation that has occurred in many areas.

Expect surprises and consider maintaining a broad range of management options. Expect rare events; they have always influenced the majority of the landscape.

- **Expect surprises and consider maintaining a broad range of management options. Expect rare events; they have always influenced the majority of the landscape.** Twenty-first century climatic changes will result in conditions that differ from the pre-management era, and differ from those we are currently experiencing. Managers and scientists will work to constantly improve the accuracy of future projections, but it may remain prudent to expect the unexpected. There is much uncertainty in the complex interactions between a changing climate, environments, disturbance regimes, and the diversity of organisms and communities in our ecosystems.
- **Consider providing a full complement of vegetation cover types and successional stages within mixed-conifer landscapes.** Patterns and variability of cover types and successional stages consistent with the inherent fire regimes may be desired. Managers can reduce the need for a more highly engineered and costly resilience (that is also more uncertain as to ecological and spatial outcomes) through managing to create or recreate a landscape pattern that would be formed by the patterns and variability of native disturbance regimes.
- **Manage with entire landscapes, all ownerships, and all vegetation types in mind.** Mixed-conifer and other forest types do not exist in isolation and are not confined to ownership boundaries. Disturbance regimes and habitat conditions of neighboring types are interconnected and interrelated, and are best addressed by working together with adjacent landowners.

- **Consider maintaining a backbone of large and old early-seral trees as a primary and persistent structure of all mixed-conifer forests.** If they have been removed by timber harvest, regrow them. This can be a key to restoring climate and wildfire resilience and reestablishing many core wildlife habitat values. Consider favoring ponderosa pine in the dry mixed-conifer forests, and western larch, western white pine, sugar pine (*Pinus lambertiana*), and Douglas-fir in MMC, consistent with local conditions.
- **Consider maintaining a backbone of large standing dead and down trees, and live deformed trees** (those with broken tops and limbs, cavities, and structures for nesting and denning sites) to provide structures for wildlife use. As a result of past timber harvest and "sanitation" treatments, these fine-scale structures are in short supply in most areas. Typically, it takes decades to centuries for a once healthy tree to develop the proper characteristics of such a "wildlife" tree, but techniques are available to create and accelerate their development. Information for both snag and down wood management in green and dead stands can be found in the Decayed Wood Advisor (DecAid) (http://www.fs.fed.us/r6/nr/wildlife/decaid/). Manage these structures as needed (i.e., remove if necessary) in developed recreation areas, such as campgrounds and trailheads, where they could pose a threat to human safety.
- **Old-forest refugia located in suitable locations may be important to retain.** Dense, multilayered mixed-conifer old forest patches are typically not sustainable in many landscapes of eastern Oregon and Washington unless they reside in environmental settings (e.g., valley bottoms and north-facing slopes) that enable them to persist (i.e., suitable topo-edaphic, climatic, and disturbance contexts) by escaping common disturbances. Likewise, focus restoration efforts on developing future old-forest patches in these areas, especially where old forest exists in short supply.
- **Consider reducing the density and layering in the neighborhood surrounding old-forest refugia, and favoring fire-tolerant species to help reduce the risk of loss of multilayered old and otherwise structurally complex forest patches to high-severity fires.** Loss of some existing complex structural patches is an inevitable but reasonable tradeoff for maintaining old forests in fire-prone environments.
- **Restoring the natural variability of wildfire regimes may be a key to restoring the physical processes that create productive aquatic habitats in streams.** Anadromous and cold water fish are fire-adapted species. The natural frequency, severity, and extent of historical fires governed the pulse of erosional

events that carried wood, rocks, and soil to streams. Native fish habitat can be greatly improved through restoration of the natural fire regime.

- **Consider encouraging the natural fire regime within the riparian zones of high-gradient (steep) stream reaches.** With the exception of low-gradient (<5 percent slope) often fish-bearing valley bottom reaches, riparian ecosystems adjacent to high-gradient streams commonly exhibited the fire regime of the adjacent upslope environments. Low-gradient (flatter) reaches are routinely distinguished as flood plain depositional areas whose riparian vegetation is dominated by hardwood tree and shrub vegetation and hydrologic disturbances, whereas the riparian vegetation of higher gradient streams is remarkably similar to the upslope vegetation.

Consider focusing restoration on large, functional landscapes rather than on individual landscape attributes, goals, or risks, such as fuels reduction, timber production, or owl conservation.

- **Consider focusing restoration on large, functional landscapes rather than on individual landscape attributes, goals, or risks,** such as fuels reduction, timber production, or owl conservation. Although we acknowledge the need for short-term measures to protect key habitats, species, and resources that are currently at risk, management emphases with singular resource objectives generally marginalize other important values and eventually fail because they lack this larger focus.
- **Give adaptive management serious consideration.** It simply formalizes learning from successes and failures. The new Forest Service Planning Rule offers yet another opportunity to implement adaptive management. We realize that many prior attempts to conduct adaptive management have failed, but it still represents a rich opportunity for learning, and it is how people learn, through structured trial and experience. Flexible management approaches employing evidence-based, scientifically credible methods promote learning.
- **Consider managing forests in the context of current and potential climate change.** Rates of climate change in the past century and projected for the remainder of this century differ spatially across eastern Oregon and Washington. In some geographic settings, changes in climate in recent decades have altered fire regimes, increased insect infestations, and resulted in high levels of tree mortality. Such changes linked to climate are likely to expand to larger portions of the region in coming decades. Consider identifying rates of change in climate and ecological response over the past century and those projected for future decades and setting management goals and treatments accordingly.

Example of Landscape Management: Okanogan-Wenatchee Landscape Evaluation Decision Support Tool

In eastern Washington, scientists at the Pacific Northwest Research Station Forestry Sciences Laboratory in Wenatchee and on the Okanogan-Wenatchee National Forest have developed and implemented a landscape evaluation and decision support tool (DST) that directly aids managers with implementing a comprehensive landscape restoration strategy. The landscape restoration strategy and the DST have been fully adopted on this national forest and are being implemented on all districts for projects that undertake restoration.

We acknowledge that this particular evaluation and decision support tool represents only one example of how landscape management can be executed. In this instance the forest had access to extensive data sets and skill levels not common on national forests. This example is offered to illustrate what is possible when the necessary resources and expertise are available.

The DST is an outgrowth of a long-standing joint research and management partnership, and a peer-reviewed, forestwide restoration strategy (OWNF 2012). Under the strategy, the objectives of landscape evaluations are to:

- Transparently display how projects move landscapes toward resilience to drought, wildfire, and climate;
- Define and spatially allocate desired ecological outcomes (e.g., adequate habitat networks for listed and focal wildlife species [Gaines et al., in press] and disturbance regimes consistent with major vegetation types);
- Logically and transparently identify potential landscape treatment areas (PLTAs), treatment patches, and the associated rationale; and
- Spatially allocate desired ecological outcomes from landscape prescriptions, and estimate outputs from implemented projects.

Landscape evaluations under the strategy assemble and examine information in five topic areas: (1) current patterns and departures of vegetation structure and composition from historical and climate change reference conditions; (2) spread potential for wildfires, insect outbreaks, and disease pandemics across stands and landscapes given local weather, existing fuel and host conditions; (3) damaging interactions among road, trail, and stream networks; (4) wildlife habitat abundance, distribution, and sustainability; and (5) minimum roads analysis (i.e., which of the existing system roads are essential and affordable, and which are not) (fig. 45).

(continued on next page)

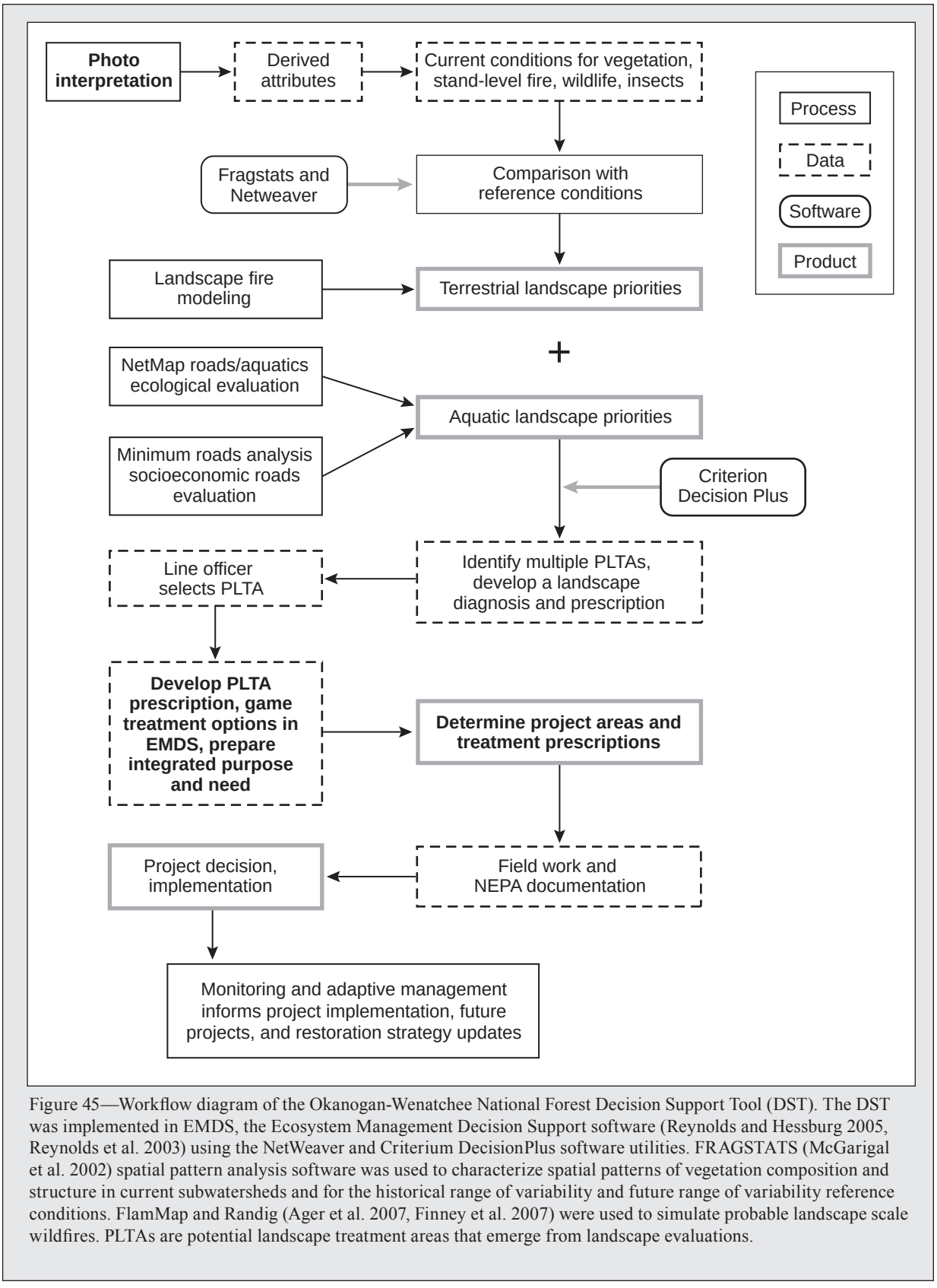


Figure 45—Workflow diagram of the Okanogan-Wenatchee National Forest Decision Support Tool (DST). The DST was implemented in EMDS, the Ecosystem Management Decision Support software (Reynolds and Hessburg 2005, Reynolds et al. 2003) using the NetWeaver and Criterium DecisionPlus software utilities. FRAGSTATS (McGarigal et al. 2002) spatial pattern analysis software was used to characterize spatial patterns of vegetation composition and structure in current subwatersheds and for the historical range of variability and future range of variability reference conditions. FlamMap and Randig (Ager et al. 2007, Finney et al. 2007) were used to simulate probable landscape scale wildfires. PLTAs are potential landscape treatment areas that emerge from landscape evaluations.

The restoration strategy is a living document, which is updated and expanded to include new relevant science and technology. Likewise, with each implemented project, new utilities are added to the decision support tool. Landscape evaluations in the DST examined current vegetation spatial pattern conditions and quantitatively compared them with both historical (past 1900s-era climate, the HRV) and future, mid-21st century climate reference conditions (the FRV), which represent plausible ranges of pattern variability for these periods. Current vegetation conditions were established via interpretation of stereo pairs of aerial photos using standard aerial photogrammetry techniques. The samples for each of the reference conditions were developed using the same vegetation attributes and these same photogrammetry techniques. Evaluated areas were typically small groupings (two or more) of modern-era subwatersheds (12-digit HUCs).

Once current vegetation conditions were interpreted and field verified, the most significant departures of local landscape pattern conditions from reconstructed early 20th century reference conditions (the HRV) were evaluated in the DST. These reconstructed conditions were obtained from the Interior Columbia Basin Ecosystem Management Project (ICBEMP) mid-scale assessment dataset (Hessburg et al. 1999a, 2000a). Since that project, these reconstructed conditions have been summarized for each of the major ecological subregions (Hessburg et al. 2000a) on the two national forests. After the initial departure analysis, departure from a second set of future warmer and drier climate change conditions (FRV) was evaluated. The FRV conditions were represented using historically reconstructed conditions of an ecological subregion whose climatic conditions best match those predicted under warming. This approach used what are often referred to as "climate change analogue conditions" and was intended to show the range of patterns that would emerge with climatic warming and the associated biotic conditions and disturbance regimes. The results of the two departure analyses were used together with equal weighting to determine the most significant changes in forest vegetation structure and composition in the evaluated subwatersheds (Hessburg et al. 2013). Equal weighting was used when considering the HRV and FRV conditions to maximize management options in future landscapes because of the scientific uncertainty surrounding predicted climate change predictions.

Reference conditions were developed for each unique ecological subregion to reflect the range in patch sizes and successional pattern conditions that are

(continued on next page)

(from page 155)

typical for the biota, climate, geology, and disturbance regimes of a physiographic region (Hessburg et al. 2000a), whether they occurred before the advent of management, or they occur at some time in the future. Results of departure analyses were reported by potential vegetation type (PVT) to provide managers with a mechanism for establishing on-the-ground treatments in response to departure analysis. Departure analysis results can inform development of landscape-level restoration prescriptions that are designed to specifically address the most significant departures. Resulting prescriptions can help restore landscape vegetation conditions that are better adapted to wildfires, native insects, pathogens, and predicted climatic warming.

In addition to the vegetation departure analysis, departure analyses were implemented for habitats of regionally listed and focal wildlife species (Gaines et al., in press), and for patch scale fire behavior attributes under a 90th percentile wildfire burn scenario (Hessburg et al. 1999a). Departure analyses were also completed that reflect landscape changes in vulnerability to a variety of major insects and pathogens using models developed for the ICBEMP project (Hessburg et al. 1999a, 1999b, 2000a).

A landscape-scale wildfire analysis was also completed and programmed into the DST, which characterizes the most probable wildfire flow across the large ecoregional landscape when typical wildfire season wind direction, wind intensity, terrain routing of wind and wildfire, and thousands of randomized ignitions are considered. The landscape-scale wildfire analysis provided concrete map depictions of the anticipated flow of large wildfires across the landscape. Managers can use these maps to determine where wildfire flow may be interrupted via strategically placed fuels treatments to reduce the likelihood of large events (Hessburg et al. 2013). Local landscape evaluations can also incorporate these insights into their landscape-level prescriptions.

New in 2013–14, aquatic landscape evaluation utilities are being added to the DST. Under construction are the addition of a minimum roads analysis subroutine, stream crossing and culvert subroutines (currently handled external to the DST), and a module designed in NetMap (Benda et al. 2007) or similar software that identifies road segments that constrain stream channel migration and natural connection with the historical flood plain, separate existing channels from off-channel features, and contribute the most to instream sediment. For additional details about the entire landscape evaluation process, see Gaines et al. (in press) and Hessburg et al. (2013).

Stand Management—Silvicultural Tools and Their Role in Landscape Management

Achieving landscape-level management objectives will require making explicit connections between patch- or stand-level and landscape-level assessments, especially among patch interactions within landscapes. We use the term "stand" to conform to the familiar nomenclature of silviculture. The term "patch" is a similar term used by some to describe a group of trees (O'Hara and Nagel 2013). The planning and operations conducted by land managers will achieve the broader objectives when making this kind of nested spatial relationship explicit in their entire planning process. Stand-level management is therefore the operational level to meet landscape objectives. Creating stand structures that meet these large-scale objectives will be a central concept to management of eastside mixed-conifer forest and riparian ecosystems. Silviculture represents the operational process and offers a matrix of options to achieve these broad-scale objectives.

Stand-level management is the operational level to meet landscape objectives. Creating stand structures that meet these large-scale objectives will be a central concept to management of eastside mixed-conifer forest and riparian ecosystems.

Reducing stand density, altering species composition, and enhancing stand and landscape complexity, where appropriate, will be the central silvicultural objectives in many eastside landscapes based on our findings and conclusions. Stand densities are too high in most locations and ecological resilience is generally lacking owing to past management. For example, logging removed a disproportionate number of large early-seral dominant trees and favored simpler stand structures where dense stands of shade-tolerant trees homogenized both stands and landscapes. Land managers are advised to evaluate the fire risks of both current conditions and what might have developed under active fire when considering how to reconstruct forest structure. Most of the ponderosa pine, and the dry and MMC forested landscapes of eastern Oregon and Washington, had a relatively open stand structure under the influence of active fire (for more information, see "Wildfire" and table 5 in chapter 2). Nonetheless, stands had a particular horizontal and vertical complexity that was characterized by a dominant matrix of relatively open canopies with tall fire-tolerant trees, canopy gaps with patches of tree regeneration or shrubs, and dense patches or scattered individuals of shade-tolerant trees. The relative proportion of these fine-scale stand and landscape elements varied with environment and disturbance regimes.

In dry ponderosa pine and dry mixed-conifer types, stands on southerly aspects were relatively open with a few dense patches of shade-tolerant Douglas-fir and grand fir. Tree regeneration and cohort development coincided with wildfires, but frequent fires killed the majority of the regenerating pines, such that relatively few survived from fire to fire, thereby yielding the appearance of many cohorts through time. In wetter areas, valley bottoms, and north aspects with longer fire

return intervals, the MMC mosaic would have had more dense patches with shade-tolerant understories or larger canopy gaps created by active or passive crown fire associated with mixed- or high-severity fire.

Restoration goals that achieve both landscape and stand objectives can be met by directing landscape units toward the species composition and diversity in age class structure, and complexity in vertical and horizontal stand structure, that are resilient in the face of fire, insects, disease, and climate change. In many cases, promoting the kind of horizontal heterogeneity of stands that occurred prior to Euro-American settlement will greatly increase resiliency to large-scale disturbances such as insect outbreaks (Fettig et al. 2007, Franklin et al. 2013, Hessburg et al. 1994, O'Hara and Ramage 2013). For many landscapes, development of a multiscale mosaic of age and size structures of fire and drought-tolerant species will be the objectives.

Another key objective, particularly in some stands where fire risk is acute, includes reducing fuels and associated potential for large-scale fires. This involves simplifying some stand structures to reduce ladder fuels or to modify understory vegetation and other fuels. Finally, some stand structures can be modified to restore old-forest single-stratum structures (e.g., O'Hara et al. 1996) where scattered overstory trees dominate and other vegetation is relatively scarce. This condition would have been common in many dry pine and dry mixed-conifer forests but also some MMC forests prior to settlement and management. These old-forest structures may be considered simple compared to contemporary stands where historical fire suppression has favored development of multiple strata, but these simple structures also exhibited a fine-scale heterogeneity of size, age, and occurrence, in clumps of varying size, and among gaps with varying size, which made these patches far more resilient to fire, insects, and drought. The result is that over the entire eastside mixed-conifer zone, and even in individual watersheds, some area (patches, stands, or small landscapes) may be directed on trajectories toward complex structures (e.g., a mosaic of open canopies and dense canopies characterized by multi-storied shade-tolerant tree species that are needed for some objectives such as northern spotted owl habitat) while the majority of others may be directed toward more open structures with a subtle but distinctive spatial, compositional, and age heterogeneity. Landscape-level planning will provide the guidance for these decisions.

Silviculture can encompass both passive and active approaches. A variety of treatment options are available to manage stands so that they develop toward desired structures. A central management objective is implementing silvicultural activities (including both mechanical treatments and prescribed burning) that

prepare areas for expected wildfire, to restore stand structures, or alter structures. Treatment options contain a wide range of methods including those that lie between traditional even-aged methods and uneven-aged methods (O'Hara 1998). Desired stand structures may be highly variable across different forest types and the treatments to direct stands toward these structures should also be variable. Implementing forest and riparian management strategies that promote the needed heterogeneity of mixed-conifer forests (dry, moist, and wet) across the landscape will require willingness to innovate on the part of land managers. There may be periods during stand development when the treated forest may not meet, or appear to meet, longer term objectives.

Stand management will often involve social or ecological tradeoffs. Some restored stand structures may not be popular with some stakeholder interests when they result in dramatic reductions in trees or cover. Additionally, many stands may have reached a state where they are prone to wind damage and cannot be manipulated with partial harvest or light thinning treatments, in which case more intensive harvest may be needed to "reset" the ecological trajectory. In other cases, prescribed burning cannot be used without substantial alterations of existing fuels. In these situations, silvicultural treatments can facilitate subsequent prescribed burning treatments. The combination of extensive areas needing treatment, air quality constraints, and work-force requirements presents enormous challenges to land managers, especially at the landscape scale (North 2012, North et al. 2012). Managers are encouraged to view their work as a series of incremental steps intended to move systems in the direction of restoring resilience of mixed-conifer forests to fire and other disturbances. Restoration will require more steps in some places than others.

Managers are encouraged to view their work as a series of incremental steps intended to move systems in the direction of restoring resilience of mixed-conifer forests to fire and other disturbances. Restoration will require more steps in some places than others.

There are opportunities for silviculture to be more cost efficient by recognizing the potential for passive treatments to achieve objectives under certain circumstances. Passive silviculture relies on natural processes including wildfire and regeneration to achieve target stand structures. For example, mixtures of tree species with differential growth rates can result in complex, stratified stand structures even though the stands are even-aged. The rapid growth of western larch and lodgepole pine (*Pinus contorta* Douglas ex Loudon) in comparison to grand fir, evident in many mixed-conifer areas in eastern Oregon and Washington, is one example (e.g., see Cobb et al. 1993).

Another cost-saving strategy involves offsetting expenses of active treatments through commercial activities that help maintain local industries. Active components of silviculture include mechanical removal of low- and mid-story vegetation

to restore a stand dominated by the largest early-seral trees. These restoration treatments will often involve treatments that result in removal of some commercially valuable trees. To meet the ecological objectives, the commercial volume could come from larger diameter, shade-tolerant species. Ideally, the byproduct of landscape restoration is wood fiber from ecologically undesirable components of stands that can help offset treatment costs, which can sometimes be quite high.

Silvicultural treatments of stands will be more effective when directly tied to a landscape analysis and prescription, and tailored to resolve many concurrent issues. Both single- and multi-aged stand structures are naturally part of eastside forest landscapes. Single cohort structures often result from stand-replacement fires, which can be structurally mimicked by several types of silvicultural techniques, if a significant large dead wood component is provided. However, there is no direct substitute for fire and its effects (McIver et al. 2012, Stephens et al. 2012). Fine-scale multi-aged conditions, on the other hand, were much more common in dry ponderosa pine, dry mixed conifer, and MMC forests, especially where surface fire effects dominated, and fires were relatively frequent. Multi-aged stand management at a variety of scales offers a means to create complex structures and emulate the structural complexity found in forests subject to mixed-severity fire regimes. However, traditional uneven-aged management methods are generally inappropriate to achieve these ends. These tools focus on achieving certain diameter frequency distributions rather than meaningful structural characteristics such as numbers of canopy strata, crown coverage, or light penetration for regeneration (O'Hara 1996, 1998; O'Hara and Valappil 1999). These tools also tend to encourage stand structures that are constant from one location to the next and over time.

Instead, managers can focus on retaining meaningful structures that build on existing structural features that vary from site to site and where patchiness of cohorts within stands may vary from fine (groups of trees) to rather coarse (acres to parts of acres) grains. For example, some large and old ponderosa pine and other large young forest dominants would ideally be retained on sites where they are scarce, regardless of the effect on a diameter distribution curve. Simpler two-aged stands offer the opportunity to form structures that fit historical disturbance regimes, retain some cover at all times, and provide structural diversity within stands and across landscapes. The multi-aged approaches in eastside forests may therefore not resemble traditional uneven-aged silviculture (e.g., O'Hara and Gersonde 2004). Instead, guides with a high level of flexibility will be needed to encompass a wide range of stand structural features. Examples of flexible prescriptions and stand structures are available for ponderosa pine (O'Hara et al. 2003) and lodgepole pine (O'Hara and Kollenberg 2003).

In some MMC forests where native disturbance regimes previously created patches of high-severity fire and, in turn, patches of early-seral grass, shrubs, or forest, the wildlife habitat associated with early-seral conditions may be lacking. This may be due to a lack of stand-replacement disturbance or because recent timber harvest has consisted of partial removal treatments that consistently left some of the more dominant trees. In situations where early-seral structure is clearly underrepresented, treatments targeted at creating early-seral grass, shrub, seedling, sapling, and pole-sized tree patches within the forest may be needed, complete with large snags and down logs, as appropriate. Variable retention systems that leave residual trees after harvest (e.g., Beese et al. 2003, Mitchell and Beese 2002) are one way to develop these stand structures.

Existing stands without desired variability in stand structure may be managed to enhance stand-level variation with variable-density thinning (VDT) and other similar methods. VDT is used to enhance variability in homogeneous stands by thinning to a range of densities within a single stand (Carey 2003, O'Hara et al. 2012). This general concept can be applied to any stand to any degree where increased variability is an objective (e.g., see Harrod et al. 1999). However, generalized VDT protocols do not exist because these protocols are usually not transferable from one stand to another, so prescriptions will be needed for individual stands.

Systematically achieving variability in managed forest landscapes is a major change from past practices because traditional silviculture emphasized homogeneity rather than heterogeneity.

Systematically achieving variability in managed forest landscapes is a major change from past practices because traditional silviculture emphasized homogeneity rather than heterogeneity. The challenge will be finding ways to systematically integrate variability into stand management. Recent efforts are making meaningful progress toward development of operational marking rules and procedures for implementing VDT in a variety of vegetation types (O'Hara et al. 2012). Larson and Churchill (2012) cautioned that typical global pattern analysis ignores within-pattern variation that is often the key feature of forest restoration. They recommended maintaining mosaic structures within patches that often exist at quite small spatial scales (<0.4 ha [1 ac]) and developing marking guidelines that focus on creating or maintaining individuals, clumps, and openings (ICO) as key structural elements (Churchill et al. 2013, Larson and Churchill 2012) (fig. 46). This approach has been employed recently and demonstrates the innovation that is emerging in forest management to achieve these varied landscape objectives (Churchill et al. 2013, Franklin et al. 2013, Stine and Conway 2012). More extensive datasets are needed from additional physiographic regions and potential vegetation type settings to better understand the variability in within-patch clumpiness that can inform marking guidelines and silvicultural prescriptions throughout the mixed-conifer forest.

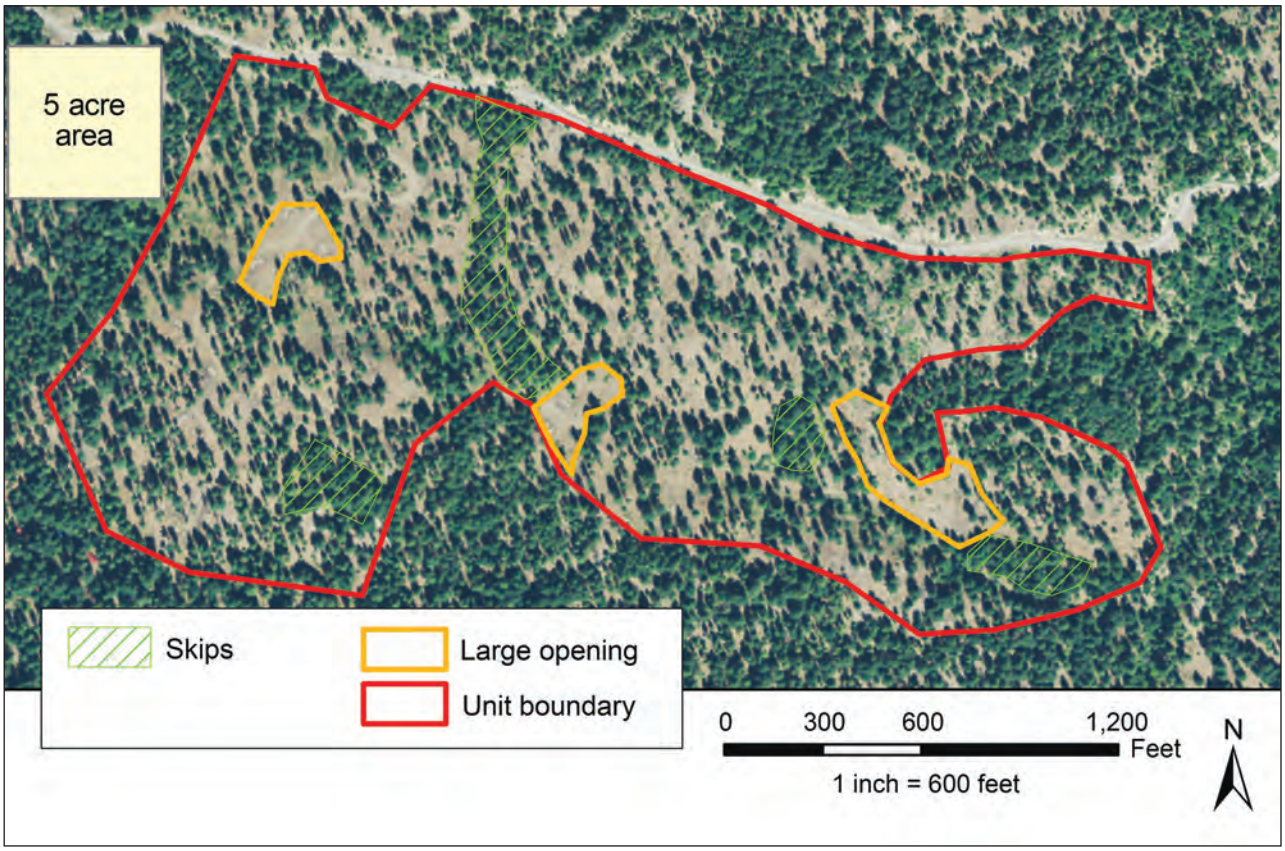


Figure 46—Example of a 32-ha (80-ac) ponderosa pine and Douglas-fir treatment from the Okanogan-Wenatchee National Forest. The treatment was designed to restore a pattern of individual trees, clumps, and openings consistent with prefire exclusion conditions. The prescription included specific guidelines for retentions of clumps of different sizes, as well as openings (Churchill et al. 2013). Large openings were flagged out during layout and were often sinuous in shape. Smaller openings occurred as a result of leaving clumps. Large skips (0.2 to 1.2 ha [0.5 to 3 ac]) were included to protect a riparian buffer in the middle of the unit and other biological hotspots such as large Douglas-fir with dwarf mistletoe, concentrations of downed logs, and multistory patches. Note how the unit boundaries were used to create an additional "finger" skip that extends into the stand. A 2-ha (5-ac) square area is shown to indicate the approximate size of an area that should contain a skip or large clump to break up siting distances. For more details on this approach, see http://www.cfc.umt.edu/forestecology/files/ICO_Manager_Guide_V2.pdf.

In the case of the diverse mixed-conifer forests of eastern Oregon and Washington (dry, moist, wet) the ICO method identifies important components of heterogeneity at fine spatial scales that should be considered in any silviculture prescription. Knowledge about the landscape context, disturbance history, environment, and other management goals will need to inform how the ICO goals are set. For example, in MMC where grand-fir invasion has created large areas of dense canopies, a stand-level silvicultural prescription may be focused first on creating relatively open conditions by removal of most grand fir stems (subject to other management objectives) and second on the spatial patterning of individuals, clumps, and openings in the remaining early-seral species-dominated stand. These considerations may be sequenced or concurrent, depending upon the particular vegetation conditions, and other relevant contexts.

Offsite or nonlocal seed sources were commonly used to replant many plantations in previous decades. These stands frequently exhibit poor survival and growth. Individual trees that are clearly maladapted to a site can be removed, but the presence of these trees should not necessitate special operations to remove them. Often such trees are not producing either pollen or seed and their presence may be of limited ecological importance.

Salvage treatments are an option to produce some timber from stands where trees have been killed by fire, insects, or pathogens. In addition to potentially providing wood resources to local communities, salvage treatments can mitigate future damages from wildfires, especially if salvage removes the smaller trees and associated fine fuels. However, there is typically little ecological justification for salvage of dead trees (Lindenmayer et al. 2008, Spies et al. 2012). Treatments to remove fire- or insect-killed trees are best focused on first achieving residual stand structural goals determined through landscape analysis including retention of snags and downed logs for wildlife habitat considerations (O'Hara and Ramage 2013). Additionally, salvage treatments can be a necessary safety measure in developed recreation areas, near communities, and along roads to reduce hazards.

Upper diameter limit restrictions on tree harvesting have been implemented to improve retention of larger trees on some public lands (e.g., OWNF 2012). Conservation of remaining large and old trees makes sense in many ecological settings where these structures are in short supply, especially where remaining old trees are fire-tolerant, shade-intolerant species. However, strict application of this restriction can prevent managers from having flexibility to achieve ecological objectives. For example, Abella and Covington (2006) found that in Southwestern ponderosa pine forests, upper diameter limits hindered abilities to achieve ecosystem goals and instead served primarily as an economic constraint. Likewise, in some forest patches, large and old trees may be more susceptible to supporting and sustaining bark beetle infestations (Fettig et al. 2007), so some discretion is needed.

Similar constraints exist in eastside forests where these arbitrary limits on harvested tree diameters lead to an unsustainable abundance of large, shade-tolerant trees that actually impede regeneration of shade-intolerant and fire-tolerant trees. This happens on relatively productive sites where shade-tolerant trees, established after the advent of fire exclusion, have grown to relatively large diameters that exceed these arbitrary limits. The presence of such trees may also prevent restoration of openings or a patchy heterogeneity in stand structure. Many of the post-harvest stands contain large (more than about 53 cm [21 in] diameter at breast height) young trees with species compositions and stand structures that

are not representative of the native forests that we might expect to be resilient to drought stress, beetle infestation, changing climate, and other ecosystem stressors. In those situations, active management that may include the harvest of some medium- and large-size trees may produce ecologically enhanced stand structure and species compositions. Management options in these young, productive stands should take into account historical stand structure and species composition, using a landscape-scale context to help ensure that project implementation fits into overall restoration and desired future conditions. That said, large and old trees, particularly of shade-intolerant and fire-tolerant species, are essential elements to include in any eastside landscape. However, strict age or size limits on tree harvest that are not sensitive to site conditions, disturbance history, and topo-edaphic settings can hinder some restoration efforts and may reduce resiliency. Rules of thumb provide helpful guidelines but departures from these may be allowed with well-reasoned explanations.

Chapter 6—Social Agreement and Institutional Capacity for Restoring Moist Mixed-Conifer Forests

The social agreement and institutional capacity for restoring moist mixed-conifer (MMC) forests is every bit as important as the scientific foundation for doing so. The ability to institute the kinds of management changes managers will consider is directly a function of the capacity of the entire affected community to form working partnerships and a common vision. Thus, this section focuses on (1) the social acceptability of different types of restoration treatments among the general public; (2) collaboration as a means for developing, broadening, and sustaining social agreement around specific restoration projects among local stakeholders; and (3) some ideas for how the Forest Service and its partners could approach restoration on national forests that would enhance the agency's institutional capacity to implement the kinds of management strategies discussed in this synthesis document.

The social agreement and institutional capacity for restoring moist mixed-conifer forests is every bit as important as the scientific foundation for doing so.

Social Acceptability of Restoration Treatments Among Members of the Public

Public acceptance is a critical factor influencing whether or not an agency like the Forest Service can carry out its forest management goals (Shindler 2007). It is generally not enough for decisions about forest management to be scientifically sound and economically feasible; they must also be socially acceptable (Shindler 2007). Scientific evidence clearly attests to the need for forest restoration, as this science synthesis demonstrates, and most people living in the wildland-urban interface express a high level of support for reducing fuels on public lands that exhibit high fire risk (McCaffrey et al. 2013). Research from Oregon and Washington also finds that many members of the public recognize the need for restoration treatments on federal lands because of poor forest health and high fire risk (Abrams et al. 2005, Brunson and Shindler 2004, Shindler and Toman 2003). Nevertheless, there is often social disagreement about the methods used to accomplish these treatments, and the locations where they should be carried out. Furthermore, public acceptance of fuels reduction treatments can vary by both geography and social group (Raish et al. 2007, Shindler 2007). For example, a study of nine different stakeholder groups in Oregon found that they were much more supportive of active management of lower elevation ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests than of upper elevation mixed-conifer forests, where the perceived need for treatments was controversial (Stidham and Simon-Brown 2011). This finding suggests that science-based planning—in which the ecological need for fuels reduction is demonstrated by a solid foundation of scientific evidence—is important for improving the social acceptability of restoration treatments in the mixed-conifer zone (Stidham and Simon-Brown 2011).

Social acceptability of forest restoration activities is greatest when the perceived risk of wildfire is high, forest health is believed to be poor, and proposed treatments are perceived as being cost effective and successful at achieving desired outcomes (Bright et al. 2007, Brunson and Shindler 2004, Winter et al. 2002). There is less support for management actions that are perceived as being costly, producing long-duration smoke, posing a risk of escaped or catastrophic fire, or reducing the aesthetic qualities of the landscape (Brunson and Shindler 2004, Winter et al. 2002). Moreover, when citizens believe that forest restoration and fuels treatments are likely to have positive outcomes—economic, ecological, or social—they are more likely to be supportive of them (Shindler 2007).

This science synthesis suggests that both mechanical thinning and the use of prescribed fire will be needed to restore the resilience of MMC forests. In general, there is social support for both types of treatments, though prescribed fire has been found to be less socially acceptable than mechanical thinning in some places (Abrams et al. 2005, Brunson and Shindler 2004). Regarding mechanical treatments, one survey of Oregon and Washington residents (Abrams et al. 2005) found that 88 percent of respondents supported the selective thinning of overstocked forests, and 50 percent supported selective thinning of healthy forests. There was virtually no support for clearcutting. Another study of public acceptance of mechanical fuels reduction treatments from Oregon and Utah (Toman et al. 2011) found a high level of support for mechanical thinning among survey respondents (83 percent), followed by mowing understory vegetation (68 percent).

The social acceptability of prescribed fire use appears to increase when there is confidence in those carrying out the treatments; when it is conducted in remote areas away from development; when it is implemented in a reasonably sized area and resources are present to assure its control; when people are knowledgeable about fire and fuels management and prescribed fire treatments; when people believe it will be effective in producing desired outcomes; when it is cost effective; when mitigation measures are taken to reduce negative air quality and aesthetic impacts; and when stakeholders are involved in planning and preparing the treatments (Bright et al. 2007, Brunson and Shindler 2004, Nelson et al. 2004, Ostergren et al. 2008, Shindler and Toman 2003, Toman et al. 2011, Winter et al. 2002). Ideological perspectives may also inform opinions about the use of fire as a restoration treatment. A study from Montana found that landowners who valued forests as working landscapes that produced economic value disapproved of wildland fire use and prescribed fire because they result in “wasted” timber resources (Cacciapaglia et al. 2012). These landowners also saw fire as a detrimental or unnatural force that

needed to be suppressed. They tended to view mechanical thinning in a positive light, however. In contrast, almost all of the landowners who valued land for its naturalness and ecological values supported wildland fire use (in wilderness) as well as prescribed burning, as appropriate, citing the regenerative properties of fire.

Trust and communication are key components of social acceptability. Researchers have found that the greater the trust in an agency to implement fuels treatments, the more supportive people are of their use (Olsen et al. 2012, Toman et al. 2011, Winter et al. 2002). In addition, the more informed people are about fuels management practices, the more supportive they are (Brunson and Schindler 2004). Activities that build trust between agencies and the public and increase communication and knowledge about fuels treatments are important. Communication and outreach efforts that emphasize the benefits of mechanical thinning and prescribed fire treatments for improving forest health and reducing fire risk to local residents are more likely to increase public acceptance of these treatments (Ascher et al. 2013). Highlighting the amount of control forest managers have over prescribed fire may also help increase support for it. Creating pilot demonstration projects in the places and forest types where restoration activities would be located is another approach to increasing support for them (Stidham and Simon-Brown 2011). Finally, developing fuels reduction and restoration activities through collaborative processes that include stakeholders in planning, decisionmaking, and partnerships (discussed below) is an important approach for overcoming social disagreement and lack of trust (Becker et al. 2011, Hjerpe et al. 2009, Stidham and Simon-Brown 2011, Sundstrom et al. 2012).

Shindler (2007) identified five strategies that forest managers can pursue in order to increase public acceptance of forest management activities: (1) view public acceptance as a process that evolves through building understanding, exchanging and discussing ideas, and evaluating alternatives; (2) develop agency capacity to respond to public concerns; (3) recognize trust building as the goal of public communication and outreach; (4) be sensitive to the local social and community context in which fire management activities are to be carried out, and how these activities may affect communities and forest users; and (5) encourage stable leadership so that shared understanding of forest conditions and fire management practices can develop, and so that strong agency leadership is evident in agency interactions with the public. It is important to remember, however, that social acceptability is dynamic in nature, and can change as people learn more, or when external variables shift (Shindler 2007). Thus, it is important for managers to pay continual attention to public values associated with forest restoration.

Collaboration

Decisionmaking processes play an important role in influencing public acceptance of fire and fuels management activities (Shindler 2007). One of the major constraints to increasing the rate and scale of forest restoration on national forest lands in eastern Oregon is the capacity to reach social agreement about how to achieve it (Economic Assessment Team 2012). The same is likely true in eastern Washington. The Forest Service has emphasized collaboration as a means for developing the social agreement needed among diverse stakeholder groups to carry out forest restoration projects, as demonstrated by recent investments in the Collaborative Forest Landscape Restoration Program and language in the 2012 Forest Service planning rule. Collaboration can be defined as "an approach to solving complex environmental problems in which a diverse group of autonomous stakeholders deliberates to build consensus and develop networks for translating consensus into results" (Margerum 2011: 6). Consensus can range from a simple majority to unanimous agreement regarding a decision, but usually means reaching a decision that everyone can live with. Collaboration in identifying approaches to forest restoration in MMC forests is particularly important because these forests have relatively high economic value in addition to high recreation value, and the methods needed to restore them may be complex and controversial.

There are many models for collaboration associated with forest and fire management on national forest lands (reviewed in Charnley et al. 2013); the best model will depend on local context and the nature of the issues. A number of community-based collaborative groups have formed around eastside national forests to address the ecological and economic issues associated with forest restoration, and to help implement solutions. In eastern Oregon, these include Blue Mountains Forest Partners, Umatilla Forest Collaborative Group, Wallowa-Whitman Forest Collaborative, Harney County Restoration Collaborative, and Ochoco Forest Restoration Collaborative. In eastern Washington, they include the Tapash Sustainable Forest Collaborative and the Northeast Washington Forestry Coalition.

Research has addressed what is needed for successful community-based collaborative processes. For example, McDermott et al. (2011) identified three sets of features that contribute to successful collaboration. The first factor is external sources of support. This includes the support and involvement of elected officials, agency leaders, and key decisionmakers; enabling laws and policies; and active community involvement. The second factor involves having access to sufficient resources to enable meaningful engagement of the many entities, such as funding, staffing, and information. The third factor involves the capacity to perform, which depends on effective leadership, trust, and social capital.

Bartlett (2012) laid out a logical and promising pathway for collaboration based on the collaborative process used to reach stakeholder agreement about hazardous fuels reduction projects at Dinkey Creek, on the Sierra National Forest in California. Successful collaboration there was based on a process that included five main stages: assessment, organization, education, negotiation, and implementation (see Bartlett 2012 for a description of these stages). Her experiences from California provide some key insights about what promotes effective collaboration:

- Include a broad range of participants;
- Establish a common conceptual framework, purpose and need, and long-term desired condition;
- Include scientific experts who serve as technical resources during meetings;
- Move some intractable issues forward without complete consensus if necessary;
- Include site visits to support decisionmaking and reach agreements; and
- Have an impartial mediator to promote trust and problem solving.

Other suggestions that seem to have a positive effect on collaboration include timely engagement, building trust, and developing patience with the process.

The organizational capacity of collaborative groups is critical for sustaining effective collaborative processes. Cheng and Sturtevant (2012) provide a framework for assessing the collaborative capacity of community-based collaboratives to engage in federal forest management. They identify six arenas of collaborative action: organizing, learning, deciding, acting, evaluating, and legitimizing. Within each of these arenas there are different kinds of capacities associated with individuals, the collaborative group itself, and other organizations that the group engages with. Their framework can be used to evaluate what capacities exist within local collaboratives, and what capacities could be enhanced, so that investments in building and sustaining these groups can be targeted.

Davis et al. (2012) examined the organizational capacity of community-based collaborative groups in Oregon that are engaged in natural resource management issues on public as well as private lands. They found that many of these groups have limited financial capacity and insecure funding. They also have small numbers of staff who are expected to carry out a broad range of activities, and are heavily dependent on volunteers. Most accomplish their work through partnerships, often with federal agencies. They make a valuable contribution to local-level natural resource management and community economic well-being. Finding ways to successfully engage, support, and help build the capacity of local community-based collaboratives east of the Cascades in Oregon and Washington is an important

strategy for building social agreement around the management of MMC forests, and for implementing forest restoration activities there.

Management of public lands today is as much a social experiment as it is an ecological experiment, especially when viewed through the lens of social-ecological resilience.

Management of public lands today is as much a social experiment as it is an ecological experiment, especially when viewed through the lens of social-ecological resilience. The public wants to be involved. The best efforts to engage them in this work are not only well advised but critical to the success of restoration programs. It will be prudent to engage expertise in the areas of public involvement, social science, and economics in the cadre of players who help guide these national forest planning and management efforts.

Institutional Capacity

Land managers operate within established policy, constraints, and limitations as well as in accordance with established practices and conventions. However, some of the potential changes in forest management evoked within this document represent a departure from "business as usual." Land managers will decide how to proceed, and this will depend in large part on budget, policy, local circumstances, and, ultimately, the judgment of line officers. However, there are some ideas and observations from past work, both research and management, that suggest some prudent adjustments in management approach.

Create Landscape Management Demonstration Areas

We suggest that the identified approach to project and forest planning described above dovetails quite seamlessly with the intentions and expectations of the 2012 Forest Service planning rule (36 CFR Part 219) and has value for all forms of ownership. In that vein, perhaps the findings and conclusions contained herein can be implemented both formally within the planning rule context as well as informally for current project planning on public and private lands. On public lands, Forest Service staff (or other public land managers) can identify the appropriate landscapes, sometimes including mixed ownerships, and treat them as "landscape laboratories" or landscape demonstration areas. Although the geographic scope of these "learning" landscapes is yet to be fully defined, we are generally referring to large drainage basins on the order of tens to hundreds of thousands of hectares (1 ha = about 2.5 ac).

These large landscapes can provide the context in which we evaluate past, current, and potential future conditions and then develop project plans and desired future conditions for stands, watersheds, and the entire landscape (i.e., a nested hierarchical spatial organization of a landscape) accordingly. In this way, the project and forest planners can include the crucial perspective of broader spatial and

temporal scales as they consider what to do on any given project area. It is prudent to put local project evaluations within this context of a nested landscape that can effectively consider the broader scales where the full implications of ecosystem drivers (e.g., fire, insects, and disease) and the periodicity of their occurrences can be accurately assessed.

National Forest System (NSF) staff, in collaboration with Research and Development (R&D) staff, and a variety of potential partners and collaborators will likely work together to develop this approach. Information from a wide variety of sources (e.g., experimental forests and ranges situated in the landscapes, other research results, NFS legacy data) can be used to develop better management options for public land managers and private landowners. This will also enable implementation of ecosystem restoration activities across the landscape, as well as the Department of Agriculture's guidance to consider "all lands" in our planning and management activities. Within these "landscape laboratories," Forest Service R&D, universities, and other partners with relevant information will be able to contribute long-term data records. This approach is a significant administrative and scientific challenge but it represents an important learning opportunity. The Forest Service has already made some strides in developing this concept through the relatively new Collaborative Forest Landscape Restoration Program (CFLRP). The purpose of the CFLRP is to encourage the collaborative, science-based ecosystem restoration of priority forest landscapes. Twenty projects have been established across the United States since 2010 to implement this concept. Perhaps this effort can expand to encompass larger experimental areas and a more robust role for the assistance from the scientific community.

Incorporate the "All-Lands" Initiative

The Department of Agriculture's 2010–2015 Strategic Plan contains a goal that strives to "ensure our national forests and private working lands are conserved, restored, and made more resilient to climate change, while enhancing our water resources." There are many facets to this ambitious goal and one new initiative in support of this goal involves use of a collaborative, "all lands" approach to bring public and private owners together across landscapes and ecosystems.

An all-lands approach would move landscape-level assessment and planning beyond the limits of the MMC forest type to other forest types, other land designations, and other ownerships that are often intermingled on logical landscape-level planning units. Managers can strive to involve all owners and management agencies and include all lands, even wilderness, in this kind of landscape planning. Additionally, these all-lands assessment efforts may indicate the need to treat areas such

as wilderness-designated areas with controlled ignitions and burning to achieve landscape-level goals such as fuels reduction and achieving target future ranges of variation.

Revisit Current Management Constraints; Eastside Screens

In August 1993, the Pacific Northwest Region regional forester issued a letter providing interim direction to eastside national forests on retaining old-growth attributes at the local scale and moving toward the historical range of variability (HRV) across the landscape. These became known as the "eastside screens." A subsequent decision notice in May 1994 amended all eastside forest plans to include these standards. These provisions involved a three-stage process for screening projects to evaluate effects:

- Riparian Screen. Defers timber harvest in riparian areas.
- Ecosystem Screen. Compares the acres of old forest stages in a watershed with the HRV for that structural stage.
- Wildlife Screen. Maintains options for future wildlife habitat requirements for old growth-dependent species.

Eastside screens for large trees (>21 in [about 53 cm] in diameter) were intended to be an 18-month interim measure to screen out projects that could potentially harvest significant amounts of old forest and of remnant medium- and large-size trees. Managers were advised to avoid removal of trees above a certain diameter limit for a variety of reasons. The eastside forest health assessment in eastern Oregon and Washington had shown that remnant large trees and old-forest patches had been heavily targeted for timber harvest, and were seriously depleted (Everett et al. 1994). Public concern for loss of large and old trees also became significant beginning in the late 1980s and has continued to the present. Forest managers had to rapidly "screen" timber sales and then exclude parcels from those sales that included these large trees. Tree diameter was also used as a rapid and conservative but crude surrogate for old growth to limit removal of larger and older trees—because analyses had not been completed to characterize old forests and old trees—across the variety of forest types and productivities.

The team that developed the large tree screen designed it to be replaced by more in-depth landscape evaluations that considered the key departures in forest structural and compositional patterns from HRV. In fact, in 1994 the regional forester stated that "projects need to be designed according to the principles of landscape ecology and conservation biology." Nonetheless, these screens have been employed for 20 years now. We are not aware of how much variation in these

procedures has been exercised since the screens were instituted, but the screens are still being used. Restoration of patterns that support natural processes and terrestrial species habitat arrangements is better achieved through evaluations that lead to landscape prescriptions. We know of no research that has evaluated the effects of the screens since they were implemented. However, other research on the ecology and history of pine and mixed-conifer forest (Hessburg et al. 1999a, 2005; Merschel 2012; Perry et al. 2004) indicates that many shade-tolerant trees more than 51 cm (20 in) in diameter were established after fire exclusion in the early 1900s. Consequently, restoration guided by size alone will not remove all of the individuals of species and ages of trees that are products of the altered disturbance regimes of these forests.

Furthermore, a recent report on climate change impacts on Western forests indicates that increased fire frequency and severity, insect outbreaks, and drought stress will challenge managers with novel conditions that fall outside what was identified from the 500+ years prior to Euro-American settlement (Fettig et al. 2013). To develop adaptation strategies, including ones that allow for new species composition and changes in forest structure across the landscape, managers will need more flexibility than is provided under one-size-fits-all rules for silviculture, such as those imparted by the eastside screens. Local variability coupled with an uncertain climate future requires an ability to adjust to site conditions and be nimble, as better and more complete information becomes available.

Rather than simple rules based only on stand structure, managers can be guided by multi-scale evaluations that include landscape and site-level criteria.

Rather than simple rules based only on stand structure, managers can be guided by multi-scale evaluations that include landscape and site-level criteria. Such approaches would consider and remedy the key departures in forest structural and compositional patterns relative to their HRV and future range of variability (FRV), the latter of which incorporates climate change. This integration of historical and potential future conditions is likely to conserve more desired components of ecosystems than would occur under the use of HRV or the FRV alone. The departure analyses using the HRV and the FRV are not meant as a recipe, but as guidance about the nature of pre-management-era patterns that supported native species habitats and disturbance regimes. With climate warming we use the FRV in the same way as HRV—as guidance about the nature of the patterns that may emerge as species distributions and disturbance regimes (e.g., ecological envelopes) shift as climate interacts with land use to create novel environmental conditions and behaviors. As we are seeing in eastern Washington ecoregions, these envelopes of HRV and FRV can actually overlap quite a bit, but are clearly being deformed by warmer and drier conditions.

As managers reevaluate their planning approaches using the concepts and findings contained in this report, they might also consider phasing out these interim directions. As mentioned, these screens were a short-term solution to prevent harvesting of larger trees. The diameter limits were intended as a crude and conservative filter to avoid harvesting old trees, pending the development of more precise definitions and tools. These limits are arbitrary with respect to meeting any ecological objectives because they applied to all sites regardless of the number or species of large trees present, or the potential of these areas to grow large trees. The limits on removing any tree larger than about 53 cm (21 in) whatsoever, regardless of geographic context, or age, or species, or relative abundance, or other considerations (e.g., forest health) within a patch can inhibit regeneration in some stands, lack any real landscape objectives, and impede landscape-level management and restoration.

The concepts presented in this report address the underlying ecological objectives of the eastside screens. As these concepts are explored and implemented by managers, the ecological goals intended by the eastside screens can be met. Some individual features (i.e., nesting, roosting, and resting sites for wildlife) may continue to merit short-term conservation measures. However, employing a landscape approach to assessment, planning, and execution of forest management will improve our ability to effectively restructure forests to a more resilient condition and cope with impending change. Moving landscapes toward these desired conditions will be expensive, thus some flexibility in treatment options is needed. Treatments designed based on the considerations herein are capable of generating some revenue that will offset a portion of the costs of achieving landscape-level objectives. Flexibility will also help managers address long-term socio-political and operational issues related to eastside screens.

Chapter 7—Conclusions

Active management of vegetation in moist mixed-conifer (MMC) forests in eastern Oregon and Washington has declined over the last two decades because of uncertainties about management. During this time, shade-tolerant and fire-intolerant trees have regenerated, grown, and densified forests in many locations. Consequently much of the landscape of ponderosa pine and dry and MMC forests of eastern Oregon and Washington is in a non-resilient condition. Some of the MMC landscape would benefit from active vegetation and fire management to restore or create vegetation conditions and landscape patterns that are better adapted to fire, drought, insects and disease, and climate change than conditions and patterns managed passively. Although managers have a scientific foundation and some amount of social license to conduct active restoration in pine and dry mixed-conifer types, there is far less consensus on what should be done in MMC types. This report offers scientific findings and management considerations to help managers take informed steps toward restoring resilience to MMC forests.

This report offers scientific findings and management considerations to help managers take informed steps toward restoring resilience to moist mixed-conifer forests.

Dry, moist, and wet mixed-conifer forests coexist in landscape mosaics that have been altered by settlement and land use activities. On balance, the array of changes over the last 100 to 150 years make these forests and landscapes subject to high-severity and sometimes large fires (with varying degrees of mixed- and low-severity components), insect outbreaks, and drought-related tree mortality that negatively affect many ecological and social values. During the presettlement era, the dry **and** MMC forest landscapes were sculpted by low-, mixed-, and high-severity wildfires (tables 8 through 13 in app. 3) that maintained relatively open canopies and understories. Landscapes were mosaics, dominated by a mix of tree species, sizes, and ages (tables 8 through 13 in app. 3). Some ecoregions exhibited more mixed- and high-severity fire than others.

Environments and vegetation patterns are diverse and complex in the MMC forest (e.g., historical disturbance regimes differ within potential vegetation types as a result of topography and landscape context). We lack uniform vegetation classifications, maps, and disturbance regime information that can be applied at local landscape scales. This information is sorely needed. Despite these challenges, we were able to identify and develop a working definition of the MMC types (potential vegetation types, disturbance regimes, ecoregions) within the broader mixed-conifer mosaic, where structure, composition, and processes have been significantly altered by Euro-American activities.

In many respects the impacts of postsettlement activity on forests and implications to restoration are the same in MMC forests as those in the ponderosa pine and dry mixed-conifer forests. The disturbance regimes were similar in the dry and moist environments, but in the productive MMC forest environments the large

increases in understory density were composed of shade-tolerant species like grand fir or Douglas-fir rather than ponderosa pine. We identify that in the wettest mixed-conifer types, restoration of resilient vegetation patterns is much less needed or inappropriate given their low frequency disturbance regimes.

Given the stated restoration goals of the Forest Service, we identify a set of objectives and actions at stand and landscape levels that would move forests and landscapes on a trajectory toward resilience in the face of fire, insects, disease, and climate change. These include creating diverse, fire-resilient vegetation types over a large portion of the MMC landscape, creating seral-stage diversity and patterns at stand and landscape scales, using topography as a guide, maintaining habitats for key wildlife species, including those that need landscapes with patches of dense mixed-conifer forests, and maintaining ecological and physical processes that favorably reconnect terrestrial and aquatic ecosystems and support habitat for fish.

Stands (patches) and local landscapes, conjoined with regional landscape-scale perspectives, are needed to achieve restoration goals. Although we address all three scales in this report, we have emphasized local landscape perspectives because they are newer and the theory and practice is rapidly developing through research and innovative management. For those seeking more detail on the latest stand-level considerations for mixed-conifer forests, other resources exist (e.g., Franklin et al. 2013). The geographic scope and context of forest restoration dictates an "all lands" approach to address the challenges of the 21st century. Vegetation succession and disturbance dynamics emerging from wildfires, insect and disease outbreaks, exotic species invasions, and multiple ownerships and management directions—set against a backdrop of climate change—do not observe local forest patch boundaries, land lines, or administrative boundaries. More effective land management can be realized through action grounded in collaboration and a landscape perspective.

A list of management considerations is provided for planners and managers when managing for restoration and resilience at landscape scales (see app. 1). The list includes guidance on development and use of historical reference conditions (historical range variation is a useful guide), addressing climate change (using potential future range of variation in designing landscapes), and a workflow plan. Several eastside national forests and other forest landowners in this region now actively employ some principles of restoration management at a landscape scale. The example provided from the Okanogan-Wenatchee National Forest is one of a number of bottom-up initiatives that explore innovative approaches to forest management. Many of the concepts presented in this report may be known to land

managers, but they are not yet in common practice. Understandably, new innovations and scientific insights take time and often require experimentation to integrate into standard operations.

It makes sense for both the management and research communities to work together to learn about restoration and collectively stop every few years and take stock of where we are and what we have learned in implementing these ideas. This is, in essence, the conceptual core of adaptive management, and we encourage such flexible management approaches that promote learning and sharing. It also makes sense to build stronger day-to-day ties between management and research to enhance the real-time flow of information, improve researcher insights about ongoing and newly emergent problems, and to improve management by experimentation and adaptation. Regional land management, with all of its uncertainties and risks, and the significant and growing public scrutiny, is an enterprise that could benefit from increased adaptive management and enhanced science-management collaboration.

Land management activities necessarily integrate many policy and societal considerations, while utilizing the best available science. Managers can rely on well-tested, dependable methods and approaches of our respective professions, but can also continually avail themselves of developing innovations and technologies to better enable decisions and implementation. That, we believe, is evident in the synthesis presented in this report. We have presented a synopsis of the best available science, old and new, combined with an array of management concepts and principles that have yet to become common practice. We have also assessed the best of both traditional scientific and management approaches with some recent innovations that substantially improve our ability to understand how complex forest ecosystems function and how management influences those processes.

Finally, when viewed through the lens of socioecological resilience, creating ecologically resilient landscapes cannot occur without support and consideration of the institutions and socioeconomic components. Restoration and renewal of resiliency in eastside forest landscapes requires economic support, forest management infrastructure, and social license and partnerships between management agencies and various publics. Human activities over the last 150 years have reduced the resilience of mixed-conifer forests across millions of acres of federal lands. This problem, a long time building and currently widespread, will require a sustained, comprehensive, and collaborative approach to remedy.

Restoration and renewal of resiliency in eastside forest landscapes requires economic support, forest management infrastructure, and social license and partnerships between management agencies and various publics.

Acknowledgments

In the preparation of this report, many more people contributed to the final product than simply the listed authors. Accordingly, we thank the following for their meaningful efforts: Becky Gravenmier for helping coordinate our efforts in so many ways; Keith Routman for considerable expertise in editing and formatting the document for final publication; Tom DeMeo, Rod Clausnitzer, Sabine Mellmann-Brown, Dave Powell, and Mike Simpson for their input into developing table 2 and suggestions for text related to potential vegetation types; Ayn Shlisky for reviewing portions of earlier drafts and preparing some graphics; the Umatilla National Forest staff, particularly Dave Powell, who hosted our August 2012 workshop and field tour and helped with arrangements for the December 2013 workshop in Pendleton; the peer reviewers; and many others who offered comments on earlier drafts.

Metric Equivalents

When you know:	Multiply by:	To get:
Inches (in)	2.54	Centimeters
Feet (ft)	.305	Meters
Miles (mi)	1.609	Kilometers
Square miles (mi^2)	2.59	Square kilometers
Acres (ac)	.405	Hectares

Literature Cited

Abella, S.R.; Covington, W.W. 2006. Forest ecosystems of an Arizona *Pinus ponderosa* landscape: multifactor classification and implications for ecological restoration. Journal of Biogeography. 33: 1368–1383.

Abrams, J.B.; Kelly, E.; Shindler, B.; Wilton, J. 2005. Value orientation in forest management: the forest health debate. Environmental Management. 36: 495–505.

Agee, J.K. 1988. Successional dynamics in forest riparian zones. In: Raedeke, K.J., ed. Streamside management: riparian wildlife and forestry interactions. Proceedings of a symposium on riparian wildlife interactions. Seattle, WA: University of Washington: 31–44.

Agee, J.K. 1990. The historical role of fire in Pacific Northwest forests. In: Walstad, J.D.; Radosevich, S.R; Sandberg, D.V., eds. Natural and prescribed fire in Pacific Northwest forests. Corvallis, OR: Oregon State University Press: 25–38.

Agee, J.K. 1993. Fire ecology of Pacific Northwest Forests. Washington, DC: Island Press. 493 p.

Agee, J.K. 1994. Fire and weather disturbances in terrestrial ecosystems of the eastern Cascades. In: Hessburg, P.F., ed. Eastside forest ecosystem health assessment. Gen. Tech. Rep. PNW-GTR-320. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 52 p.

Agee, J.K. 1998. The landscape ecology of western forest fire regimes. Northwest Science. 72: 24–34.

Agee, J.K. 2003. Historical range of variability in eastern Cascades forests, Washington, USA. Landscape Ecology. 18: 725–740.

Agee, J.K.; Skinner, C.N. 2005. Basic principles of fuel reduction treatments. Forest Ecology and Management. 211: 83–96.

Ager, A.A.; Finney, M.A.; Kerns, B.K.; Maffei, H. 2007. Modeling wildfire risk to northern spotted owl (*Strix occidentalis caurina*) habitat in central Oregon, USA. Forest Ecology and Management 246: 45–56.

Aguilar, F.; Garrett, H.E. 2009. Perspectives of woody biomass for energy: survey of state foresters, state energy biomass contacts, and national council of forestry association executives. Journal of Forestry. 107: 297–306.

Alexander, M.E.; Hawksworth, F.G. 1975. Wildland fires and dwarf mistletoe: a literature review of ecology and prescribed burning. Gen. Tech. Rep. RM-GTR-14. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 12 p.

Anderson P.D.; Larson D.J.; Chan S.S. 2007. Riparian buffer and density management influences on microclimate of young headwater forests of western Oregon. Forest Science. 53: 254–269.

Arno, S.F. 1988. Fire ecology and its management implications in ponderosa pine forests. In: Baumgartner, D.M.; Lotan, J.E., eds. Ponderosa pine: the species and its management: Proceedings of a symposium. Pullman, WA: Washington State University Extension: 133–139.

Asah, S.T.; Blahna, D.J.; Ryan, C.M. 2012. Involving forest communities in identifying and constructing ecosystem services: millennium assessment and place specificity. Journal of Forestry. 110: 149–156.

Ascher, T.J.; Wilson, R.S.; Toman, E. 2013. The importance of affect, perceived risk, and perceived benefit in understanding support for fuels management among wildland-urban interface residents. International Journal of Wildland Fire. 22: 267–276.

Aubry, K.B.; Koehler, G.M.; Squires, J.R. 2000. Ecology of Canada lynx in southern boreal forests. In: Ruggiero, L.F.; Aubry, K.B.; Buskirk, S.W.; Koehler, G.M.; Krebs, C.J.; McKelvey, K.S.; Squires, J.R., eds. Ecology and conservation of lynx in the United States. Gen. Tech. Rep. RMRS-GTR-30. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 373–396.

Aubry, K.B.; McKelvey, K.S.; Copeland, J.P. 2010. Distribution and broadscale habitat relationships of the wolverine in the contiguous United States. Journal of Wildlife Management. 71: 2147–2158.

Ault, T.R.; Cole, J.E.; St. George, S. 2012. The amplitude of decadal to multi-decadal variability in precipitation simulated by state-of-the-art climate models. Geophysical Research Letters. 39:10.1929/2012GL053424.

Bailey, R.G. 1995. Description of the ecoregions of the United States. Misc. Publ. 1391. Washington, DC: U.S. Department of Agriculture. 108 p.

Baker, C.S.; Batchelder, H.P.; Epps, C.; Garcia, T.S.; Haig, S.M.; Letelier, R.M.; Lytle, D.A.; Menge, B.A.; Miller, J.C.; Noakes, D.L.G.; Peterson, W.T.; Rice, J.M.; Rumrill, S.S.; Schreck, C.B.; Suryan, R.M.; Sytsma, M.D.; White, A.E. 2010. Oregon's fish and wildlife in a changing climate. In: Dello, K; Mote, P., eds. Oregon Climate Assessment Report. Corvallis, OR: Oregon State University, Oregon Climate Change Research Institute. Chapter 7. http://occri.net/wp-content/uploads/2011/04/chapter7ocar.pdf. (17 January 2014).

Baker, W.L. 2012. Implications of spatially extensive historical data from surveys for restoring dry forests of Oregon's eastern Cascades. Ecosphere. 3(3): 23.

Barbour, J.R.; Fried, J.S.; Daugherty, P.J.; Christensen, G.; Fight, R. 2008. Potential biomass and logs from fire hazard reduction treatments in Southwest Oregon and Northern California. Forest Policy and Economics. 10: 400–407.

Bartlett, G. 2012. Developing collaboration and cooperation. In: North, M., ed. Managing Sierra Nevada forests. Gen. Tech. Rep. PSW-GTR-237. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 81–88.

Bartos, D.L. 2000. Landscape dynamics of aspen and conifer forests. Aspen Bibliography. Paper 782. http://digitalcommons.usu.edu/aspen_bib/782. (17 January 2014).

Baxter C.V.; Fausch K.D.; Murakami, M.; Chapman, P.L. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology. 85: 2656–2663.

Becker, D.R.; Larson, D.; Lowell, E.C. 2009. Financial considerations of policy options to enhance biomass utilization for reducing wildfire hazards. Forest Policy and Economics. 11: 628–635.

Becker, D.R.; McCaffrey, S.M.; Abbas, D.; Halvorsen, K.E.; Jakes, P.; Moseley, C. 2011. Conventional wisdoms of woody biomass utilization on federal public lands. Journal of Forestry. 109: 208–218.

Bednarz, J.C.; Ripper, D.; Radley, P.M. 2004. Emerging concepts and research directions in the study of cavity-nesting birds: keystone ecological processes. The Condor. 106: 1–4.

Beebe, J.; Everett, R.; Scherer, G.; Davis, C. 2002. Effect of fertilizer applications and grazing exclusion on species composition and biomass in wet meadow restoration in Eastern Washington. Res. Pap. PNW-RP-542. Portland OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station. 15 p.

Beechie, T.; Bolton, S. 1999. An approach to restoring salmonid habitat-forming processes in Pacific Northwest watersheds. Fisheries. 24: 6–15.

Beese, W.J.; Dunsworth, B.G.; Zielke, K.; Bancroft, B. 2003. Maintaining attributes of old-growth forests in coastal BC through variable retention. Forestry Chronicle. 79: 570–578.

Belsky, J.A.; Matzke, A.; Uselman, S. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation. 54: 419–431.

Benda, L.; Miller, D.; Andras, K.; Bigelow, P.; Reeves, G.; Michael, D. 2007. NetMap: a new tool in support of watershed science and resource management. Forest Science. 52: 206–219.

Benda, L.; Miller, D.; Bigelow, P.; Andras, K. 2003. Effects of post-wildfire erosion on channel environments, Boise River, Idaho. Forest Ecology and Management. 178: 105–119.

Benitez-Lopez, A.; Alekemade, R.; Verweij, P.A. 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biological Conservation 143: 1307–1316.

Bennett, A.F. 2003. Linkages in the landscape: the role of corridors and connectivity in wildlife conservation. IUCN Forest Conservation Programme, Conserving Forest Ecosystems Series No. 1. Gland, Switzerland: IUCN. 254 p.

Bentz, B.J.; Régnière, J.; Fettig, C.J.; Hansen, E.M.; Hayes, J.L.; Hicke, J.A.; Kelsey, R.G.; Negrón, J.F.; Seybold, S.J. 2010. Climate change and bark beetles of the western U.S. and Canada: Direct and indirect effects. Bioscience. 60: 602–613.

Berkes, F.; Ross, H. 2013. Community resilience: toward an integrated approach. Society and Natural Resources. 26: 5–20.

Beschta, R.L.; Donahue, D.L.; DellaSala, D.A.; Rhodes, J.J.; Karr, J.R.; O'Brien, M.H.; Fleischner, T.L.; Deacon Williams, C. 2012. Adapting to climate change on western public lands: addressing the ecological effects of domestic, wild, and feral ungulates. Environmental Management. 51: 474–491.

Beschta, R.L.; Ripple, W.J. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation. 142: 2401–2414.

Betancourt, J.L.; Van Devender, T.R.; Martin, P.S. 1990. Packrat middens: the last 40,000 years of biotic change. Tucson, AZ: University of Arizona Press. 469 p.

Betts, M.G.; Hagar, J.; Rivers, J.; Alexander, J.; McGarigal, K.; McComb, B.C. 2010. Thresholds in songbird occurrence in relation to early seral broadleaf forest. Ecological Applications. 20: 2116–2130.

Binckley, C.A.; Wipfli, M.S.; Medhurst, R.B.; Polivka, K.; Hessburg, P.; Salter, R.B.; Kill, J.Y. 2010. Ecoregion and land-use influence invertebrate and detritus transport from headwater streams. Freshwater Biology. 55: 1205–1218.

Bisson, P.A.; Rieman, B.E.; Luce, C.; Hessburg, P.F.; Lee, D.C.; Kershner, J.; Reeves, G.H.; Gresswell, R.E. 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. Forest Ecology and Management. 178: 213–229.

Bolsinger, C.L. 1978. The extent of dwarf mistletoe in six principal softwoods in California, Oregon, and Washington, as determined from forest survey records. In: Scharpf, R.F.; Parmeter, J.R. Jr., eds. Proceedings of a symposium on dwarf mistletoe control through forest management. Gen. Tech. Rep. PSW-GTR-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 45–54.

Bright, A.D.; Newman, P.; Carroll, J. 2007. Context, beliefs, and attitudes toward wildland fire management: an examination of residents of the wildland-urban interface. Human Ecology Review. 14: 212–222.

Brown, D.K.; Echell, A.A.; Propst, D.L.; Brooks, J.E.; Fisher, W.L. 2001. Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila trout (*Oncorhynchus gilae*). Western North American Naturalist. 61: 139–148.

Brown, R.N.K.; Rosenberger, R.S.; Kline, J.D.; Hall, T.E.; Needham, M.D. 2008. Visitor preferences for managing wilderness recreation after wildfire. Journal of Forestry. 106: 9–16.

Brunson, M.W.; Shindler, B.A. 2004. Geographic variation in social acceptability of wildland fuels management in the western United States. Society and Natural Resources. 17: 661–678.

Buchanan, J.B.; Irwin, L.L.; McCutchen, E.L. 1995. Within-stand nest site selection by spotted owls in the Eastern Washington Cascades. Journal of Wildlife Management. 59: 301–310.

Bull, E.L.; Heater, T.W.; Shepherd, J.F. 2005. Habitat selection by the American marten in northeastern Oregon. Northwest Science. 79: 37–43.

Bull, E.L.; Henjum, M.G. 1990. Ecology of the great gray owl. Gen. Tech. Rep. PNW-GTR-265. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 39 p.

Bull, E.L.; Holthausen, R.S. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. Journal of Wildlife Management. 57: 335–345.

Bull, E.L.; Holthausen, R.S.; Henjum, M.G. 1992. Roost trees used by pileated woodpeckers in northeastern Oregon. Journal of Wildlife Management. 56: 786–793.

Bull, E.L., Parks, C.G.; Torgerson, T.R. 1997. Trees and logs important to wildlife in the interior Columbia River basin. Gen. Tech. Rep. PNW-GTR-391. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 55 p.

Bull, E.L.; Torgersen, T.R.; Blumton, A.K.; McKenzie, C.M.; Wyland, D.S. 1995. Treatment of an old-structure stand and the effect on birds, ants, and large woody debris: a case study. Gen. Tech. Rep. PNW-GTR-353. Portland, OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station. 12 p.

Bull, E.L.; Wright, A.L.; Henjum, M.G. 1989. Nesting and diet of long-eared owls in conifer forests, Oregon. Condor. 91: 908–912.

Bull, W.B. 1991. Geomorphic responses to climate change. New York: Oxford University Press. 352 p.

Bunnell, F.L. 1995. Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia: patterns and implications for conservation. Conservation Biology. 9: 636–644.

Burton, T.A. 2005. Fish and stream habitat risks from uncharacteristic wildfire: observations from 17 years of fire-related disturbances on the Boise National Forest, Idaho. Forest Ecology and Management. 211: 140–149.

Cacciapaglia, M.A.; Yung, L.; Patterson, M.E. 2012. Place mapping and the role of spatial scale in understanding landowner views of fire and fuels management. Society & Natural Resources. 25: 453–467.

Camp, A.E. 1999. Age structure and species composition changes resulting from altered disturbance regimes on the eastern slopes of the Cascades Range, Washington. Journal of Sustainable Forestry. 9: 39–67.

Camp, A.E.; Oliver, C.D.; Hessburg, P.F.; Everett, R.L. 1997. Predicting late-successional fire refugia from physiography and topography. Forest Ecology and Management. 95: 63–77.

Carey, A.B. 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. Forestry. 76: 127–136.

Carey, A.B. 2007. AIMing for healthy forests: active, intentional management for multiple values. Gen. Tech Rep. PNW-GTR-721. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 447 p.

Carpenter, S., Walker, B.; Anderies, J.M.; Ablel, N. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems. 4: 765–781.

Cayan, D.R.; Kammerdiener, S.A.; Dettinger, M.D.; Caprio, J.M.; Peterson, D.H. 2001. Changes in the onset of spring in the western United States. Bulletin of the American Meteorological Society. 82: 399–415.

Chambers, J.; Leger, E.; Goergen, E. 2009. Cold desert fire and invasive species management: resources, strategies, tactics, and response. Rangelands. 31: 14–20.

Charnley, S.; Fischer, A.P.; Jones, E.T. 2007. Integrating traditional and local ecological knowledge into forest biodiversity conservation in the Pacific Northwest. Forest Ecology and Management. 246: 14–28.

Charnley, S.; Long, J.; Lake, F.K. 2014. Collaboration in national forest management. In: Long, J.W.; Quinn-Davidson, L.; Skinner, C.N., eds. Science synthesis to promote socioecological resilience in the Sierra Nevada and southern Cascade Range. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 661–701. Chapter 9.6.

Cheng, A.; Sturtevant, V.E. 2012. A framework for assessing collaborative capacity in community-based public forest management. Environmental Management. 49: 675–689.

Choat, B.; Jansen, S.; Brodribb, T.J.; Cochard, H.; Delzon, S.; Bhaskar, R.; Bucci, S.J.; Feild, T.S.; Gleason, S.M.; Hacke, U.G.; Jacobsen, A.L.; Lens, F.; Maherali, H.; Martínez-Vilalta, J.; Mayr, S.; Mencuccini, M.; Mitchell, P.J.; Nardini, A.; Pittermann, J.; Pratt, R.B.; Sperry, J.S.; Westoby, M.; Wright, I.J.; Zanne, A.E. 2012. Global convergence in the vulnerability of forests to drought. Nature. 491: 752–755.

Churchill, D.J.; Larson, A.J.; Dahlgreen, M.C.; Franklin, J.F.; Hessburg, P.F.; Lutz, J.A. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. Forest Ecology and Management. 291: 442–457.

Climate Impacts Group [CIG]. 2009. The Washington climate change impacts assessment: evaluating Washington's future in a changing climate. Seattle, WA: Center for Science in the Earth System, Joint Institute for the Study of the Atmosphere and Oceans, University of Washington. 407 p. http://cses.washington.edu/db/pdf/wacciareport681.pdf. (17 January 2014).

Cobb, D.F.; O'Hara, K.L.; Oliver, C.D. 1993. Effect of variations in stand structure on development of mixed species stands in eastern Washington. Canadian Journal of Forest Research. 23: 545–552.

Cook, R.C.; Cook, J.G.; Vales, D.J.; Johnson, B.K.; McCorquodale, S.M.; Shipley, L.A.; Riggs, R.A.; Irwin, L.L.; Murphie, S.L.; Murphie, B.L.; Schoenecker, K.A.; Geyer, F.; Briggs Hall, P.; Spencer, R.D.; Immell, D.A.; Jackson, D.H.; Tiller, B.L.; Miller, P.J.; Schmitz, L. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs. 184: 1–45.

Converse, S.J.; White, G.C.; Farris, K.L.; Zack, S. 2006. Small mammals and forest fuel reduction: national-scale responses to fire and fire surrogates. Ecological Applications. 16: 1717–1729.

Courtney, S.; Blakesley, J.; Bigley, R.; Cody, M.; Dumbacher, J.; Fleischer, R.; Franklin, A.; Franklin, J.; Gutierrez, R.; Marzluff, J.; Sztukowski, L. 2004. Scientific evaluation of the status of the northern spotted owl. Portland, OR: Sustainable Ecosystems Institute. 258 p.

Crisafulli, C.M. 2005. Larch Mountain salamander*, Plethodon larselli* Burns. In: Jones, L.L.C.; Leonard, W.P.; Olson, D.H, eds. Amphibians of the Pacific Northwest. Seattle, WA: Seattle Audubon Society: 132–135.

Crooks, K.R.; Sanjayan, M. 2006. Connectivity conservation. Cambridge, United Kingdom: Cambridge University Press. 712 p.

Cushman, K.A.; C.A. Pearl. 2007. A conservation assessment for the Oregon spotted frog. Portland, OR: U.S. Department of Agriculture Forest Service and U.S. Department of Interior Bureau of Land Management. 46 p.

Dale, V.H.; Joyce, L.A.; McNulty, S.; Nielson, R.P.; Ayres, M.P.; Flannigan, M.D.; Hanson, P.J.; Irland, L.C.; Lugo, A.E.; Peterson, C.J.; Simerloff, D.; Swanson, F.J.; Stocks, B.J.; Wotton, B.M. 2001. Climate change and forest disturbances. Bioscience. 51: 723–734.

Dalton, M.M.; Mote, P.W.; Snover, A.K. 2013. Climate change in the Northwest: implications for our landscapes, waters, and communities. Washington, DC: Island Press. 270 p. http://cses.washington.edu/db/pubs/allpubs.shtml. (14 January 2014).

Daly, C.; Smith, J.W.; Smith, J.I.; McKane, R.B. 2007. High-resolution spatial modeling of daily weather elements for a catchment in the Oregon Cascade Mountains, United States. Journal of Applied Meteorology and Climatology. 46: 1565–1586.

Daniels, J.M. 2004. Assessing socioeconomic resiliency in Washington Counties. Gen. Tech. Rep. PNW-GTR-607. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 35 p.

D'Antonio, C.M.; Chambers, J.C.; Loh, R.; Tunison, J.T. 2009. Applying ecological concepts to the management of widespread grass invasions. In: Inderjit, R.L., ed. Management of invasive weeds. Chapter 7. Dordrecht, The Netherlands: Springer: 123–149.

Daugherty, P.J.; Fried, J.S. 2007. Jointly optimizing selection of fuel treatments and siting of forest biomass-based energy production facilities for landscape-scale fire hazard reduction. INFOR-OTTAWA. 45: 17–30.

Davidson, D.J. 2010. The applicability of the concept of resilience to social systems: some sources of optimism and nagging doubts. Society and Natural Resources. 23: 1135–1149.

Davis, E.J. 2012. Economic development and sustainable forest stewardship in the dry forest zone: a mid-term report. Portland, OR and Eugene, OR: Sustainable Northwest and University of Oregon, Ecosystem Workforce Program, Institute for a Sustainable Environment. 24 p.

Davis, E.J.; Moseley, C.; Evers, C.; Macfarland, K.; Nielsen-Pincus, M.; Pomeroy, A.; Enzer, M.J. 2012. Community-based natural resource management in Oregon: a profile of organizational capacity. Ecosystem Workforce Program Working Paper Number 39. Eugene, OR: University of Oregon. 17 p.

Davis, E.J.; Moseley, C.; Nielsen-Pincus, M. 2010. The state of dry zone forest and its communities. Eugene, OR and Portland, OR: University of Oregon, Ecosystem Workforce Program, Institute for a Sustainable Environment. 94 p.

Daw, S.K.; DeStefano, S. 2001. Forest characteristics of northern goshawk nest stands and post-fledging areas in Oregon. Journal of Wildlife Management. 65: 59–65.

Donoghue, E.M.; Thompson, S.A.; Bliss, J.C. 2010. Tribal-federal collaboration in resource management. Journal of Ecological Anthropology. 14: 22–38.

Dramm, J.R. 1999. Small-diameter utilization issues and opportunities. In: Conference proceedings, wood technology clinic & show. Portland, OR: Miller Freeman: 30–38.

Dugger, K.M.; Anthony, R.G.; Andrews, L.S. 2011. Transient dynamics of invasive competition: barred owls, spotted owls, habitat, and the demons of competition present. Ecological Applications. 21: 2459–2468.

Dunham, J.B.; Rosenberger, A.E.; Luce, C.H.; Rieman, B.E. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. Ecosystems. 10: 335–346.

Dunham J.B.; Young M.K.; Gresswell R.E.; Rieman B.E. 2003. Effects of fires on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. Forest Ecology and Management. 178: 183–196.

Eastin, I.; Ganguly, I.; Sasatani, D.; Mason, L.; Lipple, B. 2009. Economic contribution of the forestry and wood processing sectors in the State of Washington, executive summary. Working paper 116. Seattle, WA: Center for International Trade in Forest Products. 2 p.

Ebersole, J.L.; Liss, W.J.; Frissell, C.A. 1997. Restoration of stream habitats in the western United States: restoration as reexpression of habitat capacity. Environmental Management. 21: 1–14.

Englin, J.; Loomis, J.; Gonzalez-Caban, A. 2001. The dynamic path of recreational values following a forest fire: a comparative analysis of states in the Intermountain West. Canadian Journal of Forestry Research. 31: 1837–1844.

Everett R.L.; Hessburg, P.F.; Jensen, M.; Bormann, B. 1994. Volume I: executive summary. Eastside forest health assessment. Gen. Tech. Rep. PNW-GTR-317. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 61 p.

Everett, R.L.; Schellhaas, R.; Keenum, D.; Spurbeck, D.; Ohlson, P. 2000. Fire in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. Forest Ecology and Management. 129: 207–225.

Everett, R.; Schellhaas, R.; Ohlson, P.; Spurbeck, D.; Keenum, D. 2003. Continuity in fire disturbance between riparian and adjacent sideslope Douglas-fir forests. Forest Ecology and Management. 175: 31–47.

Everett, R.; Schellhaas, D.; Spurbeck, D.; Ohlson, P.; Keenum, D.; Anderson, T. 1997. Structure of northern spotted owl nest stands and their historical conditions on the eastern slope of the Pacific Northwest Cascades, USA. Forest Ecology and Management. 94: 1–14.

Fetherston, K.L.; Naiman, R.J.; Bilby, R.E. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Geomorphology. 13: 133–144.

Fettig, C.J. 2012. Forest health and bark beetles. In: North, M., ed. Managing Sierra Nevada forests. Gen. Tech. Rep. PSW-GTR-237. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 13–22. Chapter 2.

Fettig, C.J.; Klepzig, K.D.; Billings, R.F.; Munson, A.S.; Nebeker, T.E.; Negrón, J.F.; Nowak, J.T. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle outbreaks in coniferous forests of the western and southern United States. Forest Ecology and Management. 238: 24–53.

Fettig, C.J.; Reid, M.L.; Bentz, B.J.; Sevanto, S.; Spittlehouse, D.L.; Wang, T. 2013. Changing climates, changing forests: a western North American perspective. Journal of Forestry. 111: 214–228.

Filip, G.M. 1990. Effect of tree harvesting on Armillaria root disease in an old-growth mixed-conifer stand in northeastern Oregon. Northwest Environmental Journal. 6: 412–413.

Filip, G.M.; Goheen, D.J. 1982. Tree mortality caused by a root pathogen complex on the Deschutes National Forest, Oregon. Plant Disease. 66: 240–243.

Filip, G.M.; Goheen, D.J. 1984. Root diseases cause severe mortality in white and grand fir stands of the Pacific Northwest. Forest Science. 30: 138–142.

Filip, G.M., Maffei, H.M.; Chadwick, K.L.; Max, T.A. 2010. Armillaria root disease-caused tree mortality following silvicultural treatments (shelterwood or group selection) in an Oregon mixed-conifer forest: insights from a 10-year case study. Western Journal of Applied Forestry. 25: 136–143.

Filip, G.M.; Schmitt, C.L. 1979. Susceptibility of native conifers to laminated root rot east of the Cascade Range in Oregon and Washington. Forest Science. 25: 261–265.

Filip, G.M.; Schmitt, C.L.; Hosman, K.P. 1992. Effects of harvesting season and stump size on incidence of annosum root disease of true fir. Western Journal of Applied Forestry. 7: 54–57.

Finney, M.A.; Seli, R.C.; McHugh, C.W.; Ager, A.A.; Bahro, B.; Agee, J.K. 2007. Simulation of long-term landscape-level fuel treatment effects on large wildfires. International Journal of Wildland Fire. 16: 712–727.

Fischer, W.C.; Bradley, A.F. 1987. Fire ecology of western Montana forest habitat types. Gen. Tech. Rep. INT-GTR-223. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 95 p.

Folke, C. 2006. Resilience: the emergence of a perspective for socio-ecological systems analyses. Global Environmental Change. 16: 253–267.

Forsman, E.D. 1983. Methods and materials for locating and studying spotted owls. Gen. Tech. Rep. PNW-GTR-162. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 8 p.

Forsman, E.D.; Anthony, R.; Dugger, K.; Glenn, E.; Franklin, A.; White, G.; Schwarz, C.; Burnham, K.; Anderson, D.; Nichols, J.; Hines, J.; Lint, J.; Davis, R.; Ackers, S.; Andrews, L.; Biswell, B.; Carlson, P.; Diller, L.; Gremel, S.; Herter, D.; Higley, J.; Horn, R.; Reid, J.; Rockweit, J.; Schaberl, J.; Snetsinger, T.; Sovern, S. 2011. Population demography of northern spotted owls. Studies in Avian Biology No. 40. Los Angeles, CA: University of California Press. 120 p.

Forsman, E.D.; Anthony, R.G.; Meslow, E.C.; Zabel, C.J. 2004. Diets and foraging behavior of northern spotted owls in Oregon. Journal of Raptor Research. 38: 214–230.

Forsman, E.D.; Otto, I.A.; Sovern, S.G.; Taylor, M.; Hays, D.W.; Allen, H.; Roberts, S.L.; Seaman, D.E. 2001. Spatial and temporal variation in diets of Spotted Owls in Washington. Journal of Raptor Research. 35: 141–150.

Franceschi, V.R.; Krokene, P.; Christiansen, E.; Krekling, T. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytologist. 167: 353–376.

Franklin, J.F.; Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-GTR-008. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 427 p.

Franklin, J.F.; Dyrness, C.T. 1988. Natural vegetation of Oregon and Washington. Corvallis, OR: Oregon State University Press. 464 p.

Franklin, J.F.; Johnson, K.N. 2012. A restoration framework for federal forests in the Pacific Northwest. Journal of Forestry. 110: 429–439.

Franklin, J.F.; Johnson, K.N.; Churchill, D.; Hagmann, K.; Johnson, D.; Johnston, J. 2013. Restoration of dry forests in eastern Oregon: a field guide. Portland, OR: The Nature Conservancy. 202 p.

Franklin, J.F.; Lindenmayer, D.; MacMahon, J.A.; McKee, A.; Magnuson, J.; Perry, D.A.; Waide, R.; Foster, D. 2000. Threads of continuity: there are immense differences between even-aged silvicultural disturbances (especially clearcutting) and natural disturbances, such as windthrow, wildfire, and even volcanic eruptions. Conservation in Practice. 1: 8–17.

Frissell, C.A.; Liss, W.J.; Gresswell, R.E.; Nawa, R.K.; Ebersole, J.L. 1997. A resource in crisis: changing the measure of salmon management. In: Stouder, D.J.; Bisson, R.A.; Naiman, R.J., eds. Pacific salmon and their ecosystems: status and future options. New York: Chapman & Hall: 411–444.

Gaines, W.L.; Harrod, R.J.; Dickinson, J.D.; Lyons, A.L.; Halupka, K. 2010. Integration of northern spotted owl habitat and fuels treatments in the eastern Cascades, Washington, USA. Forest Ecology and Management. 260: 2045–2052.

Gaines, W.L.; Singleton, P.H.; Gold, A.L. 2000. Conservation of rare carnivores in the North Cascades Ecosystem, western North America. Natural Areas Journal. 20: 366-375.

Gaines, W.L.; Singleton, P.H.; Ross, R.C. 2003. Assessing the cumulative effects of linear recreation routes on wildlife habitats on the Okanogan and Wenatchee National Forests. Gen. Tech. Rep. PNW-GTR-586. Portland OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station. 79 p.

Gaines, W.L.; Wales, B.C.; Suring, L.H.; Begley, J.S.; Mellen-McLean, K.; Mohoric, S. [In press]. Terrestrial species viability assessments for the national forests in northeastern Washington. Gen. Tech. Rep. Portland OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station.

Galbraith, W.A.; Anderson, E.W. 1991. Grazing history of the Northwest. Rangelands. 13: 213–218.

Garza, E.S. 1995. Fire history and fire regimes of East Humbug and Scorpion Creeks, and their relation to the range of *Pinus lambertiana* Dougl. Portland, OR: Oregon State University. 75 p. M.F. thesis.

Gedalof, Z.; Peterson, D.L.; Mantua, N.J. 2005. Atmospheric, climatic, and ecological controls on extreme wildfire years in the northwestern United States. Ecological Applications. 15: 154–174.

Goheen, D.J.; Filip, G.M. 1980. Root pathogen complexes in Pacific Northwest forests. Plant Disease. 64: 793–794.

Goheen, E.M.; Willhite, E.A. 2006. Field guide to common diseases and insect pests of Oregon and Washington conifers. R6-NR-FID-PR-01-06. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 327 p.

Graf, M.; Reid, M.L.; Aukema, B.H.; Lindgren, B.S. 2012. Association of tree diameter with body size and lipid content of mountain pine beetles. The Canadian Entomologist. 144: 467–477.

Grant, G.; Tague, C.; Allen, C.D. 2013. Watering the forest for the trees: an emerging priority for managing water in forest landscapes. Frontiers in Ecology and the Environment. 11: 314–321.

Gregory, S.V.; Swanson, F.J.; McKee, W.A.; Cummins, K.W. 1991. An ecosystem perspective of riparian zones: focus on links between land and water. BioScience. 41: 540–551.

Greenwald, D.N.; Crocker-Bedford, D.C.; Broberg, L.; Suckling, K.F.; Tibbitts, T. 2005. A review of northern goshawk habitat selection in the home range and implications for forest management in the western United States. Wildlife Society Bulletin. 33: 120–128.

Gresswell, R.E. 1999. Fire and aquatic ecosystems in forested biomes of North America. Transactions of the American Fisheries Society.128: 193–221.

Gresswell, R.E.; Liss, W.J.; Larson, G.L. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences. 51: 298–309.

Gude, P.H.; Rasker, R.; van den Noort, J. 2008. Potential for future development on fire-prone lands. Journal of Forestry. 106: 198–205.

Gunderson, L.H. 2000. Ecological resilience—in theory and application. Annual Review of Ecological Systems. 31: 425–439.

Gutierrez, R.J.; Cody, M.; Courtney, S.; Franklin, A.B. 2007. The invasion of barred owls and its potential effect on the spotted owl: a conservation conundrum. Biological Invasions. 9: 181–196.

Hadfield, J.S.; Goheen, D.G.; Filip, G.M.; Schmitt, C.L.; Harvey, R.D. 1986. Root diseases in Oregon and Washington conifers. R6-FPM-250-86. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Forest Pest Management. 27 p.

Hagar, J.C. 2007. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: A review. Forest Ecology and Management. 246: 108–122.

Hagmann, R.K.; Franklin, J.F.; Johnson, K.N. 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. Forest Ecology and Management. 304: 492–504.

Hall, T.E.; Heaton, H.; Kruger, L.E. 2009. Outdoor recreation in the Pacific Northwest and Alaska: trends in activity participation. Gen. Tech. Rep. PNW-GTR-778. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 108 p.

Halofsky, J.E.; Donato, D.C.; Hibbs, D.E.; Campbell, J.L.; Donaghy Cannon, M.; Fontaine, J.B.; Thompson, J.R.; Anthony, R.G.; Bormann, B.T.; Kayes, L.J.; Law, B.E.; Peterson, D.L.; Spies, T.A. 2011. Mixed-severity fire regimes: lessons and hypotheses from the Klamath-Siskiyou ecoregion. Ecosphere. 2(4): art40. doi: 10.1890/ES10-00184.1.

Hamlet, A.F.; Mote, P.W.; Clark, M.P.; Lettenmaier, D.P. 2005. Effects of temperature and precipitation variability on snowpack trends in the western United States. Journal of Climate. 18: 4545–4561.

Hamlet, A.F.; Mote, P.W.; Clark, M.P.; Lettenmaier, D.P. 2007. Twentieth-century trends in runoff, evapotranspiration, and soil moisture in the western United States. Journal of Climate. 20: 1468–1486.

Hann, W.J.; Jones, J.L.; Karl, M.G.; Hessburg, P.F.; Keane, R.E.; Long, D.G.; Menakis, J.P.; McNicoll, C.H.; Leonard, S.G.; Gravenmier, R.A.; Smith, B.G. 1997. An assessment of landscape dynamics of the basin. In: Quigley, T.M.; Arbelbide, S.J., eds. An assessment of ecosystem components in the Interior Columbia Basin and portions of the Klamath and Great Basins. Gen. Tech. Rep. PNW-GTR-405. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 337–1055.

Hansen, A.J.; Knight, R.; Marzluff, J.; Powell, S.; Brown, K.; Hernandez, P.; Jones, K. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, research needs. Ecological Applications. 15: 1893–1905.

Hansen, A.J.; Phillips, L.; Flather, C.H.; Robison-Cox, J. 2011. Carrying capacity for species richness as a context for conservation: a case study of North American breeding birds. Global Ecology and Biogeography. 20: 817–831.

Hansen, A.J.; Phillips, L.; Loehle, C.; Waring, R.H. 2006. Species energy theory and regional scale bird diversity: implications for conservation. Technical Report. Bozeman, MT: Montana State University, Landscape Biodiversity Lab.

Harrington, M.G. 1991. Fire management in interior Douglas-fir forests. In: Baumgartner, D.M.; Lotan, J.E., eds. Interior Douglas-fir: the species and its management. Proceedings of a symposium. Pullman, WA: Washington State University Cooperative Extension: 209–214.

Harris, C.; McLaughlin, W.; Brown, G.; Becker, D.R. 2000. Rural communities in the Inland Northwest: An assessment of small rural communities in the Interior and Upper Columbia River Basins. Gen. Tech. Rep. PNW-GTR-477. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station and U.S. Department of the Interior, Bureau of Land Management. 120 p.

Harris, J.A.; Hobbs, R.J.; Higgs, E.H.; Aronson, J. 2006. Ecological restoration and global climate change. Restoration Ecology. 14: 170–176.

Harrod, R.J.; McRae, B.H.; Hartl, W.E. 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. Forest Ecology and Management. 114: 433–446.

Harvey, A.E.; Geist, J.M.; McDonald, G.I.; Jurgensen, M.F.; Cochran, P.H.; Zabowski, D.; Meurisse, R.T. 1994. Biotic and abiotic processes in eastside ecosystems: the effects of management on soil properties, processes, and productivity. In: Hessburg, P.F., ed., Eastside Forest Ecosystem Health Assessment. Gen. Tech. Rep. PNW-GTR-323. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 71 p.

Haugo, R.D.; Hall, S.A.; Gray, E.M.; Gonzalez, P.; Bakker, J.D. 2010. Influences of climate, fire, grazing, and logging on woody species composition along an elevation gradient in the eastern Cascades, Washington. Forest Ecology and Management. 260: 2204–2213.

Haugo, R.D.; Halpern, C.B. 2007. Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. Canadian Journal of Botany. 85: 285–298.

Hawksworth, F.G. 1958. Rate of spread and intensification of dwarf mistletoe in young lodgepole pine stands. Journal of Forestry. 56: 404–407.

Hawksworth, F.G. 1960. Distribution of ponderosa pine dwarf mistletoe in the vicinity of an Arizona volcano. Ecology. 41: 799–800.

Hawksworth, F.G.; Nicholls, T.H.; Merrill, L.M. 1987. Long-distance dispersal of lodgepole pine dwarf mistletoe. In: Troendle, C.A.; Kaufmann, M.R.; Hamre, R.H.; Winokur, R.P., tech. coords. Management of subalpine forests: building on 50 years of research. Gen. Tech. Rep. RM-GTR-149. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 220–226.

Hayes, J.L.; Daterman, G.E. 2001. Bark beetles (Scolytidae) in eastern Oregon and Washington. Northwest Science. 75: 21–30.

Hayes, J.L.; Ragenovich, I. 2001. Non-native invasive forest insects of eastern Oregon and Washington. Northwest Science. 75: 77–84.

Healey, M.C.; Prince, A. 1995. Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype. In: Nielsen, J., ed. Evolution and the aquatic ecosystem: defining unique units in population conservation. Bethesda, MD: American Fisheries Society: 176–184.

Hedrick, D.W.; Young, J.; McArthur, J.; Keniston, R. 1968. Effects of forest and grazing practices on mixed coniferous forests of northeastern Oregon. Technical Bulletin 103. Corvallis, OR: Oregon State University Agricultural Experiment Station. 24 p.

Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research. 3: 329–382

Heller, N.E.; Zavaleta, E.S. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation. 142: 14–32.

Henderson, J.A.; Lesher, R.D.; Peter, D.H.; Ringo, C.D. 2011. A landscape model for predicting potential natural vegetation of the Olympic Peninsula USA using boundary equations and newly developed environmental variables. Gen. Tech. Rep. PNW-GTR-841. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 35 p.

Hessburg, P.F.; Agee, J.K.; Franklin, J.F. 2005. Dry mixed-conifer forests and wildland fires of the Inland Northwest: contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management. 211: 117–139.

Hessburg, P.F.; James, K.M.; Salter, R.B. 2007. Re-examining fire severity relations in pre-management era mixed-conifer forests: inferences from landscape patterns of forest structure. Landscape Ecology. 22: 5–24.

Hessburg, P.F.; Mitchell, R.G.; Filip, G.M. 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. In: Hessburg, P.F., ed. Eastside Forest Ecosystem Health Assessment. Gen. Tech. Rep. PNW-GTR-327. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 72 p.

Hessburg, P.F.; Reynolds, K.M.; Salter, R.B.; Dickinson, J.D.; Gaines, W.L.; Harrod, R.J. 2013. Landscape evaluation for restoration planning on the Okanogan-Wenatchee National Forest, USA. Sustainability. 5: 805–840.

Hessburg, P.F.; Reynolds, K.M.; Salter, R.B.; Richmond, M.B. 2004. Using a decision support system to estimate departures of present forest landscape patterns from historical conditions: an example from the Inland Northwest Region of the United States. In: Perera, A.H.; Buse, L.J.; Weber, M.G., eds. Emulating natural forest landscape disturbances: concepts and applications. New York: Columbia University Press: 158–175.

Hessburg P.F.; Salter, R.B.; Richmond, M.B.; Smith, B.G. 2000a. Ecological subregions of the Interior Columbia Basin, USA. Applied Vegetation Management. 3: 163–180.

Hessburg, P.F.; Smith, B.G.; Kreiter, S.G.; Miller, C.A.; Salter, R.B.; McNicholl, C.H.; Hann, W.J. 1999a. Historical and current forest and range landscapes in the Interior Columbia River Basin and portions of the Klamath and Great Basins. Part 1. Linking vegetation patterns and landscape vulnerability to potential insect and pathogen disturbances. Gen. Tech. Rep. PNW-GTR-458. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 357 p.

Hessburg, P.F.; Smith, B.G.; Miller, C.A.; Kreiter, S.G.; Salter, R.B. 1999b. Modeling change in potential landscape vulnerability to forest insect and pathogen disturbances: methods for forested subwatersheds sampled in the mid-scale Interior Columbia River Basin assessment. Gen, Tech. Rep. PNW-GTR-454. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 56 p.

Hessburg, P.F.; Smith, B.G.; Salter, R.B. 1999c. Detecting change in forest spatial patterns from reference conditions. Ecological Applications. 9: 1232–1252.

Hessburg, P.F.; Smith, B.G.; Salter, R.B. 1999d. Using natural variation estimates to detect ecologically important change in forest spatial patterns: a case study of the eastern Washington Cascades. Res. Pap. PNW-RP-514. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 65 p.

Hessburg, P.F.; Smith, B.G.; Salter, R.B.; Ottmar, R.D.; Alvarado, E. 2000b. Recent changes (1930s–1990s) in spatial patterns of interior northwest forests, USA. Forest Ecology and Management. 136: 53–83.

Hesseln, H.; Loomis, J.B.; Gonzalez-Caban, A. 2004. Comparing the economic effects of fire on hiking demand in Montana and Colorado. Journal of Forest Economics. 10: 21–35.

Hesseln, H.; Loomis, J.B.; Gonzalez-Caban, A.; Alexander, S. 2003. Wildfire effects on hiking and biking demand in New Mexico: a travel cost study. Journal of Environmental Management. 69: 359–368.

Hessl, A.E.; McKenzie, D.; Schellhaas, R. 2004. Fire and climatic variability in the inland Pacific Northwest. Ecological Applications. 14: 425–442.

Heyerdahl, E.K.; Brubaker, L.B.; Agee, J.K. 2001. Spatial controls of historical fire regimes: a multi-scale example from the Interior West, USA. Ecology. 82: 660–678.

Heyerdahl, E.K.; Falk, D.A.; Loehman, R.A. 2013. Data archived with the International Multiproxy Paleofire Database, IGBP PAGES/World Data Center for Paleoclimatology. Boulder, CO: NOAA/NCDC Paleoclimatology Program. http://www.ncdc.noaa.gov/paleo/impd/paleofire.html. (4 February 2014).

Heyerdahl, E.K.; McKenzie, D.; Daniels, L.D.; Hessl, A.E.; Littell, J.S.; Mantua, N.J. 2008. Climate drivers of regionally synchronous fires in the inland Northwest (1651–1900). International Journal of Wildland Fire. 17: 40–49.

Hicke, J.A.; Jenkins, J.C. 2008. Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the western United States. Forest Ecology and Management. 255: 1536–1547.

Hicke, J.A.; Johnson, M.C.; Hayes, J.L.; Preisler, H.K. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management. 271: 81−90.

Hilty, J.A.; Lidicker, W.Z.; Merenlender, A.M. 2006. Corridor ecology: the science and practice of linking landscapes for biodiversity and conservation. Washington, DC: Island Press. 323 p.

Hjerpe, E.; Abrams, J.; Becker, D.R. 2009. Socioeconomic barriers and the role of biomass utilization in southwestern ponderosa pine restoration. Ecological Restoration. 27: 169–177.

Hobbs, R.J.; Hallett, L.M.; Ehrlich, P.R.; Mooney, H.A. 2011. Intervention ecology: applying ecological science in the twenty-first century. BioScience. 61: 442–450.

Hollenbeck, J.P.; Bate, L.J.; Saab, V.A.; Lehmkuhl, J.F. 2013. Snag distributions in relation to human access in ponderosa pine forests. Wildlife Society Bulletin. 37: 256–266.

Huff, M.H.; Ottmar, R.D.; Lehmkuhl, J.F.; Hessburg, P.F.; Everett, R.L.; Alvarado, E.; Vihanek, R.H. 1995. Historical and current forest landscapes of eastern Oregon and Washington. Part II: potential fire behavior and smoke production. In: Hessburg, P.F., ed., Eastside Forest Ecosystem Health Assessment. Gen. Tech. Rep. PNW-GTR-355. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 43 p.

Intergovernmental Panel on Climate Change [IPCC]. 2013. Summary for policymakers. In: Climate change 2013: the physical science basis. Stocker, D.F.; Qin, D.; Plattner, G.-K.; Tignor, M.; Allen, S.K.; Boschung, J.; Nauels, A.; Xia, Y.; Bex, V.; Midgley, P.M., eds. Working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom, and New York: Cambridge University Press. 27 p.

Intertribal Timber Council [ITC]. 2013. Fulfilling the promise of the Tribal Forest Protection Act of 2004, executive summary. Portland, OR: Intertribal Timber Council.

Intertribal Timber Council and Resource Innovations. 2006. Tribal wildfire resource guide. Eugene, OR: University of Oregon, Resource Innovations. 146 p.

Isaak, D.J.; Luce, C.H.; Rieman, B.E.; Nagel, D.E.; Peterson, E.E.; Horan, D.L.; Parkes, S.; Chandler, G. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. Ecological Applications. 20: 1350–1371.

Jain, T.B.; Battaglia, M.A.; Han, H.; Graham, R.T.; Keyes, C.R.; Fried, J.S.; Sandquist, J.E. 2012. A comprehensive guide to fuel management practices for dry mixed-conifer forests in the northwestern United States. Gen. Tech. Rep. RMRS-GTR-292. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 344 p.

Jain, S.; Lall, U. 2001. Floods in a changing climate: Does the past represent the future? Water Resources Research. 37: 3193–3206.

Jenkins, M.J.; Runyon, J.B.; Fettig, C.J.; Page, W.G.; Bentz, B.J. 2014. Interactions among the mountain pine beetle, fires, and fuels. Forest Science. 60: 489–501.

Johnson, C. 2007. Rangeland exclosures of northeastern Oregon: stories they tell (1936–2004). Gen. Tech. Rep. PNW-GTR-724. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 33 p.

Johnson, C.G., Jr. 2004. Alpine and subalpine vegetation of the Wallowa, Seven Devils, and Blue Mountains. R6-NR-ECOL-TP-03-04. Portland OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 612 p.

Johnson, C.G., Jr.; Clasunitzer, R.R. 1992. Plant associations of the Blue and Ochoco Mountains. R6-ERW-TP-036-92. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 208 p.

Johnson, C.G.; Clausnitzer, R.R.; Mehringer, P.J.; Oliver, C.D. 1994. Biotic and abiotic processes in eastside ecosystems: the effects of management on plant and community ecology, and on stand and landscape vegetation dynamics. Gen. Tech. Rep. PNW-GTR-322. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 66 p.

Johnson, C.G., Jr.; Simon, S.A. 1987. Plant associations of the Wallowa-Snake Province. R6-ECOL-TP-255A-86. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 400 p. plus appendixes.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology. 61: 65–71.

Johnson, D.J.; O'Neil, T.A. 2001. Wildlife-habitat relationships in Oregon and Washington. Corvallis, OR: Oregon State University Press. 736 p.

Jolly, W.M.; Parsons, R.A.; Hadlow, A.M.; Cohn, G.M.; McAllister, S.S.; Popp, J.B.; Hubbard, R.M.; Negrón, J.F. 2012. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. Forest Ecology and Management. 269: 52–59.

Kauffman, J.B. 1988. The status of riparian habitats in Pacific Northwest forests. In: Raedeke, K.J., ed. Streamside management: riparian wildlife and forestry interactions. College of Forest Resources Institute of Forest Resources Contribution 59. Seattle, WA: University of Washington: 45–55.

Keane, R.E.; Hessburg, P.F.; Landres, P.B.; Swanson, F.J. 2009. The use of historical range and variability (HRV) in landscape management. Forest Ecology and Management. 258: 1025–1037.

Keegan III, C.E.; Morgan, T.A.; Gebert, K.M.; Brandt, J.P.; Blatner, K.A.; Spoelma, T.P. 2006. Timber-processing capacity and capabilities in the western United States. Journal of Forestry. 104: 262–268.

Kellogg, L.K.B.; McKenzie, D.; Peterson, D.L.; Hessl, A.E. 2008. Spatial models for inferring topographic controls on historical low-severity fire in the eastern Cascade Range of Washington, USA. Landscape Ecology. 23: 227–240.

Kemp, W.P.; Everson, D.O.; Wellington, W.G. 1985. Regional climate patterns and western spruce budworm outbreaks. Tech. Bull. 1693. Washington, DC: U.S. Department of Agriculture, Forest Service, Cooperative State Research Service. 31 p.

Kennedy, P.L.; Fontaine, J.B. 2009. Synthesis of knowledge on the effects of fire and fire surrogates on wildlife in U.S. dry forests. Special Report 1096. Corvallis, OR: Oregon State University, Agricultural Experiment Station. 132 p.

Kiffney, P.M.; Greene C.M.; Hall J.E.; Davies J.R. 2006. Tributary streams create spatial discontinuities in habitat, biological productivity and diversity in mainstem rivers. Canadian Journal of Fisheries and Aquatic Sciences. 63: 2518–2530.

Kline, J.D. 2004. Issues in evaluating the costs and benefits of fuel treatments to reduce wildfire in the nation's forests. Res. Note PNW-RN-542. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 46 p.

Kline, J.D.; Mazzotta, M.J. 2012. Evaluating tradeoffs among ecosystem services in the management of public lands. Gen. Tech. Rep. PNW-GTR-865. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 48 p.

Klutsch, J.G.; Battaglia, M.A.; West, D.R.; Costello, S.L.; Negrón, J.F. 2011. Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. Western Journal of Applied Forestry. 26: 101−109.

Koonce, A.L.; Roth, L.F. 1980. The effects of prescribed burning on dwarf mistletoe in ponderosa pine. In: Proceedings, sixth conference on fire and forest meteorology.. Washington, DC: Society of American Foresters: 197−203.

Kotliar, N.B.; Hejl, S.J.; Hutto, R.L.; Saab, V.A.; Melcher, C.P.; McFadzen, M.E. 2002. Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. In: George, T.L.; Dobkin, D.S., eds. Effects of habitat fragmentation on birds in western landscapes: contrasts with paradigms from the eastern United States. Studies in Avian Biology No. 25. Camarillo, CA: Cooper Ornithological Society: 49–64.

Kruse, C.G.; Hubert, W.A.; Rahel, F.J. 2001. An assessment of headwater isolation as a conservation strategy for cutthroat trout in the Absaroka Mountains of Wyoming. Northwest Science. 75: 1–11.

Langston, N. 1995. Forest dreams, forest nightmares: the paradox of old growth in the Inland Northwest. Seattle, WA: University of Washington Press. 368 p.

Larson, A.J.; Churchill, D.C. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management. 267: 74–92.

Latta, G.; Temesgen, H.; Adams, D.; Barrett, T. 2010. Analysis of potential impacts of climate change on forests of the United States Pacific Northwest. Forest Ecology and Management. 259: 720–729.

Lee, D.; Sedell, J.; Rieman, B.; Thurow, R.; Williams, J. 1997. Broad-scale assessment of aquatic species and habitats. In: Quigley, T.M.; Arbelbide, S.J., eds. An assessment of ecosystem components in the Interior Columbia Basin and portions of the Klamath and Great Basins, vol. 3. Gen. Tech. Rep. PNW-GTR-405. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 1057–1430.

Lehmkuhl, J.F. 2005. Wildlife adaptations and management in eastside interior forests with mixed-severity fire regimes. Proceedings of the symposium on mixed-severity fire regimes: ecology and management, Spokane, Washington, November 17–19, 2004. Misc. Pub. 3. Davis, CA: The Association for Fire Ecology: 177–186.

Lehmkuhl, J.F.; Burger, E.D.; Drew, E.K.; Lindsey, J.P.; Haggard, M.; Woodruff, K.Z. 2007a. Breeding birds in riparian and upland dry forests of the Cascade Range. Journal of Wildlife Management. 71: 2632–2643.

Lehmkuhl, J.F.; Hessburg; P.F.; Everett; R.L.; Huff; M.H.; Ottmar, R.D. 1994. Historical and current vegetation pattern and associated changes in insect and disease hazard conditions in eastern Oregon and Washington. In: Hessburg, P.F., ed., Eastside Forest Ecosystem Health Assessment: Volume III: Assessment. Gen. Tech. Rep. PNW-GTR-328. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 88 p.

Lehmkuhl, J.F.; Kennedy, M.; Ford, E.D.; Singleton, P.H.; Gaines, W.L.; Lind, R.L. 2007b. Seeing the forest for the fuel: integrating ecological values and fuels management. Forest Ecology and Management. 246: 73–80.

Lehmkuhl, J.F.; Kistler, K.D.; Begley, J.S. 2006a. Bushy-tailed woodrat abundance in dry forests of eastern Washington. Journal of Mammalogy. 87: 371–379.

Lehmkuhl J.F.; Kistler, K.D.; Begley, J.S.; Boulanger, J. 2006b. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications. 16: 584–600.

Lehmkuhl, J.F.; Lyons, A.L.; Bracken, E.; Leingang, J.; Gaines, W.L.; Dodson, E.K.; Singleton, P.H. 2013. Forage composition, productivity, and utilization in the eastern Washington Cascade Range. Northwest Science. 87: 267–291.

Lehmkuhl, J.F.; Peffer, R.D.; O'Connell, M.A. 2008. Riparian and upland small mammals on the east slope of the Cascade Range, Washington. Northwest Science. 82: 94–107.

Lewis, J.C.; Stinson, D.W. 1998. Washington State status report for the fisher. Olympia, WA: Washington Department of Fish and Wildlife. 64 p.

Lillybridge, T.R.; Kovalchik, B.L.; Williams, C.K.; Smith, B.G. 1995. Field guide for forested plant associations of the Wenatchee National Forest. Gen. Tech. Rep. PNW-GTR-359. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station and Pacific Northwest Region, Wenatchee National Forest. 352 p.

Lindenmayer, D.; Burton, P.J.; Franklin, J.F. 2008. Salvage logging and its ecological consequences. Washington, DC: Island Press. 248 p.

Littell, J.S.; McKenzie, D.; Peterson, D.L.; Westerling, A.L. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecological Applications. 19: 1003–1021.

Littell, J.S.; O'Neil, E.E.; McKenzie, D.; Hicke, J.A.; Lutz, J.A.; Norheim, R.A.; Elsner, M.M. 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. Climatic Change. 102: 129–158

Loehle, C. 2011. Criteria for assessing climate change impacts on ecosystems. Ecology and Evolution 1: 63–72.

Long, R.A.; Rachlow, J.L.; Kie, J.G.; Vavra, M. 2008. Fuels reduction in a western coniferous forest: effects on quantity and quality of forage for elk. Rangeland Ecology and Management. 61: 302–313.

Loomis, J.; Gonzalez-Caban, A.; Englin, J. 2001. Testing for differential effects of forest fires on hiking and mountain biking demand and benefits. Journal of Agricultural and Resource Economics. 26: 508–522.

Lotan, J.E.; Alexander, M.E.; Arno, S.F.; French, R.E.; Langdon, O.G.; Loomis, R.M.; Morum, R.A.; Rothermel, R.C.; Schmidt, W.C.; van Wagtendonk, J. 1981. Effects of fire on flora: a state of knowledge review. Gen. Tech. Rep. WO-GTR-16. Washington, DC: U.S. Department of Agriculture, Forest Service. 71 p.

Luce, C.H.; Abatzoglou, J.T.; Holden, Z.A. 2013. The missing mountain water: slower westerlies decrease orographic enhancement in the Pacific Northwest USA. Science 342: 1360–1364.

Luce, C.; Morgan, P.; Dwire, K.; Isaak, D.; Holden, Z.; Rieman, B. 2012. Climate change, forests, fire, water, and fish: Building resilient landscapes, streams, and managers. Gen. Tech. Rep. RMRS-GTR-290. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 207 p.

Luce, C.H.; Rieman, B.E.; Dunham, J.B.; Clayton, J.L.; King, J.G.; Black, T.A. 2001. Incorporating aquatic ecology into decisions on prioritization of road decommissioning. Water Resources Impact. May: 8–14.

Luce, C.; Staab, B.; Kramer, M.; Wenger, S.; Isaak, D.; McConnell, C. 2014. Sensitivity of summer stream temperatures to climate variability in the Pacific Northwest. Water Resources Research 50, doi:10.1002/2013WR014329.

Ludwig, D.; Hilborn, R.; Walters, C. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Science. 260: 35–36.

Lyon, L.; Christensen, A.G. 2002. Elk and land management. In: Toweill, D.E.; Thomas, J.W., eds., North American Elk: Ecology and Management. Washington, DC: Wildlife Management Institute: 531–556.

Lyons, A.L.; Gaines, W.L.; Lehmkuhl, J.F.; Harrod, R.J. 2008. Short-term effects of fire and fire surrogate treatments on foraging tree selection by cavity-nesting birds in dry forests of central Washington. Forest Ecology and Management. 255: 3201–3211.

Lyons, A.L.; Gaines, W.L.; Servheen, C. 2003. Black bear resource selection in the northeast Cascades, Washington. Biological Conservation. 113: 55–62.

Magis, K. 2010. Community resilience: an indicator of social sustainability. Society and Natural Resources. 23: 401–416.

Malamud, B.D.; Millington, J.D.A.; Perry, G.L.W. 2005. Characterizing wildfire regimes in the United States. Proceedings of the National Academy of Sciences of the United States of America. 102: 4694–4699.

Malamud, B.D.; Morein, G.; Turcotte, D.L. 1998. Forest fires: an example of self-organized critical behavior. Science. 281: 1840–1842.

Mantua, N.J.; Hare, S.R. 2002. The Pacific decadal oscillation. Journal of Oceanography. 58: 35–44.

Mantua, N.J.; Hare, S.R.; Zhang, Y.; Wallace, J.M.; Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society. 78: 1069–1079.

Marcot, B.G.; Mellen, K.; Livingston, S.A.; Ogden, C. 2002. The DecAID advisory model: wildlife component. In: Shea, P.J.; Laudenslayer Jr., W.F.; Valentine, B.; Weatherspoon, C.P., eds. Proceedings of the symposium on the ecology and management of dead wood in western forests. Gen. Tech. Rep. PSW-GTR-181. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 561–590.

Margerum, R.D. 2011. Beyond consensus: improving collaborative planning and management. Cambridge, MA: The MIT Press. 416 p.

Marsh, R.; Helliwell, R.; Rodgers, J. 1987. Plant association guide for the commercial forest of the Warm Springs Indian reservation. Warm Springs, OR: Warm Springs Indian Reservation. 142 p.

Martin, K.; Aitken, K.E.H.; Wiebe, K.L. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia. The Condor. 106: 5–19.

Maser, C.; Anderson, R.G.; Cromak Jr., K.; Williams, J.T.; Martin, R.E. 1979. Dead and down woody material. In: Thomas, J.W., ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agricultural Handbook 553. Washington, DC: U.S. Department of Agriculture, Forest Service: 78–95.

McAllister, K.R.; Leonard, W.P. 1997. Washington State status report for the Oregon spotted frog. Olympia, WA: Washington Department of Fish and Wildlife. 38 p.

McCaffrey, S.; Toman, E.; Stidham, M.; Shindler, B. 2013. Social science research related to wildfire management: an overview of recent findings and future research needs. International Journal of Wildland Fire. 22: 15–24.

McComb, W.C. 2001. Management of within-stand forest habitat features. In: Johnson, D.H.; O'Neil, T.A., managing directors. Wildlife–habitat relationships in Oregon and Washington. Corvallis, OR: Oregon State University Press: 140–153.

McDermott, M.H.; Moote, M.A.; Danks, C. 2011. Effective collaboration: overcoming external obstacles. In: Dukes, E.F.; Firehock, K.E.; Birkhoff, J.E., eds. Community-based collaboration: bridging socio-ecological research and practice. Charlottesville: University of Virginia Press: 81–110.

McGarigal, K.; Cushman, S.A.; Neel, M.C.; Ene, E. 2002. FRAGSTATS 3.0: spatial pattern analysis program for categorical maps. Amherst, MA: University of Massachusetts. http://www.umass.edu/landeco/research/fragstats/documents/fragstats_documents.html. (July 3, 2014).

McGlone, C.M.; Springer, J.D.; Laughlin, D.C. 2009. Can pine forest restoration promote a diverse and abundant understory and simultaneously resist nonnative invasion? Forest Ecology and Management. 258: 2638–2646.

McIver, J.; Stephens, S.; Agee, J.; Barbour, J.; Boerner, R.; Edminster, C.; Erickson, K.; Farris, K.; Fettig, C.; Fiedler, C.; Haase, S.; Hart, S.; Keeley, J.; Knapp, E.; Lehmkuhl, J.; Moghaddas, J.; Otrosina, W.; Outcalt, K.; Schwilk, D.; Skinner, C.; Waldrop, T.; Weatherspoon, P.; Yaussy, D.; Youngblood, A.; Zack, S. 2012. Ecological effects of alternative fuel reduction treatments: highlights of the national Fire and Fire Surrogate study (FFS). International Journal of Wildland Fire. 22: 63–82.

McKelvey, K.S.; Copeland, J.P.; Schwartz, M.K.; Littell, J.S.; Aubry, K.B.; Squires, J.R.; Parks, S.A.; Elsner, M.M.; Mauger, G.S. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. Ecological Applications. 21: 2882–2897.

McKinney, M.L. 2002. Urbanization, biodiversity, and conservation. BioScience. 52: 883–890.

Medhurst, R.B.; Wipfli, M.S.; Binckley, C.; Polivka, K.M.; Hessburg, P.F.; Salter, R.B. 2010. Headwater streams and forest management: Does ecoregional context influence logging effects on benthic communities? Hydrobiologia. 641: 71–83.

Merschel, A.G. 2012. Mixed-conifer forests of central Oregon: structure, composition, history of establishment, and growth. Portland, OR: Oregon State University. 167 p. M.S. thesis.

Meyer, G.A.; Pierce, J. 2003. Climatic control of fire-induced sediment pulses in Yellowstone National Park and Central Idaho: a long-term perspective. Forest Ecology and Management. 178: 89–104.

Meyer, G.A.; Wells, S.G.; Balling Jr., R.C.; Jull, A.J.T. 1992. Response of alluvial systems to fire and climate change in Yellowstone National Park. Nature. 357: 147–150.

Miller, D.; Luce, C.; Benda, L. 2003. Time, space, and episodicity of physical disturbance in streams. Forest Ecology and Management. 178: 121–140.

Miller, J.D.; Skinner, C.N.; Safford, H.D.; Knapp, E.E.; Ramirez, C.M. 2012. Trends and causes of severity, size, and number of fires in northwestern California, USA. Ecological Applications. 22: 184–203.

Minshall, G.W. 2003. Responses of stream benthic macroinvertebrates to fire. Forest Ecology and Management. 178: 155–161.

Mitchell, S.J.; Beese, W.J. 2002. The retention system: reconciling variable retention with the principles of silvicultural systems. The Forestry Chronicle. 78: 397–403.

Morgan, T.A.; Brandt, J.P.; Baldridge, J.D.; Loeffler, D.R. 2011. Use of financial and economic analyses by federal forest managers for woody biomass removal. Western Journal of Applied Forestry. 26: 5–12.

Moritz, M.A.; Hessburg, P.F.; Povak, N.A. 2011. Native fire regimes and landscape resilience. In: McKenzie, D.; Miller, C.; Falk, D.A., eds. The landscape ecology of fire. New York: Springer: 51–86.

Moritz, M.A.; Hurteau, M.D.; Suding, K.N.; D'Antonio, C.M. 2013. Bounded ranges of variation as a framework for future conservation and fire management. Annals of the New York Academy of Sciences. 1286: 92–107.

Morrison, D.J.; Williams, R.E.; Whitney, R.D. 1991. Infection, disease development, diagnosis, and detection. In: Shaw, C.G., III; Kile, G.A., eds. Armillaria root disease. Agric. Handb. 691. Washington, DC: U.S. Department of Agriculture, Forest Service: 62–75.

Morrison, M.L.; Marcot, B.G.; Mannan, R.W. 1998. Wildlife-habitat relationships: concepts and applications. 2nd ed. Madison, WI: University of Wisconsin Press. 435 p.

Mote, P.W. 2003. Trends in snow water equivalent in the Pacific Northwest and their climatic causes. Geophysical Research Letters 30: 1601. doi:10.1029/2003GL017258.

Mote, P.W. 2009. Update to data originally published in: Mote, P.W.; Hamlet, A.F.; Clark, M.P.; Lettenmaier, D.P. 2005. Declining mountain snowpack in Western North America. Bulletin of the American Meteorological Society. 86: 39–49.

Mote, P.W.; Hamlet, A.F.; Clark, M.P.; Lettenmaier, D.P. 2005. Declining mountain snowpack in western North America. Bulletin of the American Meteorological Society. 86: 39–49.

Mote, P.W.; Parson, E.A.; Hamlet, A.F.; Ideker, K.N.; Keeton, W.S.; Lettenmaier, D.P.; Mantua, N.; Miles, E.L.; Peterson, D.W.; Peterson, D.L.; Slaughter, R.; Snover, A.K. 2003. Preparing for climate change: the water, salmon, and forests of the Pacific Northwest. Climatic Change. 61: 45–88.

Mote, P.W.; Salathé, E.P. 2010. Future climate in the Pacific Northwest. Climatic Change. 102: 29–50.

Munger, T.T. 1917. Western yellow pine in Oregon. USDA Bulletin No. 418. Washington, D.C.: U.S. Government Printing Office. 48 p.

Munzing, D.; Gaines, W.L. 2008. Monitoring American marten on the east-side of the North Cascades of Washington. Northwestern Naturalist. 89: 67–75.

Naiman, R.J.; Bilby, R.E.; Bisson, P.A. 2000. Riparian ecology and management in the Pacific coastal rain forest. Bioscience 50: 996–1011.

Naiman, R.J.; Decamps, H. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics. 28: 621–658.

Naiman, R.J.; Decamps, H.; Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications. 3: 209–212.

Naiman, R.J.; Fetherston, K.L.; McKay, S.J.; Chen, J. 1998. Riparian forests. In: Naiman, R.J.; Bilby, R.E., eds. River ecology and management: lessons from the Pacific Coastal Ecoregion. New York: Springer-Verlag: 289–323.

Nakano, S.; Miyasaka, H.; Kuhara, N. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80: 2435–2441.

National Research Council (NRC). 1992. Restoration of aquatic ecosystems. Washington, DC: The National Academy Press. 532 p.

National Research Council (NRC). 1996. Upstream: salmon and society in the Pacific Northwest. Washington, DC: The National Academy Press. 472 p.

Naylor, L.M.; Wisdom, M.J.; Anthony. R.G. 2009. Behavioral responses of North American elk to recreational activity. Journal of Wildlife Management. 73: 328–338.

Nechodom, M.; Becker, D.R.; Haynes, R. 2008. Evolving interdependencies of community and forest health. In: Donoghue, E.M.; Sturtevant, V.E., eds. Forest community connections: implications for research, management, and governance. Washington, DC: Resources for the Future: 91–108.

Nelson, K.; Monroe, M.; Johnson, J.; Bowers, A. 2004. Living with fire: homeowner assessment of landscape values and defensible space in Minnesota and Florida, USA. International Journal of Wildland Fire. 13: 413–425.

Neville, H.; Dunham, J.D.; Rosenberger, A.; Umek, J.; Wilson, B. 2009. Influences of wildfire, habitat size, and connectivity on trout in headwater streams revealed by patterns of genetic diversity. Transactions of the American Fisheries Society 138: 1314–1327.

Nicholls, D.L.; Monserud, R.A.; Dykstra, D.P. 2008. A synthesis of biomass utilization for bioenergy production in the western United States. Gen. Tech. Rep. PNW-GTR 753. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 52 p.

Nielsen-Pincus, M.; Charnley, S.; Moseley, C. 2012. The influence of market proximity on national forest hazardous fuels treatments. Forest Science. 59: 566–577.

Nonaka, E.; Spies, T.A. 2005. Historical range of variability in landscape structure: a simulation study in Oregon, USA. Ecological Applications. 15: 1727–1746.

North, M. 2012. Managing Sierra Nevada forests. Gen. Tech. Rep. PSW-GTR-237. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 184 p.

North, M.P.; Collins, B.M.; Stephens, S.L. 2012. Using fire to increase the scale, benefits and future maintenance of fuels treatments. Journal of Forestry. 110: 392–401.

North M.; Stine, P.; O'Hara, K.; Zielinski, W.; Stephens, S. 2009. An ecosystem management strategy for Sierran mixed-conifer forests. Gen. Tech. Rep. PSW-GTR-220. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 49 p.

Nuñez, T.A.; Lawler, J.J.; McRae, B.H.; Pierce, D.J.; Krosby, M.B.; Kavanagh, D.M.; Singleton, P.H.; Tewksbury, J.J. 2013. Connectivity planning to address climate change. Conservation Biology. 27: 407–416.

O'Hara, K.L. 1996. Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. Forest Science. 42: 1–34, Suppl. 33.

O'Hara, K.L. 1998. Silviculture for structural diversity: a new look at multi-aged systems. Journal of Forestry. 96: 4–10.

O'Hara, K.L.; Gersonde, R.F. 2004. Stocking control concepts in uneven-aged silviculture. Forestry. 77: 131–143.

O'Hara, K.L.; Kollenberg, C.L. 2003. Stocking control procedures for multi-aged lodgepole pine stands in the northern Rocky Mountains. Western Journal of Applied Forestry. 18: 15–21.

O'Hara, K.L.; Latham, P.A.; Hessburg, P.; Smith, B.G. 1996. A structural classification for inland northwest forest vegetation. Western Journal of Applied Forestry. 11: 97–102.

O'Hara, K.L.; Leonard, L.; Keyes, C.R. 2012. Variable-density thinning and a marking paradox: comparing prescription protocols to attain stand variability in coast redwood. Western Journal of Applied Forestry. 27: 143–149.

O'Hara, K.L.; Nagel, L.M. 2013. The stand: revisiting a central concept in forestry. Journal of Forestry. 111: 335–340.

O'Hara, K.L.; Ramage, B.S. 2013. Silviculture in an uncertain world: utilizing multi-aged management systems to integrate disturbance. Forestry. doi: 10.1093/forestry/cpt012.

O'Hara, K.L.; Valappil, N.I. 1999. MASAM: a flexible stand density management model for meeting diverse structural objectives in multi-aged stands. Forest Ecology and Management. 118: 57–71.

O'Hara, K.L.; Valappil, N.I.; Nagel, L.M. 2003. Stocking control procedures for multi-aged ponderosa pine stands in the Inland Northwest. Western Journal of Applied Forestry. 18: 5–14.

Okanogan-Wenatchee National Forest [OWNF]. 2012. The Okanogan-Wenatchee National Forest Restoration Strategy: adaptive ecosystem management to restore landscape resiliency. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 119 p. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5340103.pdf. (17 January 2014).

Oliver, C.D.; Larson, B.C. 1996. Forest stand dynamics-update edition. New York: John Wiley & Sons. 544 p.

Olsen, C.S.; Mallon, A.L.; Shindler, B. 2012. Public acceptance of disturbance-based forest management: factors influencing support. Forestry 2012: Article ID 594067, 10 p. doi:10.5402/2012/594067.

Olson, D.H.; Hagar, J.; Carey, A.; Cissel, J.; Swanson, F. 2001. Wildlife of westside and high montane forests. In Johnson, D.H.; O'Neil, T.A., eds. Wildlife-habitat relationships in Oregon and Washington. Corvallis, OR: Oregon State University Press: 187–212.

Olson, D.L. 2000. Fire in riparian zones: a comparison of historical fire occurrence in riparian and upslope forests in the Blue Mountains and southern Cascades of Oregon. Seattle, WA: University of Washington. 274 p. M.S. thesis.

Olson, D.L; Agee, J.K. 2005. Historical fires in Douglas-fir dominated riparian forests of the southern Cascades, Oregon. Fire Ecology. 1: 50–74.

Oregon Forest Resources Institute [OFRI]. 2012. The 2012 forest report: an economic assessment of Oregon's forest and wood products manufacturing sector. 181 p. http://theforestreport.org/downloads/2012_Forest_Report.pdf. (17 January 2014).

Ormsbee, P.C.; McComb, W.C. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade Range. Journal of Wildlife Management. 62: 596–603.

Ostergren, D.M.; Abrams, J.B.; Lowe, K.A. 2008. Fire in the forest: public perceptions of ecological restoration in north-central Arizona. Ecological Restoration. 26: 51–60.

Otrosina, W.J.; Cobb Jr., F.W. 1989. Biology, ecology, and epidemiology of *Heterobasidion annosum*. In: Otrosina, W.J.; Scharpf, R.F., eds. Research and management of annosus root disease (*Heterobasidion annosum*) in western North America. Gen. Tech. Rep. PSW-GTR-116. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 26–33.

Page, W.G.; Jenkins, M.J. 2007. Predicted fire behavior in selected mountain pine beetle infested lodgepole pine. Forest Science. 53: 662−674.

Page, W.G.; Jenkins, M.J.; Runyon, J.B. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. Canadian Journal of Forest Research. 42: 1631−1647.

Pan, F.; Han, H.-S.; Johnson, L.R.; Elliot, W.J. 2008. Production and cost of harvesting, processing, and transporting small-diameter (≤ 5 inches) trees for energy. Forest Products Journal. 58: 47−53.

Parks, C.G.; Bull, E.L.; Tinnin, R.O.; Shepherd, J.F.; Blumton, A.K. 1999. Wildlife use of dwarf mistletoe brooms in Douglas-fir in northeast Oregon. Western Journal of Applied Forestry. 14: 100−105.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics. 37: 637–669.

Parmeter, J.R., Jr. 1978. Forest stand dynamics and ecological factors in relation to dwarf mistletoe spread, impact, and control. In: Scharpf, R.F.; Parmeter, J.R., Jr., eds. Dwarf mistletoe control through forest management. Gen. Tech. Rep. PSW-GTR-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 16–30.

Pederson, J.L.; Smith, G.A.; Pazzaglia, F.J. 2001. Comparing the modern, quaternary, and neogene records of climate-controlled hillslope sedimentation in southeast Nevada. Geological Society of America Bulletin. 113: 305–319.

Peñuelas, J.; Canadell, J.G.; Ogaya, R. 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. Global Ecology and Biogeography. 20: 597–608.

Perry, D.A.; Hessburg, P.F.; Skinner, C.N.; Spies, T.A.; Stephens, S.L.; Taylor, A.H.; Franklin, J.F.; McComb, B.; Riegel, G. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. Forest Ecology and Management. 262: 703–717.

Perry, D.A.; Jing, H.; Youngblood, A.; Oetter, D.R. 2004. Forest structure and fire susceptibility in volcanic landscapes of the Eastern High Cascades, Oregon. Conservation Biology. 18: 913–926.

Perry, D.A.; Ram, O.; Hart, S.C. 2008. Forest ecosystems. 2nd edition. Baltimore, MD: Johns Hopkins University Press. 632 p.

Pess, G.R.; Montgomery, D.R.; Steel, E.A.; Bilby, R.E.; Feist, B.E.; Greenberg, H.M. 2002. Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences. 59: 613–623.

Peterson, G.D. 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. Ecosystems. 5: 329–338.

Peterson, G.D.; Allen, C.R.; Holling, C.S. 1998. Ecological resilience, biodiversity, and scale. Ecosystems. 1: 6–18.

Pfister, R.D.; Arno, S.F. 1980. Classifying forest habitat types based on potential climax vegetation. Forest Science. 26: 52–70.

Pickett S.T.A.; Cadenasso, M.L.; Grove, J.M.; Nilson, C.H.; Pouyat, R.V.; Zipperer, W.C.; Costanza, R. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics. 32: 127–157.

Pilliod, D.S.; Bull, E.L.; Hayes, J.L.; Wales, B.C. 2006. Wildlife and invertebrate response to fuel reduction treatments in dry coniferous forests of the Western United States: a synthesis. Gen. Tech. Rep. RMRS-GTR-173. Fort Collins, CO: U. S. Department of Agriculture Forest Service, Rocky Mountain Research Station. 34 p.

Poff, N.L.; Allan, J.D.; Bain, M.B.; Karr, J.R.; Prestegaard, K.L.; Richter, B.D.; Sparks, R.E.; Stromber, J.C. 1997. The natural flow regime: a paradigm for river conservation and restoration. Bioscience. 47: 769–784.

Poff, N.L.; Brinson, M.M.; Day Jr., J.W. 2002. Aquatic ecosystems and global climate change: potential impacts on inland freshwater and coastal wetland ecosystems in the United States. Report from the Pew Center on Global Climate Change. http://www.c2es.org/docUploads/aquatic.pdf. (17 January 2014).

Polivka, K.M.; Friedli, L.M.; Green, E.C. 2013. Stream inflow and predation risk affect littoral habitat selection by benthic fish. Freshwater Biology. 58: 986–994.

Poole, G.; Dunham, J.; Hicks, M.; Keenan, D.; Lockwood, J.; Materna, E.; McCullough, D.; Mebane, C.; Risley, J.; Sauter, S.; Spalding, S.; Sturdevant, D. 2001. Scientific issues relating to temperature criteria for salmon, trout, and char native to the Pacific Northwest. A Summary Report submitted to the Policy Workgroup of the EPA Region 10 Water Temperature Criteria Guidance Project, EPA Region 10 Office, Seattle, WA.

Powell, D.C.; Johnson Jr., C.G.; Crowe, E.A.; Wells, A.; Swanson, D.K. 2007. Potential vegetation hierarchy for the Blue Mountains section of northeastern Oregon, southeastern Washington, and west-central Idaho. Gen. Tech. Rep. PNW-GTR-709. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 87 p.

Preisler, H.K.; Hicke, J.A.; Ager, A.A.; Hayes, J.L. 2012. Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. Ecology. 93: 2421−2434.

Radeloff, V.C.; Hammer, R.B.; Stewart, S.I.; Fried, J.S.; Holcomb, S.S.; McKeefry, J.F. 2005. The wildland–urban interface in the United States. Ecological Applications. 15: 799–805.

Rainville, R.; White, R.; Barbour, J., tech. eds. 2008. Assessment of timber availability from forest restoration within the Blue Mountains of Oregon. Gen. Tech. Rep. PNW-GTR-752. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 65 p.

Raish, C.; Gonzalez-Caban, A.; Martin, W.; Martin, I.; Bender, H. 2007. Cultural variation in public perceptions concerning fire use and management. In: Daniel, T.C.; Carroll, M.S.; Moseley, C.; Raish, C. eds. People, fire, and forests. Corvallis, OR: University of Oregon Press: 70–88.

Rasmussen, K.; Hibbard, M.; Lynn, K. 2007. Wildland fire management as conservation-based development:an opportunity for reservation communities? Society and Natural Resources. 20: 497–510.

Reeves, G.H.; Benda, L.E.; Burnett, K.M.; Bisson, P.A.; Sedell, J.R. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. In: Nielsen, J., ed. Evolution and the aquatic ecosystem, Proceedings of the 17th Symposium of the Bethesda, MD: American Fisheries Society: 334–349.

Reeves, G.H.; Bisson, P.A.; Dambacher, J.M. 1998. Fish communities. In: Naiman, R.J.; Bilby, R.E., eds. River ecology and management: lessons from the Pacific Coastal ecoregion. New York: Springer-Verlag: 200–234.

Rehfeldt, G.E.; Crookston, N.L.; Saenz-Romero, C.; Campbell, E.M. 2012. North American vegetation model for land-use planning in a changing climate: a solution to large classification problems. Ecological Applications. 22: 119–141.

Reid, M.L.; Purcell, J.R.C. 2011. Condition-dependent tolerance of monoterpenes in an insect herbivore. Arthropod-Plant Interactions 5: 331−337.

Reyna, N.E. 1998. Economic and social characteristics of communities in the Interior Columbia Basin. In: Interior Columbia Basin Ecosystem Management Project, Economic and Social Conditions of Communities. Walla Walla, WA: U.S. Department of Agriculture, Forest Service and U.S. Department of Interior, Bureau of Land Management: 3–81.

Reynolds, K.M.; Hessburg, P.F. 2005. Decision support for integrated landscape evaluation and restoration planning. Forest Ecology and Management. 207: 263–278.

Reynolds, K.M.; Rodriguez, S.; Bevans, K. 2003. User guide for the ecosystem management decision support system, version 3.0. Redlands, CA: Environmental Systems Research Institute. 82 p.

Rieman, B.E.; Dunham, J.B. 2000. Metapopulation and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish. 9: 51–64.

Rieman, B.E.; Hessburg, P.F.; Lee, D.C.; Thurow, R.F.; Sedell, J.R. 2000. Toward an integrated classification of ecosystems: defining opportunities for managing fish and forest health. Environmental Management. 25: 425–444.

Rieman B.E.; Hessburg, P.F.; Luce, C.; Dare, M.R. 2010. Wildfire and management of forests and native fishes: Conflict or opportunity for convergent solutions? BioScience. 60: 460–468.

Rieman, B.E.; Isaak, D.J.; Adams, S.; Horan, D.; Nagel, D.; Luce, C.; Myers, D. 2007. Anticipated climate warming effects on bull trout habitats and populations across the Interior Columbia River Basin. Transactions of the American Fisheries Society. 136: 1552–1565.

Rieman, B.E.; Lee, D.C.; Burns, D.; Gresswell, R.; Young, M.; Stowell, R.; Rinne, J.; Howell, P. 2003. Status of native fishes in the western United States and issues for fire and fuels management. Forest Ecology and Management. 178: 197–212.

Riggs, R.A.; Tiedemann, A.R.; Cook, J.G.; Ballard, T.M.; Edgerton, P.J.; Vavra, M.; Krueger, W.C.; Hall, F.C.; Bryant, L.D.; Irwin, L.L.; Delcurto, T. 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains ecological province. Res. Pap. PNW-RP-527. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 77 p.

Roath, L.R.; Krueger, W.C. 1982. Cattle grazing influences on a mountain riparian zone. Journal of Range Management. 35: 100–104.

Robbins, W.G. 1997. Landscapes of promise: the Oregon story, 1800–1940. Seattle, WA: University of Washington Press. 392 p.

Robbins, W.G. 1999. Landscape and environment: ecological change in the Intermontane Northwest. In: Boyd, R., ed. Indians, fire, and the land in the Pacific Northwest. Corvallis, OR: Oregon State University Press: 219–237.

Robbins, W.G.; Wolf, D.W. 1994. Landscape and the Intermontane Northwest: an environmental history. In: Hessburg, P.F., ed. Eastside Forest Ecosystem Health Assessment. Gen. Tech. Rep. PNW-GTR-319. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 32 p.

Roghair, C.N.; Dollof, C.A.; Underwood, M.K. 2002. Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. Transactions of the American Fisheries Society. 131: 718–730.

Roni, P.; Beechie, T.J.; Bilby, R.E.; Leonetti, F.E.; Pollock, M.M.; Pess, G.R. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. North American Journal of Fisheries Management. 22: 1–20.

Rosenberger, A.E.; Dunham, J.B.; Neuswanger, J.R.; Railsback, S.F. [N.d.]. Population and individual responses of rainbow trout to wildfire and channel reorganization: an integrated analysis of observation and models. In review. Freshwater Science. On file with: A.E. Rosenberger, U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri, Columbia, Missouri 65211.

Rosenzweig, C.; Karoly, D.; Vicarelli, M.; Neofotis, P.; Wu, Q.; Casassa, G.; Menzel, A.; Root, T.L.; Estrella, N.; Seguin, B.; Tryjanowski, P.; Liu, C.; Rawlins, S.; Imeson, A. 2008. Attributing physical and biological impacts to anthropogenic climate change. Nature. 453: 353–358.

Running, S.W.; Nemani, R.R.; Heinsch, F.A.; Zhao, M.; Reeves, M.; Hashimoto, H. 2004. A continuous satellite-derived measure of global terrestrial primary productivity: future science and applications. Bioscience. 56: 547–560.

Russell, R.E; Royle, J.A.; Saab, V.A.; Lehmkuhl, J.F.; Block, W.M.; Sauer, J.R. 2009. Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. Ecological Applications. 19: 1253–1263.

Ryan, R.B. 1997. Before and after evaluation of biological control of the larch casebearer (Lepidoptera: Coleophoridae) in the Blue Mountains of Oregon and Washington, 1972-1995. Environmental Entomology. 26: 703–715.

Sabo, K.E.; Sieg, C.H.; Hart, S.C.; Bailey, J.D. 2009. The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA. Forest Ecology and Management. 257: 1656–1662.

Sallabanks, R.; Heglund, P.; Haufler, J.B.; Gilbert, B.; Wall, W. 1999. Forest fragmentation in the inland West: issues, definitions, and potential study approaches for birds. In: Rochelle, J.; Lehmann, L.; Wisniewski, J., eds. Forest fragmentation: wildlife and management implications. Leiden, The Netherlands: Brill Publishers: 187–199.

Sallabanks, R.; Marcot, B.; Riggs, R.; Mehl, C.; Arnett, E. 2001. Wildlife of eastside (interior) forests and woodlands. In: Johnson, D.H.; O'Neil, T.A., managing directors. Wildlife–habitat relationships in Oregon and Washington. Corvallis, OR: Oregon State University Press: 213–238.

Sallabanks R.; Riggs, R.A.; Cobb, L.E. 2002. Bird use of forest structural classes in grand fir forests of the Blue Mountains, Oregon. Forest Science. 48: 311–321.

Schmitt, C.L.; Goheen, D.G.; Gregg, T.F.; Hessburg, P.F. 1991. Effects of management activities and stand type on pest-caused losses in true fir and associated species on the Wallowa-Whitman National Forest, Oregon. BMPMZ-01-91. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Wallowa-Whitman National Forest. 78 p.

Schmitt, C.L.; Goheen, E.M.; Frankel, S.J. 1984. Effects of management activities and dominant species type on pest-caused mortality losses in true fir on the Fremont and Ochoco National Forests. Portland, OR: U.S. Department of Agriculture, Forest Service, Forest Pest Management. 34 p.

Schommer, T.J.; Woolver, M.M. 2008. A review of disease related conflicts between domestic sheep and goats and bighorn sheep. Gen. Tech. Rep. RMRS-GTR-209. Fort Collins, CO: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station. 16 p.

Schultz, C.A.; Jedd, T.; Beam, R.D. 2012. The Collaborative Forest Landscape Restoration Program: a history and overview of the first projects. Journal of Forestry. 110: 381–391.

Schumm, S.A.; Hadley, R.J. 1957. Arroyos and the semi-arid cycle of erosion. American Journal of Science. 225: 161–174.

Seibert, J.; McDonnell, J.J.; Woodsmith, R.D. 2010. Effects of wildfire on catchment runoff response: a modelling approach to detect changes in snow-dominated forested catchments. Hydrology Research. 41: 378–390.

Shindler, B. 2007. Public acceptance of wildland fire conditions and fuel reduction practices: challenges for federal forest managers. In: Daniel, T.C.; Carroll, M.S.; Moseley, C.; Raish, C. eds. People, fire, and forests. Corvallis, OR: University of Oregon Press: 37–54.

Shindler, B.; Toman, E. 2003. Fuel reduction strategies in forest communities. Journal of Forestry. 101: 8–15.

Shirk, A.J.; Wallin, D.O.; Cushman, S.A.; Rice, C.G.; Warheit, K.I. 2010. Inferring landscape effects on gene flow: a new model selection framework. Molecular Ecology. 19: 3603–3619.

Shirley, D.M.; Erickson, V. 2001. Aspen restoration in the Blue Mountains of northeast Oregon. In: Shepperd, W.D.; Binkley, D.; Bartos, D.L.; Stohlgren, T.J.; Eskew, L.G., comps. Sustaining aspen in western landscapes: symposium proceedings. Proceedings RMRS-P-18. Fort Collins, CO: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station: 13–15.

Shmida, A.; Wilson, M.V. 1985. Biological determinants of species diversity. Journal of Biogeography. 12: 1–20.

Simpson, W.G. 2009. American pikas inhabit low-elevation sites outside the species' previously described bioclimatic envelope. Western North American Naturalist. 69: 243–250.

Singleton, P.H. 2013. Barred owls and northern spotted owls in the eastern Cascade Range, Washington. Seattle, WA: University of Washington. 198 p. Ph.D. dissertation.

Singleton, P.H.; Gaines, W.L.; Lehmkuhl, J.F. 2002. Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. Res. Pap. PNW-RP-549. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 89 p.

Singleton, P.H.; Lehmkuhl, J.F.; Gaines, W.L.; Graham, S.A. 2010. Barred owl space use and habitat selection in the eastern Cascades, Washington. Journal of Wildlife Management. 74: 285–294.

Simpson, M. 2007. Forested plant associations of the Oregon East Cascades. Tech. Pap. R6-NR-ECOL-TP-03-2007. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 590 p.

Skinner, C.N. 1997. Fire history in riparian reserves of the Klamath Mountains. In: Cooper, S.; Sugihara, N., eds. Proceedings—fire in California ecosystems: integrating ecology, prevention, and management. Davis, CA: California Association for Fire Ecology.

Skovlin, J.M.; Bryant, L.D.; Edgerton, P.J. 1989. Timber harvest affects elk distribution in the Blue Mountains of Oregon. Res. Pap. PNW-RP-415. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 10 p.

Skovlin, J.M.; Thomas, J.W. 1995. Interpreting long-term trends in Blue Mountains ecosystems from repeat photography. Gen. Tech. Rep. PNW-GTR-315. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 102 p.

Smith, D. 2012. Washington mill survey, 2010. Olympia, WA: Washington State Department of Natural Resources. 100 p.

Smith, J.K. ed. 2000. Wildland fire in ecosystems: effects of fire on fauna. Gen. Tech. Rep. RMRS-GTR-42-vol. 1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 83 p.

Smith, N.; Deal, R.; Kline, J.; Blahna, D.; Patterson, T.; Spies, T.A.; Bennett, K. 2011. Ecosystem services as a framework for forest stewardship: Deschutes National Forest overview. Gen. Tech Rep. PNW-GTR-852. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 46 p.

Southwood, T.R.E. 1977. Habitat, the template for ecological strategies? Journal of Animal Ecology. 46: 337–365.

Sovern, S.G.; Taylor, M.; Forsman, E.D. 2011. Nest reuse by northern spotted owls on the east slope of the Cascade Range, Washington. Northwestern Naturalist. 92: 101–106.

Spies, T.A. 1998. Forest structure: a key to the ecosystem. Northwest Science. 72: 34–39.

Spies, T.A.; Duncan, S.L. 2009. Searching for old growth. In: Spies, T.A.; Duncan, S.L., eds. Old growth in a new world: a Pacific Northwest icon reexamined. Washington, DC: Island Press. 344 p.

Spies, T.A.; Hemstrom, M.A.; Youngblood, A.; Hummel, S. 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. Conservation Biology. 20: 351–362.

Spies, T.A.; Lindenmayer, D.B.; Gill, A.M.; Stephens, S.L.; Agee, J.K. 2012. Challenges and a checklist for biodiversity conservation in fire-prone forests: perspectives from the Pacific Northwest of USA and southeastern Australia. Biological Conservation. 145: 5–14.

Spies, T.A.; Turner, M.G. 1999. Dynamic forest mosaics. In: Hunter, M.L., ed. Maintaining biodiversity in forest ecosystems. Cambridge, United Kingdom: Cambridge University Press: 95–160.

Springsteen, B.; Christofk, T.; Eubanks, S.; Mason, T.; Clavin, C.; Storey, B. 2011. Emission reductions from woody biomass waste for energy as an alternative to open burning. Journal of the Air and Waste Management Association. 61: 63–68.

Squires, J.R.; Kennedy, P.L. 2006. Northern goshawk ecology: an assessment of current knowledge and information needs for conservation and management. Studies in Avian Biology. 31: 8–62.

State of Oregon. 2012. National forest health restoration: an economic assessment of forest restoration on Oregon's eastside national forests. Prepared for Governor John Kitzhaber and Oregon's legislative leaders. 84 p. http://www.oregon.gov/gov/docs/OR_Forest_Restoration_Econ_Assessment_Nov_2012.pdf. (17 January 2014).

Staudinger, M.C.; Carter, S.L.; Cross, M.S.; Dubois, N.S.; Duffy, J.E.; Endquist, C.; Griffis, R.; Hellmann, J.J.; Lawler, J.L.; O'Leary, J.; Morrison, S.A.; Sneddon, L.; Stein, B.; Thompson, L.M.; Turner, W. 2013. Biodiversity in a changing climate: a synthesis of current and projected trends in the U.S. Frontiers in Ecology and the Environment. 11: 465–473.

Stephens, G.L.; L'Ecuyer, T.; Forbes, R.; Gettlemen, A.; Golaz, J.-C.; Bodas-Salcedo, A.; Suzuki, K.; Gabriel, P.; Haynes, J. 2010. Dreary state of precipitation in global models. Journal of Geophysical Research. 115: D24211.

Stephens, S.L.; McIver, J.D.; Boerner, R.E.J.; Fettig, C.J.; Fontaine, J.B.; Hartsough, B.R.; Kennedy, P.L.; Schwilk, D.W. 2012. Effects of forest fuel-reduction treatments in the United States. Bioscience. 62: 549–560.

Stewart, I.; Cayan, D.; Dettinger, M. 2005, Changes towards earlier streamflow timing across western North America. Journal of Climate. 18: 1136–1155.

Stidham, M.; Simon-Brown, V. 2011. Stakeholder perspectives on converting forest biomass to energy in Oregon, USA. Biomass and Bioenergy. 35: 203–213.

Stine, P.A.; Conway, S. 2012. Applying GTR-220 Concepts on the Sagehen Experimental Forest. In: North, M. ed. Managing Sierra Nevada forests. Gen. Tech. Rep. PSW-GTR-237. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 184 p.

Strong, N.; Stringer, D.; Welch, T.; Littlefield, B. 2010. Land manager's guide to aspen management in Oregon. Corvallis, OR: Oregon State University, Agricultural Extension Service. http://ir.library.oregonstate.edu/xmlui/handle/1957/18399. (14 January 2014).

Sturrock, R.N.; Frankel, S.J.; Brown, A.V.; Hennon, P.E.; Kliejunas, J.T.; Lewis, K.J.; Worrall, J.J.; Woods, A.J. 2011. Climate change and forest diseases. Plant Pathology. 60: 133–149.

Sundstrom, S.; Nielsen-Pincus, M.; Moseley, C.; McCaffrey, S. 2012. Woody biomass use trends, barriers, and strategies: perspectives of US Forest Service managers. Journal of Forestry. 110: 16–24.

Suring, L.H.; Gaines, W.L.; Wales, B.C.; Mellen-McLean, K.; Begley, J.S.; Mohoric, S. 2011. Maintaining populations of terrestrial wildlife through land management planning: a case study. Journal of Wildlife Management. 75: 945–958.

Sutherland, S.; Nelson, C.R. 2010. Nonnative plant response to silvicultural treatments: a model based on disturbance, propagule pressure, and competitive abilities. Western Journal of Applied Forestry. 25: 27–33.

Swan, L.; Tokarczyk, J.; Kaetzel, B. 2012. Eastern Oregon primary wood products processing facilities and operations, Final Draft. Vallejo, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, State and Private Forestry. 21 p.

Swanson, M.E.; Franklin, J.F.; Beschta, R.L.; Crisafulli, C.M.; DellaSala, D.A.; Hutto, R.L.; Lindenmayer, D.B.; Swanson, F.J. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment. 9: 117–125.

Swenson, J.J.; Waring, R.H. 2006. Modeled photosynthesis predicts woody plant richness at three geographic scales across northwestern USA. Global Ecology and Biogeography. 15: 470–485.

Tague, C.; Grant, G. 2009. Groundwater dynamics mediate low-flow response to global warming in snow-dominated alpine regions. Water Resources Research. 45: W07421. 12 p.

Taylor, A.H.; Skinner, C.N. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management. 111: 285–301.

Taylor, A.H.; Skinner, C.N. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications. 13: 704–719.

Theobald, D.M.; Crooks, K.R.; Norman, J.B. 2011. Assessing effects of land use on landscape connectivity: loss and fragmentation of western U.S. forests. Ecological Applications. 21: 2445–2458.

Theobald, D.M.; Reed, S.E.; Fields, K.; Soule, M. 2012. Connecting natural landscapes using a landscape permeability model to prioritize conservation activities in the United States. Conservation Letters. 5: 123–133.

Thomas, J.W. ed. 1979. Wildlife habitat in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: U.S. Department of Agriculture, Forest Service. 512 p.

Thomas, J.W.; Anderson, R.G.; Maser, C.; Bull, E.L. 1979a. Snags. In: Thomas, J.W., ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: U.S. Department of Agriculture, Forest Service: 60–77.

Thomas, J.W.; Forsman, E.D.; Lint, J.B.; Meslow, E.C.; Noon, B.B.; Verner, J. 1990. A conservation strategy for the northern spotted owl. Interagency scientific committee to address the conservation of the northern spotted owl. Portland, OR: U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior Bureau of Land Management, Fish and Wildlife Service, and National Park Service. 427 p.

Thomas, J.W.; Maser, C.; Rodiek, J.E. 1979b. Edges. In: Thomas, J.W., ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: U.S. Department of Agriculture, Forest Service: 48–59.

Tiedemann, A.R.; Berndt, H.W. 1972. Vegetation and soils of a 30-year deer and elk exclosure in central Washington. Northwest Science. 46: 59–66.

Tiedemann, A.R.; Woodard, P.M. 2002. Multiresource effects of a stand-replacement prescribed fire in the *Pinus contorta-Abies lasiocarpa* vegetation zone of central Washington. Gen. Tech. Rep. PNW-GTR-535. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 26 p.

Tinnin, R.O. 1981. Interrelationships between *Arceuthobium* and its hosts. American Midland Naturalist. 106: 126–132.

Tinnin, R.O. 1984. The effect of dwarf mistletoe on community ecology. In: Hawksworth, F.G.; Scharpf, R.F., eds. Biology of dwarf mistletoes. Gen. Tech. Rep. RM-GTR-111. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 117–122.

Tinnin, R.O.; Hawksworth, F.G.; Knutson, D.M. 1982. Witches' broom formation in conifers infected by *Arceuthobium douglasii*: an example of parasitic impact on community dynamics. American Midland Naturalist. 107: 351–359.

Tinnin, R.O.; Knutson, D.M. 1980. Growth characteristics of the brooms on Douglas-fir caused by *Arceuthobium douglasii*. Forest Science. 26: 149–158.

Toman, E.; Stidham, M.; Schindler, B.; McCaffrey, S. 2011. Reducing fuels in the wildland-urban interface: community perceptions of agency fuels treatments. International Journal of Wildland Fire. 20: 340–349.

Topik, C.; Halverson, N.M.; T. High, T. 1988. Plant association and management guide for the ponderosa pine, Douglas-fir, and grand fir zones, Mount Hood National Forest. R6 Ecol. Tech. Pap. 004-88. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 132 p.

Torgersen, T.R. 2001. Defoliators in eastern Oregon and Washington. Northwest Science. 75: 11–20.

Torgersen, T.R.; Powell, D.C.; Hosnan, K.P.; Schmidt, F.H. 1995. No long-term impact of carbaryl treatment on western spruce budworm and host trees in the Malheur National Forest, Oregon. Forest Science. 41: 851−863.

Underwood, E.C.; Viers, J.H.; Quinn, J.F.; North, M.P. 2010. Using topography to meet wildlife and fuels treatment objectives in fire-suppressed landscapes. Journal of Environmental Management. 46: 809–819.

U.S. Department of Agriculture, Forest Service [USDA FS]. 1996. Status of the Interior Columbia River Basin: summary of scientific findings. Gen. Tech. Rep. PNW-GTR-385. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 151 p.

U.S. Department of Agriculture, Forest Service [USDA FS]. 2013. Ecological restoration policy. Federal Register Vol. 78, No. 177. RIN 0596-AC82. P. 56202.

U.S. Department of Agriculture [USDA]. 2010. Strategic plan: FY 2010–2015. Washington, DC: U.S. Department of Agriculture. 58 p.

U.S. Department of the Interior, Fish and Wildlife Service [USFWS]. 1997. Grizzly bear recovery plan supplement: North Cascades Ecosystem Recovery Plan. Missoula: MT: U.S. Fish and Wildlife Service. 64 p.

U.S. Department of the Interior, Fish and Wildlife Service [USFWS]. 2011. Revised recovery plan for the northern spotted owl (*Strix occidentalis caurina*). Portland, OR: U.S. Fish and Wildlife Service. 277 p.

Van Pelt, R. 2008. Identifying old trees and forests in eastern Washington. Washington State Dept. of Natural Resources, Olympia WA. 166 p. http://www.dnr.wa.gov/ResearchScience/Topics/ForestResearch/Pages/lm_oldgrowth_guides.aspx. (14 January 2014).

Vavra, M.; Walburger, K.; Delcurto, T. 2005. Ungulate ecology of ponderosa pine ecosystems in the Northwest. In: Ritchie, M.; Maguire, D.; Youngblood, A., eds. Proceedings of the symposium on ponderosa pine: issues, trends, and management. Gen. Tech.Rep. PSW-GTR-198. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 145–158.

Verschuyl, J.P.; Hansen, A.J.; McWethy, D.B.; Sallabanks, R.; Hutto, R.L. 2008. Is the effect of forest structure on bird diversity modified by forest productivity? Ecological Applications. 18: 1155–1170

Vinyeta, K.; Lynn, K. 2013. Exploring the role of traditional ecological knowledge in climate change initiatives. Gen. Tech. Rep. PNW-GTR-879. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 37 p.

Voggesser, G.; Lynn, K.; Daigle, J.; Lake, F.K.; Ranco, D. 2013. Cultural impacts to tribes from climate change influences on forests. Climatic Change. [online]. doi: 10.1007/s10584-013-0733-4.

Volney, W.J.A.; Fleming, R.A. 2007. Spruce budworm (*Choristoneaura* spp.) biotype reactions to forest and climate characteristics. Global Change Biology. 13: 1630−1643.

Wagener, W.W. 1965. Dwarf mistletoe removal and reinvasion in Jeffrey and ponderosa pine, northeastern California. Res. Note PSW-RN-73. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 8 p.

Wales, B.C.; Mellen-McLean, K.; Gaines, W.L.; Suring, L. 2011. Focal species assessment of current condition and the proposed action (alternative B) for the Blue Mountains forest plan revisions (draft Oct. 2011). Unpublished paper. On file with: U.S. Department of Agriculture, Forest Service, Wallowa-Whitman National Forest, Blue Mountain Forest Plan Revision Team, Baker City, OR 97814.

Walker, B.; Holling, C.S.; Carpenter, S.R.; Kinzig, A. 2004. Resilience, adaptability and transformability in social–ecological systems. Ecology and Society. 9: 5. http://www.ecologyandsociety.org/vol9/iss2/art5/. (17 January 2014).

Walker, B.; Salt, D. 2006. Resilience thinking: Sustaining ecosystems and people in a changing world. Washington, DC: Island Press. 174 p.

Wallin, D.O.; Swanson, F.J.; Marks, B. 1994. Landscape pattern response to changes in pattern generation rules: land-use legacies in forestry. Ecological Applications. 4: 569–580.

Walther G.; Post, E.; Convey, P.; Menzel, A.; Parmesan, C.; Beebee, T.J.C.; Fromentin, J.; Hoegh-Guldberg, O.; Bairlein, F. 2002. Ecological responses to recent climate change. Nature. 416: 389−395.

Waring, R.H.; Coops, N.C.; Running, S.W. 2011. Predicting satellite-derived patterns of large-scale disturbances in forests of the Pacific Northwest Region in response to recent climatic variation. Remote Sensing of Environment. 115: 3554−3566.

Washington State Department of Natural Resources [WA DNR]. 2007. The future of Washington forests. Olympia, WA: DNR Communications Group. 76 p.

Washington Wildlife Habitat Connectivity Working Group [WHCWG]. 2010. Washington connected landscapes project: statewide analysis. Olympia, WA: Washington Departments of Fish and Wildlife, and Transportation. 223 p.

Wasserman, T.N.; Cushman, S.A.; Shirk, A.S.; Landguth, E.L.; Littell, J.S. 2012. Simulating the effects of climate change on population connectivity of American marten *(Martes americana*) in the northern Rocky Mountains, USA. Landscape Ecology. 27: 211–225.

Watson, D.M. 2001. Mistletoe—a keystone resource in forests and woodlands worldwide. Annual Review of Ecology and Systematics. 32: 219–249.

Weaver, H. 1974. Effects of fire on temperate forests: western United States. In: Kozlowski, T.T.; Ahlgren, C.E., eds. Fire and ecosystems. New York: Academic Press: 279–320.

Weins, J.A.; Haywood, G.D.; Safford, H.D.; Catherine, C.M. 2012. Historical environmental variation in conservation and natural resource management. Hoboken, NJ: John Wiley & Sons. 337 p.

Wenger, S.J.; Isaak, D.J.; Luce, C.H.; Neville, H.M.; Fausch, K.D.; Dunham, J.B.; Dauwalter, D.C.; Young, M.K.; Elsner, M.M.; Rieman, B.E.; Hamlet, A.F.; Williams, J.E. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences of the United States of America. 108: 14175–14180.

Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006. Warming and earlier spring increase western US forest wildfire activity. Science. 313: 940–943.

Westman, W.E. 1978. Measuring the inertia and resilience of ecosystems. Bioscience 28: 705–710.

White, R. 1983. The altered landscape: social change and land in the Pacific Northwest. In: Robbins, W.G., Frank, R.J., Ross, R.E., eds. Regionalism and the Pacific Northwest. Corvallis, OR: Oregon State University Press. 109–128.

White, R. 1991. It's your misfortune and none of my own: a new history of the American West. Norman, OK: University of Oklahoma Press. 644 p.

White, R. 1992. Discovering nature in North America. Journal of American History. 79: 874–891.

White, R. 1999. Indian land use and environmental change. In: Boyd, R., ed. Indians, fire, and the land in the Pacific Northwest. Corvallis, OR: Oregon State University Press: 36–49.

Whitlock, C.; Knox, M.A. 2002. Prehistoric burning in the Pacific Northwest: Humans versus climate influences. In: Vale, T., ed. Fire, native peoples, and the natural landscape. Washington, DC: Island Press: 195–232.

Whitlock, C.; Shafer, S.; Marlon, J. 2003. The role of climate and vegetation change in shaping past and future fire regimes in the northwestern USA and implications for ecosystem management. Forest Ecology and Management. 178: 5–21.

Whitlock, M.C. 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. The American Naturalist. 148: S65–S77.

Whyte, K.P. 2013. Justice forward: tribes, climate adaptation and responsibility. Climatic Change. 120: 517–530.

Wickman, B.E. 1992. Forest health in the Blue Mountains: the influence of insects and diseases. Gen. Tech. Rep. PNW-GTR-295. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 15 p.

Wienk, C.L.; Sieg, C.H.; McPherson, G.R. 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. Forest Ecology and Management. 192: 375−393.

Wiens, J.A.; Hayward, G.D; Holthausen, R.S.; Wisdom, M.J. 2008. Using surrogate species and groups for conservation planning and management. BioScience. 58: 241–252.

Williams, A.P.; Allen, C.D.; Macalady, A.K.; Griffin, D.; Woodhouse, C.A.; Meko, D.M.; Swetnam, T.W.; Rauscher, S.A.; Seager, R.; Grissino-Mayer, H.D.; Dean, J.S.; Cook, E.R.; Gangodagamage, C.; Cai, M.; McDowell, N.G. 2012. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change. doi:10.1038/nclimate1693.

Williams, C.K.; Kelley, B.F.; Smith, B.G.; Lillybridge, T.R. 1995. Forested plant associations of the Colville National Forest. Gen.Tech. Rep. PNW-GTR-360. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 370 p.

Williams, C.K.; Lillybridge, T.R. 1983. Forested plant associations of the Okanogan NF. R6 Ecol 132-1983. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 116 p.

Williams, D.W.; Liebhold, A.M. 1995. Herbivorous insects and global change: potential changes in the spatial distribution of forest defoliator outbreaks. Journal of Biogeography. 22: 665–671.

Williams, M.A.; Baker, W.L. 2012. Comparison of the higher-severity fire regime in historical (A.D. 1800) and modern (A.D. 1984–2009) montane forests across 624,156 ha of the Colorado Front Range. Ecosystems. 15: 832–847.

Wimberly, M.C.; Spies, T.A. 2001. Modeling landscape patterns of understory tree regeneration in the Pacific Northwest, USA. Applied Vegetation Science. 4: 277–286.

Winter, G.; Vogt, C.; Fried, J.S. 2002. Fuel treatments at the wildland-urban interface- common concerns in diverse regions. Journal of Forestry. 100: 15–21.

Winthers, E.; Fallon, D.; Haglund, J.; DeMeo, T.; Nowacki, G.; Tart, D.; Ferwerda, M.; Robertson, G.; Gallegos, A.; Rorick, A.; Cleland, D.T.; Robbie, W. 2005. Terrestrial Ecological Unit Inventory technical guide. Washington, DC: U.S. Department of Agriculture, Forest Service, Washington Office, Ecosystem Management Coordination Staff. 245 p.

Wipfli, M.S.; Richardson, J.S.; Naiman, R.J. 2007. Ecological linkages between headwaters and downstream ecosystems: transport of organic matter, invertebrates, and wood down headwater channels. Journal of the American Water Resources Association. 43: 72–85.

Wisdom M.J.; Holthausen, R.S.; Wales, B.C. 2000. Source habitats for terrestrial vertebrates of focus in the Interior Columbia River Basin: broad-scale trends and management implications. Vol. 1—Overview. Gen. Tech. Rep. PNW-GTR-485. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 156 p.

Wissmar, R.C.; Smith, J.E.; McIntosh, B.A.; Li, H.W.; Reeves, G.H.; Sedell, J.R. 1994a. A history of resource use and disturbance in riverine basins of eastern Oregon and Washington (early 1880s–1990s). Northwest Science. 68: 1–35.

Wissmar, R.C.; Smith, J.E.; McIntosh, B.A.; Li, H.W.; Reeves, G.H.; Sedell, J.R. 1994b. Ecological health of river basins in forested regions of eastern Oregon and Washington. In: Hessburg, P.F., ed. Eastside Forest Ecosystem Health Assessment. Gen. Tech. Rep. PNW-GTR-326. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 65 p.

Wondzell, S.M.; King, J.G. 2003. Postfire erosional processes in the Pacific Northwest Rocky Mountain regions. Forest Ecology and Management. 78: 75–87.

Woodard, P.M. 1977. Effects of prescribed burning on two different-aged high elevation plant communities in eastern Washington. Seattle, WA: University of Washington. 228 p. Ph.D. dissertation.

Wright, C.S.; Agee, J.K. 2004. Fire and vegetation history in the eastern Cascade Mountains, Washington. Ecological Applications. 14: 443–459.

Wu, J.; Loucks, O.L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. The Quarterly Review Biology. 70: 439–466.

Wu, J.; David, J.L. 2002. A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. Ecological Modelling. 153: 7–26.

Appendix 1—List of Practical Considerations for Landscape Evaluation and Restoration Planning

This list of management considerations is intended to provide an example of the kinds of key steps that could be taken in achieving restoration and resilience goals. The list does not establish a rigid process nor required steps in project planning; rather, these are reminders of the types of planning actions that can enable managers to achieve a broad range of landscape restoration objectives. Their application to a specific project is at the discretion of the responsible official, depending on the purpose of the action. The six major elements of this example process are presented first, followed by a more detailed discussion of the kinds of activities that can contribute knowledge through this process:

- **Local landscapes can be prioritized within ecoregions for restoration.** Local landscapes might be individual or groups of subwatersheds or watersheds. Local landscape domains should represent land units that are useful to terrestrial and aquatic system evaluations. Broad-scale assessment methodology can be used to base prioritization on the degree of vegetation departure from historical and future climate change reference conditions (including exotic plant invasions); vulnerability to large-scale, high-severity fire, drought, insect, and pathogen-caused tree mortality events; and priorities for terrestrial and aquatic habitat restoration and regional linkages, especially as they relate to listed and focal species. Other criteria may also be important.
- **Consider engaging in stakeholder processes early and as often as is practical.**
- **Characterization of the current vegetation conditions of high-priority local landscapes is recommended.** Using a meso-scale assessment methodology, estimate and spatially allocate the departure of current conditions from historical and climate change reference conditions; landscape vulnerability to large-scale, high-severity fire, drought, insect, and pathogen-caused tree mortality events; noxious and nonnative plant and animal invasions; and priorities for listed and focal species (terrestrial and aquatic) habitat restoration and improved connectivity.
- **For local landscapes, we recommend developing target frequency and patch size histograms (distributions) of desired vegetation conditions,** including physiognomic types, cover types, structural classes, canopy cover classes, density and age classes, and other related conditions, considering the potential vegetation type, the topographic setting, local soils, historical

disturbance regimes and range of variability, expected climate change and future range of variability, special legacy wildlife concerns, and other ecological, operational, or socioeconomic factors as needed.

- **Consider developing a method to spatially allocate and distribute these patch size distributions to local landscapes.** Fine tune target distributions based on landscape context and special legacy considerations.
- **Consider developing Proposed Landscape Treatment Areas (PLTAs) in local landscapes based on ecological and socioeconomic criteria**, including stakeholder input.

The following more detailed steps may be considered for local landscape evaluations where appropriate to the purpose of the project or planning action:

- **Characterizing and mapping the current vegetation conditions of entire local landscapes; include all potential vegetation types (PVTs) is recommended.** Motivating questions are:
  - What are the current patterns of physiognomic types, cover types, structural stages or successional classes, stand density, and basal area classes?
  - What is the density and distribution of large, old, fire-tolerant/intolerant trees, and the density and basal area of shade-tolerant trees?
  - What are current surface and canopy fuel conditions?
  - What is the vulnerability of the current vegetation to major insect and pathogen disturbances?
  - What is the vulnerability of the current vegetation and fuelbeds to wildfires?
- **For each ecoregion, we suggest characterizing historical reference conditions (ca. 1880–1900) for all PVTs.** Motivating questions are:
  - What were the historical patterns of physiognomic types, cover types, structural stages or successional classes, stand density, and basal area classes?
  - What was the historical pattern and distribution of large, old, fire-tolerant trees?
  - What was the historical pattern and distribution of shade-tolerant trees? How did their basal area and density vary? How were these patterns distributed with respect to topography, PVTs, and dominant processes?
  - What is a set of guiding reference conditions (potential restoration and resilience targets) based on historical patterns of structure and composition?

  - What is a desired set of class and landscape pattern metrics to characterize these reference conditions?

  Develop reference conditions that enable a direct comparison of the current conditions with the historical reference conditions.

- **Consider comparing current vegetation with reference conditions** (structure, composition, disturbance regimes). Motivating questions are:
  - Where within the local landscapes have disturbance regimes and vegetation structure and composition have been significantly altered by Euro-American activities?
  - How does this departure vary by topography, soils, and PVT setting, and by disturbance regime?
- **To strengthen understanding of sustainable landscape-scale ecological condition, future climate change reference conditions (ca. 2010–2050) for all PVTs can be characterized for each ecoregion.** Motivating questions are:
  - What do climate change models predict to be the most likely climate change scenarios for each ecoregion? Identify one or two most likely climate change scenarios for each ecoregion; use existing information from models or expert opinion.
  - What are predicted future patterns of physiognomic types, cover types, structural stages or successional classes, stand density, and basal area classes?
  - What is a set of guiding reference conditions (potential restoration and resilience targets) based on future patterns of structure and composition?
  - What is a desired set of class and landscape pattern metrics to characterize these reference conditions?

  Develop reference conditions that enable a direct comparison of the current conditions with the future climate change reference conditions.

- **Assessment of the risk of high-severity fire under current fuel conditions is suggested.**
  - Tools such as FlamMap, a fire behavior mapping and analysis program, are currently being used for this.
  - Terrain-routed wind flow projections can be obtained from Wind Ninja, Wind Wizard, or similar simulation tools.
  - To initialize wind speeds and directions, use meteorological data from nearby weather stations where available, or expert advice as needed.

- Determine the mapped distribution of burn probability, probable flame length, fireline intensity, rate of spread, crown fire ignition, and spread potential.
- Note the hotspots on the landscape for high-probability flame length and fireline intensity.
- Note the corridors on the landscape that most strongly tend to spread fire.

- **Assessment of the departures from historical and climate change reference conditions in patch-scale fire behavior attributes.** Motivating questions are:
  - How have spatial patterns of surface and canopy fuels changed with respect to these references?
  - How will changes translate to changes in expected fire behavior?
  - What are the key changes by PVT setting?
  - How are changes in expected fire behavior spatially distributed?

- **Evaluating the wildlife habitat conditions (distribution, abundance, and connectivity of different habitat types) and assessing current conditions. The following steps have been used for regional-scale wildlife habitat assessment (Suring et al. 2011), but can be adjusted to address planning at other scales:**
  - Identify species of conservation concern.
  - Describe habitats and other important factors (e.g., sensitivity to activities associated with roads or residential developments).
  - Group species according to habitat associations and other threats.
    - Select species for assessment. Appropriate assessment target species could include threatened, endangered, or sensitive species, or focal species selected based on their association with specific habitat conditions and particular threats associated with human activities.
    - Develop assessment models for each focal species.
    - Develop conservation strategies that address management of habitat and other risks.
    - Design monitoring and adaptive management plans.

- **A terrestrial landscape diagnosis of habitat retention and vegetation restoration needs can be developed by considering items above.**
  - Evaluation of the road network associated with the current landscape is recommended.
  - Identify all roads crossing streams, culverts, and other fish passage barriers.
  - Identify road segments that confine stream channels, reduce access to off-channel features, and contribute the most sediment.

  - Identify portions of the road network that most reduce subsurface water flow and accelerate runoff.
  - Identify the portions of the road network that are most essential for access.

- **Evaluation of the stream network of the current landscape is recommended.**
  - Identify and map existing anadromous and cold water fish habitats, especially for listed or focal species.
  - Identify and map habitats with inherent potential for these same species.
  - Identify and map the cold water upwelling areas within the stream network and the extent of their influence on water temperature.

- **Evaluation of the surface erosion and mass failure potential within the landscape is recommended.**
  - Identify anadromous and cold water fish habitats that are prone to erosion, especially those of regionally listed or focal species.
  - Identify habitats with inherent potential for these same species that are especially prone to erosion effects.

- **An aquatic landscape diagnosis of habitat restoration needs can be derived by considering items above.**

- **Terrestrial and aquatic landscape and road restoration needs can be diagnosed using considerations items above.**

- **Using integrated risk and vulnerability assessments and socioeconomic opportunity factors can be effective in spatially allocating treatment priorities and identifying proposed landscape treatment areas (PLTAs)** (fig. 47). Spatial decision support tools can help users jointly consider the spatial allocation of treatment priorities across a multitude of factors.
  - Assess and map current land use and land designations and whatever constraints, challenges, or opportunities this suggests.
  - Develop and identify PLTAs that restore key concerns identified in analysis.
  - Among the PLTAs, vary the emphasis among the concerns to provide a wide variety of management alternatives to consider.
  - Array and compare the social and economic benefits and costs of each alternative.
  - Identify transitioning issues: How do we transition from a tenuous current condition to a more desirable and resilient future? How do we provide specific attention to species at risk and the elements of the landscape that need conservation in the near term while transitioning to the future?

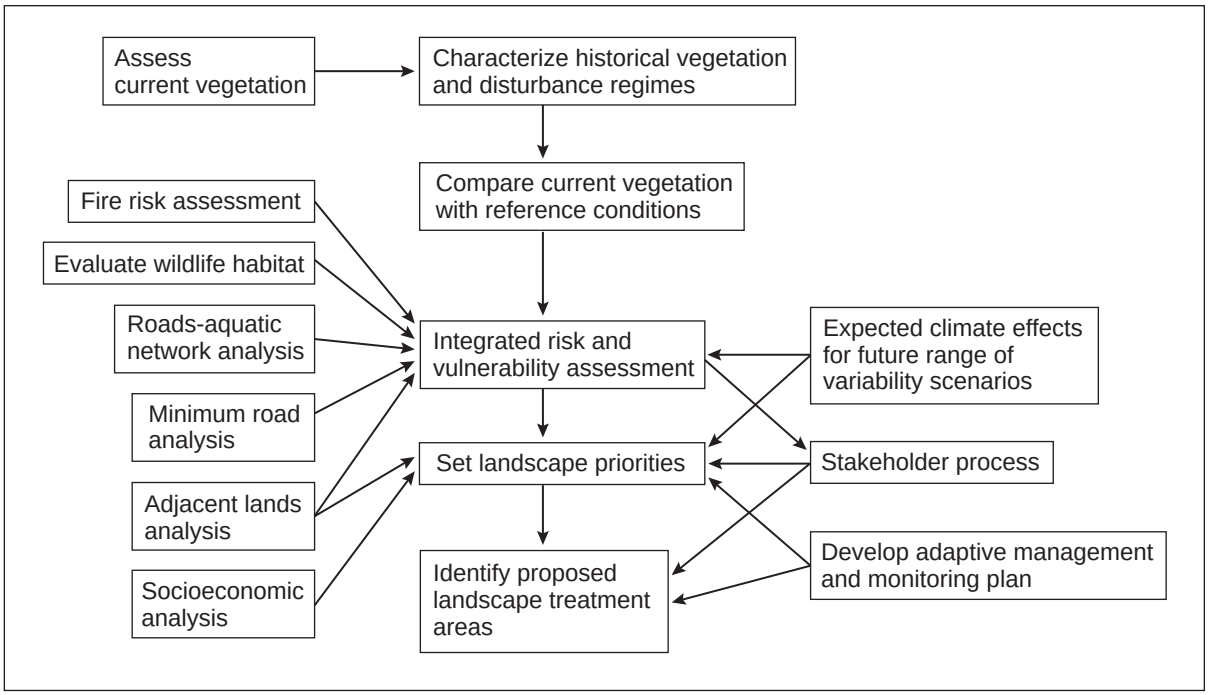


Figure 47—Schematic diagram of a suggested landscape evaluation workflow.

- Develop a landscape diagnosis and prescription for the best subset of alternatives based on stakeholder inputs and the condition of the resources.
- Assess potential effects of proposed work on adjoining lands and possible effects of ongoing activities on adjacent lands.

- **Develop a plan for monitoring implementation and effectiveness of the proposed treatments.** Monitoring programs take many different forms depending on specific objectives and available resources. Careful planning of a monitoring strategy is important to enable scientifically effective and reliable data collection and analysis for the intended purposes. The Forest Service planning rule provides detailed guidance for Forest Plan monitoring (36 CFR 219.12) including both a broad and local-scale approach. This plan also includes the option for jointly developed (i.e., more than one forest) plans that will effectively address broader-scale needs.

- **Regularly assess new scientific findings and adjust plans accordingly.**

Disclaimer: As stated above, the preceding elements are provided for the consideration of managers in conducting landscape evaluations to achieve sustainable land management objectives. These specific elements are not meant to suggest strict requirements; rather they are examples of the kinds of considerations that enable managers to obtain the best available scientific information for project planning.

Appendix 2—Regional-Scale Fire Regimes Group Classification for Oregon and Washington[1]

Most Moist Mixed-Conifer (MMC) Fire Regimes Fall Within Types I and III a and b.

0 to 35 years, low severity—
Typical climax plant communities include ponderosa pine, eastside/dry Douglas-fir, pine-oak woodlands, Jeffrey pine on serpentine soils, oak woodlands, and very dry white fir. Large stand-replacing fire can occur under certain weather conditions, but are rare events (i.e., every 200+ years).

0 to 35 years, mixed and high severity—
Includes true grasslands (Columbia basin, Palouse, etc.) and savannahs with typical return intervals of less than 10 years; mesic sagebrush communities with typical return intervals of 25 to 35 years and occasionally up to 50 years, and mountain shrub communities (bitterbrush, snowberry, ninebark, ceanothus, Oregon chaparral, etc.) with typical return intervals of 10 to 25 years. Certain specific communities include mountain big sagebrush and low sagebrush-fescue communities. Grasslands and mountain shrub communities are not completely killed, but usually only top-killed and resprout.

35 to 100+ years, mixed severity—
This regime usually results in heterogeneous landscapes. Large, high-severity fires may occur but are usually rare events. Such high-severity fires may "reset" large areas (10,000 to 100,000 ac [4050 to 40 500 ha]) but subsequent mixed-severity fires are important for creating landscape heterogeneity. Within these landscapes a mix of stand ages and size classes are important characteristics; generally, the landscape is not dominated by one or two age classes. In southeastern Oregon, this regime also includes aspen, riparian communities, most meadows, and wetlands.

<50 years, mixed severity—
Typical potential plant communities include mixed conifer, very dry westside Douglas-fir, and dry grand fir. Lower severity fire tends to predominate in many events.

---

[1] Evers, L. 2002. Fire regimes of Oregon and Washington. Unpublished report. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 3 p.

50 to 100 years, mixed severity—
Typical climax plant communities include well drained western hemlock; warm, mesic grand fir, particularly east of the Cascade crest; and eastside western redcedar. The relative amounts of lower and higher severity patches within a given event are intermediate between IIIa and IIIc.

100 to 200 years, mixed severity—
Typical potential plant communities include western hemlock, Pacific silver fir, and whitebark pine at or below 45° N latitude and cool, mesic grand fir and Douglas-fir. Higher-severity fire tends to dominate in many events.

35 to 100+ years, high severity—
Seral forest communities that arise from or are maintained by high-severity fires, such as lodgepole pine, aspen, western larch, and western white pine, often are important components in this fire regime. Dry sagebrush and mountain mahogany communities also fall within this fire regime. Natural ignitions within this regime that result in large fires may be relatively rare, particularly in the Cascades north of 45° N latitude.

35 to 100+ years, high severity, juxtaposed—
Typified by what would normally be considered a long-interval regime that lies immediately above a shorter interval or lower severity fire regime. Most often the fire originates lower on the slope and burns uphill into regime IVa. In southeastern Oregon, this subregime includes Wyoming big sagebrush communities on deeper soils below 5,000 ft elevation. Forest examples include lodgepole pine immediately above ponderosa pine in the eastside Washington Cascades and aspen imbedded within dry grand fir in the Blue Mountains. This regime is often found in lower elevations or drier sites than is considered typical for regime IV.

100+ years, high severity, patchy arrangement—
Typical potential forest communities include subalpine fir and mountain hemlock parkland and whitebark pine north of 45° N latitude.

Other community types include mixed Wyoming big sagebrush and low sagebrush on low productivity sites such as scablands, stiff sagebrush, and true old growth juniper savannah (<10 percent canopy closure). Some forbs are present, such as Sandberg's bluegrass, and the availability of many of these areas for burning depends on wet years that result in much greater grass production than is typical. Typical fire return interval in these communities is 100 to 150 years.

100 to 200 years, high severity—
Typical forest plant communities include subalpine mixed conifer (spruce-fir), western larch, and western white pine. Important potential forest plant communities include mountain hemlock in the Cascades and Pacific silver fir north of 45° N latitude.

Other plant communities include the intergrade between Wyoming big sagebrush and greasewood, shadscale on non-alkali soils, spiny hopsage, and alpine grasslands and heath in southeastern Oregon.

> 200 years, high severity—
This fire regime occurs at the environmental extremes where natural ignitions are very rare or virtually nonexistent, or environmental conditions rarely result in large fires. Sites tend to be very cold, very hot, very wet, very dry, or some combination of these conditions.

Typical plant communities include black sagebrush, salt desert scrub, greasewood on dunes, true old-growth juniper with at least 10 percent canopy closure and mountain-mahogany in rocky areas, and alpine communities and subalpine heath in the Blue Mountains and Cascades. Most species tend to be small and low-growing. Bare ground is common.

200 to 400 years, high severity—
Forest plant communities are at least somewhat fire-adapted. Typical plant communities include Douglas-fir, noble fir, and mountain hemlock on drier sites in parts of western Washington.

400+ years, high severity—
Forest plant communities are weakly fire-adapted or not fire-adapted. Typical plant communities include Douglas-fir, Pacific silver fir, western hemlock, western redcedar, and mountain hemlock on moister sites in western Washington.

No fire—
This regime includes forest plant communities with no evidence of fire for 500 years or more. Stands often have extremely deep duff layers on poorly developed soils. Typical plant communities include Sitka spruce and Pacific silver fir along the Oregon and Washington coast and very wet western redcedar sites.

Appendix 3—Reconstructed Historical Vegetation Conditions Within Sampled Areas of the Blue Mountains Province

This appendix is provided to highlight vegetation conditions that existed early in the 20th century in the Blue Mountains. The data are sorted by potential vegetation type (PVT); this sorting gives the reader the capacity to contrast overstory and understory size class, canopy cover, cover type, and structural class conditions for the major potential vegetation types. These insights are a companion to the body of this synthesis and are meant to amplify our observations about disturbance regimes and the sorts of patterns resulting from them. The data are adapted from Hessburg et al. (1999b, 2000a) and are available upon request. We provide these data to help the reader develop a mental picture of how the Blue Mountains landscape looked and likely functioned before forest management was in full swing (fig. 48). The vegetation conditions do not reflect a pristine condition and instead reflect some influence of early livestock grazing, timber harvest, and wildfire exclusion. Nonetheless, they are the best data we have and are based on the earliest available black-and-white, stereo-aerial photography, which was usually taken in anticipation of major future harvest activities. We found the earliest aerial photography to be an extensive reconnaissance of mostly nonharvested forest reserves. From characterizations like these, it is possible to visualize the primary directions and magnitudes of changes that occurred to the present day as a consequence of the first century of forest management.

Key to abbreviations in the tables that follow:

Potential vegetation types (PVT):

PIPO = ponderosa pine
WD PSME/ABGR = warm/dry—Douglas-fir/grand fir
CM PSME/ABGR = cool/moist—Douglas-fir/grand fir
WD ABLA2/PIEN = warm/dry—subalpine fir/Engelmann spruce
CM ALBA2/PIEN = cool/moist—subalpine fir/Engelmann spruce

Cover types:

PIPO = ponderosa pine
PSME = interior Douglas-fir
LAOC = western larch
ABGR = grand fir or white fir
Other = forest cover types not in PIPO, PSME, LAOC, or ABGR
NF = herbland, shrubland, and nonforest/nonrange types

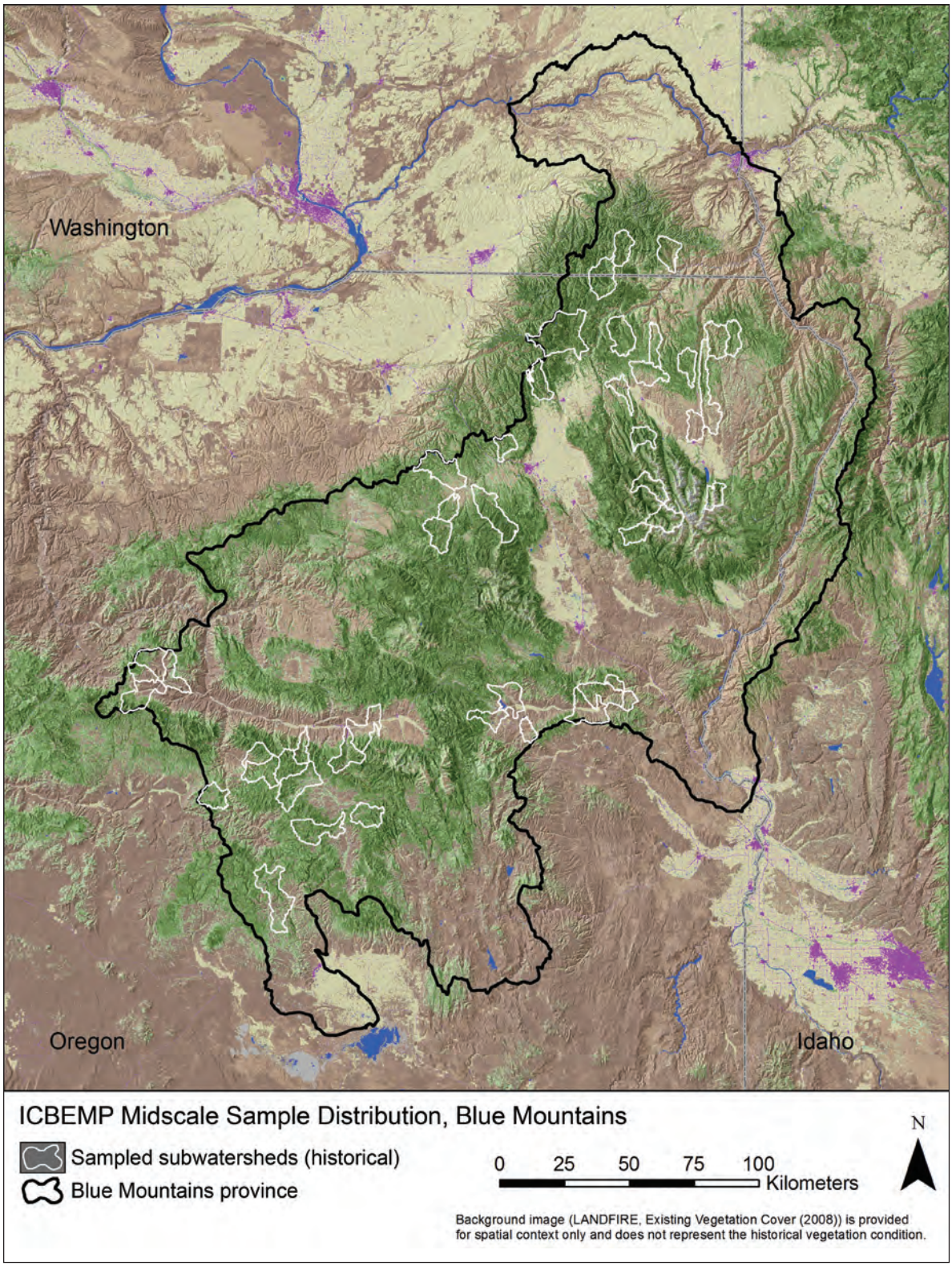


Figure 48—Subwatersheds sampled in the Blue Mountains ecological reporting unit during Interior Columbia Basin Ecosystem Management Project (ICBEMP) (Hann et al. 1997; Hessburg et al. 1999a, 2000c). The black outline delimits the sampled Blue Mountains area; the white lines delineate the reconstructed subwatersheds.

Structure class:

si = stand initiation
seoc = stem exclusion, open canopy
secc = stem exclusion, closed canopy
ur = understory reinitiation
yfms = young forest, multistory
ofms = old forest, multistory
ofss = old forest, single story
wood = woodland structures (all woodland structural classes combined)
herb = herbland (all herbland structural classes combined)
shrub = shrubland (all shrubland structural classes combined)
other = nonforest/nonrange and other anthropomorphic types

Tree size (overstory "OS," understory "US," and "Size"):

SS = seedlings and saplings (< 5.0 in diameter at breast height [d.b.h.])
PT = pole-size trees (5.1 to 8.9 in d.b.h.)
SmT = small trees (9.0 to 15.9 in d.b.h.)
MedT = medium trees (16.0 to 25.0 in d.b.h.)
LgT = large trees (>25.0 in d.b.h.)
Single story (no US) = forested patches without a visible understory
Nonforest = herbland, shrubland, and nonforest/nonrange types

Canopy cover (CC):

10–100 = percentage forest canopy cover class: 10–30, 40–60, 70–100
Single story (no US) = forested patches without a visible understory ("US_CC" tables only)
Nonforest = herbland, shrubland, and nonforest/nonrange types

Table 8 shows a total sampled area of about 415 000 ha, or more than 1 million ac. In the Blue Mountains, about 4 percent of that area resided in the dry PIPO PVT, about 10 percent in the dry mixed conifer (WD Douglas-fir/grand fir), 46 percent in the moist mixed conifer (CM Douglas-fir/grand fir) PVT, 4 percent in the dry spruce-fir PVT (WD subalpine fir/Engelmann spruce), and 8 percent in the moist and cool to cold spruce-fir PVT (CM subalpine fir/Engelmann spruce). The remainder of the area (28 percent) was occupied by early-seral forest conditions (grass, shrub, bare ground), woodlands, and other forested PVTs.

Table 8—Percentage of sampled area in the Blue Mountains ecological reporting unit (ERU) by potential vegetation type

Potential vegetation type	Area	PCT_ERU
	Hectares	*Percent*
Ponderosa pine	15 624.56	3.77
Warm/dry Douglas-fir/grand fir	40 208.19	9.70
Cool/moist Douglas-fir/grand fir	191 632.00	46.22
Warm/dry subalpine fir/Engelmann spruce	16 903.80	4.08
Cool/moist subalpine fir/Engelmann spruce	33 475.22	8.07
Total	297 843.76	71.83

Table 9 examines the distribution of overstory tree size classes (OS) combined with canopy cover class (CC) for each of the five major PVTs. The canopy cover classes are 0 (nonforest), 10 to 30 percent, 40 to 60 percent, and 70 to 100 percent. Canopy cover was originally interpreted in decile classes but reclassified here for simplicity. The size classes are given in the key that precedes these tables. Note the amount of each PVT that was occupied by early-seral nonforest conditions. One quarter of the area in the PIPO PVT was not forested, but in grass, shrub, or bare ground condition at any one time. This was also true of about 10 to 20 percent of the area of the other PVTs. Also observe that there was a relatively small area in SS in any CC class in the PIPO PVT, but this area increased among the other PVTs. When considered along with the nonforest area by PVT, this gives some insight into the amount of stand-replacing disturbance (in grass, shrub, or forested patches that was going on at any time. Note also that regardless of PVT setting, most of the area in any OS size class falls within the lower canopy cover classes. Note as well that the area with MedT or LgT in the overstory consistently ranges from 40 to 60 percent of the PVT area (PIPO = 42.7 percent, WD PSME/ABGR = 55.6 percent, CM PSME/ABGR = 59.75 percent, WD ABLA2/PIEN = 38.2 percent, and CM ABLA2/PIEN = 44.42 percent), and most of that area is in the lower CC classes. Finally, note that each PVT shows a considerable area in PT and SmT trees (PIPO = 31.5 percent, WD PSME/ABGR = 36.1 percent, CM PSME/ABGR = 31.1 percent, WD ABLA2/PIEN = 37.1 percent, and CM ABLA2/PIEN = 46.3 percent), suggesting that mixed- and high-severity fire occurrence has to be a part of the fire history story.

Table 9—Percentage of the sampled area in the Blue Mountains province by historical potential vegetation type, overstory size class, and canopy cover class combination

	Potential vegetation type				
Overstory size × CC	**PIPO**	**WD PSME/ABGR**	**CM PSME/ABGR**	**WD ABLA2/PIEN**	**CM ABLA2/PIEN**
			Percent		
SS_10–30	0.09	0.51	0.17	0.22	
SS_40–60		0.01	0.03	0.23	0.22
SS_70–100		0.07	0.10	5.43	1.43
PT_10–30	4.07	3.46	2.15	3.38	3.47
PT_40–60	0.15	0.59	0.82	2.50	2.56
PT_70–100	0.12	0.61	1.65	1.50	3.42
SmT_10–30	25.91	24.04	13.42	12.52	15.19
SmT_40–60	0.69	5.14	7.10	10.10	13.96
SmT_70–100	0.52	2.21	5.95	7.09	7.73
MedT_10–30	35.89	32.30	29.57	12.32	11.80
MedT_40–60	3.34	9.14	14.16	10.95	12.85
MedT_70–100	0.12	1.59	3.66	3.96	6.30
LgT_10–30	3.36	4.29	8.49	6.39	3.28
LgT_40–60		6.37	3.02	3.29	8.06
LgT_70–100		1.97	0.85	1.27	2.14
Nonforest	25.75	7.69	8.85	18.85	7.59
Total	100.00	100.00	100.00	100.00	100.00

CC = canopy cover; PIPO = ponderosa pine; WD PSME/ABGR = warm/dry Douglas-fir/grand fir; CM PSME/ABGR = cool/moist Douglas-fir/grand fir; WD ABLA2/PIEN = warm/dry subalpine fir/Engelmann spruce; CM ALBA2/PIEN = cool/moist subalpine fir/Engelmann spruce; SS = seedlings and saplings; PT = pole-size trees; SmT = small trees; MedT = medium trees; LgT = large trees.

Table 10 examines the distribution of understory tree size classes (US) combined with canopy cover class (CC) for each of the five major PVTs. It is a companion to the previous table and provides insights about the understories of the forested PVTs, when that is the focal point. The canopy cover classes are 0 (nonforest), 10 to 30 percent, 40 to 60 percent, and 70 to 90 percent; obviously 100 percent US CC cannot exist for it to remain a US rather than an OS layer. Canopy cover was originally interpreted in decile classes but reclassified here for simplicity. The size classes are given in the key that precedes these tables. Note that as in table 9, regardless of PVT most of the area showing any US size class or CC occurs in the lowest 10 to 30 percent CC class (PIPO = 46.9 percent, WD PSME/ABGR = 51.9 percent, CM PSME/ABGR = 50.6 percent, WD ABLA2/PIEN = 38.5 percent, and CM ABLA2/PIEN = 49.1 percent). A much smaller sized area existed in any PVT in the 40 to 60 or 70 to 90 percent CC classes (PIPO = 7.6 percent, WD PSME/ABGR = 18.6 percent, CM PSME/ABGR = 24.3 percent, WD ABLA2/PIEN = 13.6 percent, and CM ABLA2/PIEN = 17.1 percent). Note also that in all PVTs, 16 to 29 percent of the patch area shows no evidence of US trees of any size class. Taken together, these results suggest that, for each of the five PVTs, most patch area

did not have dense understories, suggesting a strong influence of fire, perhaps in overlapping reburns, and from adjacent drier PVTs (e.g., those surrounding the WD and CM ABLA2/PIEN PVTs) that typically displayed more frequent fire return (the PIPO and WD and CM PSME/ABGR PVTs).

Table 10—Percentage of the sampled area in the Blue Mountains ecological reporting unit (ERU) by historical potential vegetation type, understory size class, and canopy cover class combination

Understory size × CC	Potential vegetation type				
	PIPO	WD PSME/ABGR	CM PSME/ABGR	WD ABLA2/PIEN	CM ABLA2/PIEN
			Percent		
SS_10–30	21.69	18.49	7.25	2.32	6.76
SS_40–60	2.35	6.53	1.55	2.01	2.45
SS_70–90		1.30	0.38	0.24	1.03
PT_10–30	23.45	24.61	26.22	24.94	25.15
PT_40–60	3.96	7.61	10.14	6.84	5.89
PT_70–90	1.20	0.49	1.30	1.56	1.52
SmT_10–30	1.73	8.56	15.47	11.14	17.09
SmT_40–60	0.04	2.14	8.44	2.62	5.50
SmT_70–90		0.47	0.98	0.18	0.69
MedT_10–30		0.21	1.62	0.06	0.09
MedT_40–60		0.05	1.26	0.12	
MedT_70–90			0.20		
Without any understory	19.83	21.85	16.34	29.10	26.24
Nonforest	25.75	7.69	8.85	18.85	7.59
Total	100.00	100.00	100.00	100.00	100.00

CC = canopy cover; PIPO = ponderosa pine; WD PSME/ABGR = warm/dry Douglas-fir/grand fir; CM PSME/ABGR = cool/moist Douglas-fir/grand fir; WD ABLA2/PIEN = warm/dry subalpine fir/Engelmann spruce; CM ALBA2/PIEN = cool/moist subalpine fir/Engelmann spruce; SS = seedlings and saplings; PT = pole-size trees; SmT = small trees; MedT = medium trees; LgT = large trees.

Table 11 examines the areal distribution of cover types (CT) for each of the five major PVTs. For an expanded description of the cover types see Hessburg et al. 1999a (table 7: 48–49). Note that the PIPO cover type existed in all PVTs. It was dominant in the PIPO (65.5 percent), WD PSME/ABGR (79.42 percent), and CM PSME/ABGR (44.08 percent) PVTs, and occurred in trace amounts in the ABLA2/PIEN types. Surprisingly, more area in the PIPO CT occurred in the WD PSME/ABGR than in the PIPO PVT. This was driven by the large area (about 26 percent) in patches in a nonforest physiognomy (grass and shrub cover) in the PIPO PVT. Looking across all PVTs, it appears that grass and shrub vegetation patches were integral to the forest patchwork; many patches occurred in all forested PVT settings that were otherwise capable of supporting the growth of forest cover. Undoubtedly, some of these patches were alternative stable states that experienced relatively

frequent fires and experienced difficulty establishing a dominant cover of trees. In contrast with the PIPO and WD PSME/ABGR PVTs, CT conditions in the CM PSME/ABGR PVT are increasingly complex, with 47 percent of the patch area in PSME, LAOC, ABGR, and other forest cover types. Nearly one-quarter of the CM PSME/ABGR PVT area was dominated by the ABGR (ABCO) CT, second only to the PIPO CT. A similar area in the ABGR CT occurred in the WD and CM ABLA2/PIEN PVTs, but the greatest difference was that the other forest CTs dominated the latter PVTs. These observations coupled with those from the preceding three tables suggest that several findings are plausible: (1) surface fires associated with low- and mixed-severity fires likely dominated the fire regime in the PIPO and WD PSME/ABGR PVTs; however, replacement-severity fires also occurred and they provided a nontrivial contribution; (2) low-, mixed- and high-severity fires likely occurred in the CM PSME/ABGR PVT owing to variability in fire frequency and topo-edaphic conditions, and surface fire effects from low- and mixed-severity fires were likely on par with crown fire effects from mixed- and high-severity fires; and (3) crown fire effects from mixed- and high-severity fires likely dominated in the ABLA2/PIEN PVTs.

Table 11—Percentage of the sampled area in the Blue Mountains ecological reporting unit (ERU) by historical potential vegetation type and cover type

	Potential vegetation type				
Cover type	**PIPO**	**WD PSME/ABGR**	**CM PSME/ABGR**	**WD ABLA2/PIEN**	**CM ABLA2/PIEN**
			Percent		
PIPO	65.48	79.42	44.08	1.48	0.45
PSME	0.80	4.17	15.26	10.09	4.98
LAOC	0.52	0.96	4.93	9.59	6.57
ABGR	0.06	1.45	22.67	17.82	26.07
Other forest cover types	7.39	6.30	4.21	42.17	54.33
Nonforest	25.75	7.69	8.85	18.85	7.59
Total	100.00	100.00	100.00	100.00	100.00

PIPO = ponderosa pine; WD PSME/ABGR = warm/dry Douglas-fir/grand fir; CM PSME/ABGR = cool/moist Douglas-fir/grand fir; WD ABLA2/PIEN = warm/dry subalpine fir/Engelmann spruce; CM ALBA2/PIEN = cool/moist subalpine fir/Engelmann spruce; PSME = Douglas-fir; LAOC = western larch; ABGR = grand fir.

Table 12 layers together in one location the relations existing in three of the four previous tables, excluding table 10. We integrate them all in table 13. From table 11 we saw that 65.5 percent of the PIPO PVT area supported the PIPO CT, and 26 percent of the area was nonforested. Of that 65.5 percent, 86 percent (56.3 percent of the PVT area) existed in two classes: the SmT and MedT_10 to 30 percent CC classes. Two aspects are noteworthy: canopy cover is low, in many cases less than full potential site occupancy and size class is dominated by small- and medium-sized, not large, and very large trees. In the photointerpretation, large trees were in evidence in a great many patches. To be identified as an overstory layer, LgT CC had to meet or exceed 10 percent of the CC, the lowest CC class. Where LgT cover did not meet the 10 percent CC threshold, the LgT cover was considered a remnant of a former patch and its CC was pooled with the dominant overstory size class. If, as the literature suggests, surface fires primarily thin from below but contribute <20 percent overstory mortality, then surface fire dominated regimes continuously regenerate patches affected by them, and they manifest at any point in time as multicohort, multi-aged, multisized patches. Put alternatively, if fires are occurring every 5 to 15 years in the PIPO and WD PSME/ABGR PVTs and they conservatively kill on average just 5 percent of the CC at each instance of fire, it is difficult to imagine finding many patches of PIPO CT with a high canopy cover of mostly LgT, and with many trees older than about 350 years of age. That is what is shown here. Notice the strong similarities between the PIPO and WD PSME/ABGR PVTs—but there are differences as well. In both PVTS one can see the powerful influence of surface fires in maintaining low canopy cover conditions; however, in the WD PSME/ABGR PVT, the story is less tidy; nearly 28 percent of the area is comprised of patches with a broader array of size classes, intermediate and higher canopy cover classes, and a broader range of cover types. It is apparent that fire frequency and fire severity are more variable in the WD PSME/ABGR than the PIPO PVT. This pattern continues into the CM PSME/ABGR PVT, where there is greater evidence of CT, size, CC, and hence fire regime variability.

Table 12—Percentage of the sampled area in the Blue Mountains ecological reporting unit (ERU) by historical potential vegetation type, cover type, size class, and canopy cover class

	Potential vegetation type				
Cover type	**PIPO**	**WD PSME/ABGR**	**CM PSME/ABGR**	**WD ABLA2/PIEN**	**CM ABLA2/PIEN**
			Percent		
PIPO:					
SS_10-–30		0.46	0.16		
SS_40–60		0.01			
SS_70–100		0.04	0.02		
PT_10–30	2.05	1.56	1.24	0.53	
PT_40–60	0.06	0.42	0.34		
PT_70–100	0.12	0.51	0.14		0.09
SmT_10–30	23.71	20.66	8.60	0.17	0.26
SmT_40–60	0.29	3.47	3.00	0.18	0.02
SmT_70–100		1.69	1.25		
MedT_10–30	32.56	28.75	17.93	0.51	0.08
MedT_40–60	3.26	8.22	6.56		
MedT_70–100	0.12	1.44	0.35		
LgT_10–30	3.31	3.91	3.73	0.09	
LgT_40–60		6.32	0.66		
LgT_70–100		1.94	0.09		
PSME:					
SS_10–30			0.01	0.12	
SS_40–60			0.02	0.23	
SS_70–100			0.04		
PT_10–30	0.16	0.46	0.32		0.06
PT_40–60	0.09	0.07	0.12	0.63	
PT_70–100			0.10		0.06
SmT_10–30	0.32	0.90	1.55	1.65	0.36
SmT_40–60	0.04	0.72	1.48	1.55	1.21
SmT_70–100		0.11	1.14	1.24	0.25
MedT_10–30	0.06	1.06	4.74	1.94	2.06
MedT_40–60	0.07	0.62	1.82	1.38	0.52
MedT_70–100		0.15	0.66	0.25	0.04
LgT_10–30	0.05	0.04	2.69	0.96	0.41
LgT_40–60		0.05	0.51	0.16	
LgT_70–100			0.06		
LAOC:					
SS_10–30					
SS_40–60			0.01		0.07
SS_70–100		0.02	0.01	3.31	0.28
PT_10–30		0.03	0.11		0.12
PT_40–60		0.03	0.16		0.19
PT_70–100		0.04	0.27	0.26	0.16
SmT_10–30		0.16	0.55	1.38	1.41
SmT_40–60		0.11	0.24	0.11	1.29
SmT_70–100	0.52	0.08	0.47	0.11	0.36
MedT_10–30		0.47	1.72	0.86	1.54
MedT_40–60		0.01	0.59	2.70	0.59
MedT_70–100			0.24	0.05	0.10

Table 12—Percentage of the sampled area in the Blue Mountains ecological reporting unit (ERU) by historical potential vegetation type, cover type, size class, and canopy cover class (continued)

	Potential vegetation type				
Cover	**PIPO**	**WD PSME/ABGR**	**CM PSME/ABGR**	**WD ABLA2/PIEN**	**CM ABLA2/PIEN**
			Percent		
LgT_10–30			0.20	0.80	0.46
LgT_40–60			0.36		
LgT_70–100					
ABGR:					
SS_10–30					
SS_40–60					
SS_70–100					0.08
PT_10–30			0.28	0.25	0.36
PT_40–60			0.02	0.14	0.69
PT_70–100			0.24	0.36	0.07
SmT_10–30	0.03	0.01	2.26	1.77	2.04
SmT_40–60		0.67	2.25	3.03	4.70
SmT_70–100		0.14	2.54	1.51	2.84
MedT_10–30	0.03	0.17	3.82	2.30	2.40
MedT_40–60		0.23	5.12	2.48	4.16
MedT_70–100			2.40	2.02	3.21
LgT_10–30		0.20	1.58	1.27	0.27
LgT_40–60			1.48	2.24	3.93
LgT_70–100		0.03	0.68	0.45	1.35
Other forest cover types:					
SS_10–30	0.09	0.05		0.10	
SS_40–60					0.15
SS_70–100			0.03	2.11	1.07
PT_10–30	1.86	1.42	0.21	2.61	2.93
PT_40–60		0.07	0.18	1.72	1.67
PT_70–100		0.06	0.90	0.87	3.05
SmT_10–30	1.85	2.31	0.46	7.56	11.12
SmT_40–60	0.36	0.16	0.12	5.23	6.74
SmT_70–100		0.18	0.55	4.23	4.28
MedT_10–30	3.23	1.86	1.36	6.72	5.72
MedT_40–60		0.06	0.07	4.40	7.58
MedT_70–100			0.01	1.65	2.95
LgT_10–30		0.13	0.28	3.27	2.15
LgT_40–60				0.89	4.14
LgT_70–100			0.02	0.82	0.79
Nonforest	25.75	7.69	8.85	18.85	7.59
Grand total	100.00	100.00	100.00	100.00	100.00

CC = canopy cover; PIPO = ponderosa pine; WD PSME/ABGR = warm/dry Douglas-fir/grand fir; CM PSME/ABGR = cool/moist Douglas-fir/grand fir; WD ABLA2/PIEN = warm/dry subalpine fir/Engelmann spruce; CM ALBA2/PIEN = cool/moist subalpine fir/Engelmann spruce; PSME = Douglas-fir; LAOC = western larch; ABGR = grand fir; SS = seedlings and saplings; PT = pole-size trees; SmT = small trees; MedT = medium trees; LgT = large trees.

In table 13, we layer the information from all five of the preceding tables together using structural classes of O'Hara et al. (1996). Structural classes are used because they provide a sense of the relative abundance of components of each PVT landscape resulting from the combined influences of forest succession, stand dynamics, and disturbance processes. The structural classes take the continuum of conditions and bin them into key mileposts in succession and disturbance regimes. Toggling between tables 12 and 13 is useful for visualizing this point. In the PIPO PVT, we see that stem exclusion open canopy structures (seoc, 31.4 percent) dominated, occupying nearly one half of all PIPO cover (31.4/65.5). This was followed by stand initiation structure (si, 21.2 percent), grass and herb patches (herbland, 15.62 percent), shrubland patches (9.8 percent) woodland patches where tree cover (PIPO and JUOC, western juniper) was <30 percent CC (woodland), followed by young multistory forest (yfms), and understory reinitiation (ur, 3.32 percent) structures. It is plausible that PIPO_si cover occurred in patches after severe fires or that PIPO forest was reinvading a much larger area of grass, shrub, and woodland patches under the influence of livestock grazing, fire suppression, and fire exclusion. At the time of the photointerpretation, only 2.5 percent of the total area showed any evidence of prior timber harvest, and most of this was light selection cutting. Conditions were similar to the PIPO PVT in the WD PSME/ABGR PVT; however, more closed canopy conditions are present and structural conditions are spread across a broader range of CTs. From table 11, we note that nearly 80 percent of the area in the WD PSME/ABGR PVT displayed the PIPO CT. This was distributed across all structural classes, but not evenly so; 59 percent was comprised on PIPO_si, PIPO_seoc, and PIPO_yfms conditions, PIPO_ur contributed another 9 percent, and old single and multistory forests contributed another 10 percent. At the time of the photointerpretation, one third of the WD PSME/ABGR PVT area had experienced some noticeable selection cutting. We notice a much broader distribution of CT and structural class combinations when we observe the CM PSME/ABGR PVT. Here, 33 and 23 percent of the area is comprised of yfms and seoc structures, respectively, across all cover types. At the time of the photointerpretation, 15 percent of this PVT area had experienced light selection cutting, and there was little evidence of regeneration harvesting. In both the WD and CM ABLA2/PIEN PVTs, there was trace evidence of selection and regeneration harvests. In most cases, regardless of PVT, the selection cutting dominated the observed logging in the early photos, it was obvious and recent, and the largest and oldest remnant large and very large trees were the target of opportunity.

Table 13—Percentage of the sampled area in the Blue Mountains ecological reporting unit (ERU) by historical potential vegetation type, cover type, and structural class

	Potential vegetation type				
Cover × structure	**PIPO**	**WD PSME/ABGR**	**CM PSME/ABGR**	**WD ABLA2/PIEN**	**CM ABLA2/PIEN**
			Percent		
PIPO:					
si	21.23	16.59	3.06	0.06	
seoc	31.35	27.60	11.95	0.78	0.14
secc	0.04	2.48	1.56	0.18	0.23
ur	3.32	8.72	7.70	0.19	0.08
yfms	9.44	14.51	17.64	0.27	
ofms	0.11	5.60	1.40		
ofss		3.91	0.78		
PSME:					
si		0.49	0.68	1.11	0.11
seoc	0.29	2.09	2.63	2.72	1.32
secc		0.15	1.81	1.98	0.55
ur	0.44	0.54	3.19	1.68	1.57
yfms	0.07	0.85	6.15	2.32	1.44
ofms		0.03	0.28	0.27	
ofss		0.02	0.53		
LAOC:					
si		0.02	0.45	3.85	1.07
seoc		0.13	0.14	0.11	0.27
secc	0.52	0.13	0.93	1.59	1.51
ur		0.53	1.54	2.94	2.67
yfms		0.15	1.40	0.41	1.05
ofms			0.46	0.68	
ofss			0.01		
ABGR:					
si			0.11		0.23
seoc	0.06	0.18	7.20	4.22	4.07
secc		0.50	2.65	3.15	4.74
ur		0.31	3.98	3.82	5.78
yfms		0.23	6.11	3.58	5.89
ofms		0.20	0.59	0.56	1.28
ofss		0.03	2.03	2.48	4.08
Other forest cover types:					
si	0.39	0.77	0.13	3.12	4.00
seoc		0.11	0.71	16.18	15.61
secc		0.25	1.14	8.23	7.97
ur		0.49	0.80	6.79	9.77
yfms		0.71	1.28	5.64	10.63
ofms				0.42	2.09
ofss			0.02	1.77	4.27
Woodland	7.00	3.99	0.14	0.01	
Nonforest					
Herbland	15.62	3.27	7.45	13.74	4.56
Shrubland	9.80	4.16	0.79	1.39	1.15
Nonforest/nonrange	0.34	0.27	0.61	3.73	1.89
Total	100.00	100.00	100.00	100.00	100.00

PIPO = ponderosa pine; WD PSME/ABGR = warm/dry Douglas-fir/grand fir; CM PSME/ABGR = cool/moist Douglas-fir/grand fir; WD ABLA2/PIEN = warm/dry subalpine fir/Engelmann spruce; CM ALBA2/PIEN = cool/moist subalpine fir/Engelmann spruce; PSME = Douglas-fir; LAOC = western larch; ABGR = grand fir; si = stand initiation; seoc = stem exclusion, open canopy; secc = stem exclusion, closed canopy; ur = understory reinitiation; yfms = young forest, multistory; ofms = old forest, multistory; ofss = old forest, single story.

Glossary

Adaptive management—A system of management practices based on clearly identified outcomes and monitoring to determine if management actions are meeting desired outcomes, and if not, to facilitate management changes that will best ensure that outcomes are met or reevaluated. Adaptive management stems from the recognition that knowledge about natural resource systems is sometimes uncertain (36 CFR 219.16; FSM 1905).

Composition—The biological elements within the different levels of biological organizations, from genes and species to communities and ecosystems (FSM 2020).

Connectivity (or habitat connectivity)—The degree to which intervening landscape characteristics impede or facilitate the movement of organisms or ecological processes between patches. The concept of connectivity implies that some feature or patch in the landscape is spatially related to other, similar features, and that intervening landscape characteristics influence the ecological relationship between those features. Although somewhat counterintuitively, it is important to note that a landscape can be highly fragmented or patchy, as is commonly the case in landscapes with mixed-severity fire regimes, and still be highly connected for a variety of ecological processes.

Disturbance—A force that causes significant change to the structure, composition, or function of an ecosystem through natural events such as earthquake, fire, flood, insect and disease outbreaks, weather, or wind; or by human activities such as the harvest of forest products. Many or most disturbances of interest are integral parts of and important to ecosystem function and health.

Ecophysiological—Relating to the interrelationships between an organism's function and its physical environment.

Ecosystem services—Benefits people obtain from ecosystems (FSM 2020), including:

1. **Provisioning services** such as clean air and fresh water, as well as energy, fuel, forage, fiber, and minerals;
2. **Regulating services** such as long-term storage of carbon; climate regulation; water filtration, purification, and storage; soil stabilization; flood control; and disease regulation;
3. **Supporting services** such as pollination, seed dispersal, soil formation, and nutrient cycling;
4. **Cultural services** such as educational, aesthetic, spiritual and cultural heritage values, as well as recreational experiences and tourism opportunities.

Elasticity—The speed with which a system returns after disturbance.

ENSO—El Niño/Southern Oscillation, a band of anomalously warm ocean water temperatures that occasionally develops off the western coast of South America and can cause climatic changes across the Pacific Ocean. The extremes of this climate pattern's oscillations cause extreme weather (such as floods and droughts) in many regions of the world.

Epicormic—Literally, "of a shoot or branch," this term implies growing from a previously dormant bud on the trunk or a limb of a tree.

Fire intensity—The amount of energy or heat release during fire.

Fire regime—The characteristics of fire in a given ecosystem, such as the frequency, severity, extent, and seasonality of fire.

Fire severity—The scale at which vegetation and a site are altered or disrupted by fire, from low to high severity. It is a combination of the degree of fire effects on vegetation (amount of fire caused vegetation mortality) and on soil properties.

Fragmentation—A term that has various meanings depending on the context of its use. Here we define it in two related ways (also see "connectivity"):

> **Landscape fragmentation**—The breaking up of continuous habitats into patches, thereby generating habitat loss, isolation, and edge effects.
>
> **Wildlife habitat fragmentation**—The set of mechanisms leading to the discontinuity in the spatial distribution of resources and conditions present in an area at a given scale that affects occupancy, reproduction, and survival in a particular species.

Frequency distribution—A depiction, often appearing in the form of a curve or graph, of the frequency with which possible values of a variable have occurred. In this report, we speak of the frequency of wildfire patches of various sizes.

Function—Ecological processes, such as energy flow; nutrient cycling and retention; soil development and retention; predation and herbivory; and natural disturbances such as wind, fire, and floods that sustain composition and structure (FSM 2020).

Future range of variation (FRV)—The natural fluctuation of pattern components of healthy ecosystems that may occur in the future, primarily affected by climate change, human infrastructure, and invasive species.

Heterogeneity—Any factor that induces variation in individual demographic rates.

Hierarchy theory—Ecological hierarchy theory presupposes that nature is working at multiple scales and has different levels of organization which are part of a rate-structured, nested hierarchy.

Historical range of variation (HRV)—The natural fluctuation in pattern of components of ecosystems over time.

Inertia—The resistance of a system to disturbance.

Integrity—An ecosystem has integrity if it retains its complexity, intact biotic and abiotic processes, capacity for self-organization, and sufficient diversity, within its structures and functions, to maintain the ecosystem's self-organizing complexity through time.

Interdigitate—The interlocking of (in this case) different components of the landscape like the fingers of two clasped hands. This creates an intertwining or intermingling mosaic of different vegetation or habitat conditions.

Landscape—A large land area composed of interacting ecosystems that are repeated in terms of factors such as geology, soils, climate, and human impacts. Landscapes are often used for coarse grain analysis.

Landscape hierarchy—Landscapes are systems that can be divided or decomposed into a hierarchy of nested geographic (i.e., different sized) units. This organization provides a guide for defining the functional components of a system and defines ways components at different scales are related to one another.

One common way this is conceptualized is the following organization: region = millions of hectares; landscapes = tens of thousands of hectares; watersheds = hundreds to thousands of hectares; stands (patches) = one to tens of hectares; gaps = 0.01 to 0.1 ha.

Mosaic—The contiguous spatial arrangement of elements within an area. For regions this is typically the upland vegetation patches, large urban areas, large bodies of water, and large areas of barren ground or rock. However, regional mosaics can also be land ownership, habitat patches, land use patches, or other elements. For landscapes, this is typically the spatial arrangement.

Multi-aged stands—Stands having two or more age classes and including stands resulting from variable-retention systems or other traditionally even-aged systems that leave residual or reserve trees.

Nested hierarchy—The name given to the hierarchical structure of groups within groups or branches from a trunk used to classify organisms.

Orographic—The lift of an air mass when it is forced from a low elevation to a higher elevation as it is moves over rising terrain. As the air mass gains altitude, it cools, its relative humidity increases, and clouds and sometimes precipitation result.

Patch—An area of similar vegetation, in structure and composition. Patches may range in size from a portion of a hectare to thousands of hectares.

PDO—The Pacific Decadal Oscillation is often described as a long-lived El Niño-like pattern of Pacific climate variability. As seen with the better-known El Niño/Southern Oscillation (ENSO), extremes in the PDO pattern are marked by widespread variations in Pacific Basin and North American climate.

Plant association—Plant associations are a finer level of classification in the potential vegetation hierarchy. They are defined in terms of a climax dominant overstory tree species and an understory herb or shrub species that is typical of the environmental conditions of a distinctive community of plants.

Plant association group (PAG)—A group of potential vegetation types that have similar environmental conditions and are dominated by similar types of plants (e.g., the dry shrub PVG). They are often grouped by similar types of life forms.

Potential vegetation type (PVT)—A potential vegetation type is a kind of physical and biological environment that produces a kind of vegetation, such as the dry Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) type. Potential vegetation types are identified by indicator species of similar environmental conditions. For example, Douglas-fir indicates a cooler and moister environment than ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson). Because of growth, mortality, and disturbance of the vegetation, many other kinds of vegetation will occur on this type through time. In many cases the indicator species will not be present, due to disturbance. Douglas-fir is simply an indicator, and name, for the kind of physical and biological environment stratification that is used for prediction of response.

Resilience—The capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks (FSM Chapter 2020). Resilience can be further defined to mean the amount of disturbance that an ecosystem can withstand without changing functional states. In this context, while dominant floristics may vary, a forest remains a forest as exemplified by maintenance of certain characteristic biological composition and the ecological goods and services it produces. Resiliency is the inherent capacity of a landscape or ecosystem to maintain its basic structure, function, and organization in the face of disturbances, both common and rare.

Restoration—The Forest Service defines restoration (National Forest System Land Management Planning, 36 CFR 219.19) as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed. Ecological restoration focuses on reestablishing the composition, structure, pattern, and ecological processes necessary to facilitate terrestrial and aquatic ecosystem sustainability, resilience, and health under current and future conditions.

Stand—A descriptor of a land management unit consisting of a contiguous group of trees sufficiently uniform in age-class distribution, composition and structure, and growing on a site of sufficiently uniform quality, to be a distinguishable unit.

Structure—The organization and physical arrangement of biological elements such as snags and down woody debris, vertical and horizontal distribution of vegetation, stream habitat complexity, landscape pattern, and connectivity (FSM 2020).

Sustainability—Meeting needs of the present generation without compromising the ability of future generations to meet their needs. Sustainability is composed of desirable social, economic, and ecological conditions or trends interacting at varying spatial and temporal scales, embodying the principles of multiple use and sustained yield (FSM 1905). Conditions that support native species, ecosystem services, and ecological processes are sustainable when influences on them have not resulted in significant depletion or permanent damage.

Topo-edaphic—Related to or caused by particular soil conditions, as of texture or drainage, rather than by physiographic or climatic factors within a defined region or area.

Variable density thinning—The method of thinning some sub-stand units to a different density than other sub-stand units.

Vegetation series (plant community)—An assembly of different species of plants growing together in a particular habitat; the floral component of an ecosystem. According to Powell et. al. (2007 page 12), a series is the highest level of a potential vegetation hierarchy and is defined by the dominant climax plant species.

Vegetation type—A plant community with distinguishable characteristics.

Pacific Northwest Research Station

Web site	http://www.fs.fed.us/pnw/
Telephone	(503) 808-2592
Publication requests	(503) 808-2138
FAX	(503) 808-2130
E-mail	pnw_pnwpubs@fs.fed.us
Mailing address	Publications Distribution Pacific Northwest Research Station P.O. Box 3890 Portland, OR 97208-3890



Federal Recycling Program
Printed on Recycled Paper

U.S. Department of Agriculture
Pacific Northwest Research Station
1220 SW Third Avenue, Suite 1400
P.O. Box 3890
Portland, OR 97204-3890

Official Business
Penalty for Private Use, $300

CENTRAL OREGON LANDWATCH

2843 NW Lolo Drive., Ste. 200 | Bend, OR 97703
Phone (541) 647-2930
www.colw.org

Attachment 3

2022 Expert Reports on Eastside Aquatic and Riparian Systems by Amy Stuart and Jonathan Rhodes

April 19, 2022

Oliver Stiefel
Crag Law Center
3141 E Burnside St.
Portland, OR 97214

Re: Review and Comment on the "Forest Plans Amendment – Forest Management Direction for Large Diameter Trees in Eastern Oregon and Southeastern Washington Environmental Assessment" and the Consequences and Impacts to Fish Habitat and Native Fish Populations in Riparian Areas

Dear Mr. Stiefel,

I have reviewed the environmental documents issued by the US Forest Service, Region 6, in the limited National Environmental Policy Act (NEPA) Environmental Assessment (EA) process used to remove the standard from the "Eastside Screens" that formerly protected large mature trees over 21 inches for the past 25 years on six national forests (USDA 2021a) and other related research and literature (Appendix A, Literature Cited). The following are my comments regarding the future impacts and consequences of the removal of protection of trees over 21 inches in riparian areas, including those designated as "riparian habitat conservation areas" (RHCAs), on native fish species. In my letter, I will comment on the importance of large trees in riparian areas and the consequences to native fish habitats, and the lack of adequacy of the environmental documents to fully assess and account for impacts to native fish populations, particularly species listed under the Endangered Species Act (ESA).

I am a fisheries biologist with over 38 years of experience, including 30 years with the Oregon Department of Fish and Wildlife (ODFW) before retiring in February 2014. My work for ODFW included the lands within the Project area including the John Day and Deschutes basins. I was the lead author and co-lead author for research papers on bull trout and redband trout, and restoration of anadromous fish including spring chinook and steelhead in the Deschutes basin. Attached as Appendix B is my resume.

I. Introduction

From the 1960s to the early 1990s, there were few limits on federal land management agencies to control management actions on or near streams (Roper et al. 2019). There were no safeguards to balance the risks posed by increasing timber harvest and a lengthening road system (Hicks et al. 1991; Dose and Roper 1994). This led to simplified stream channels with less instream large woody debris, increased fine sediments in streambeds, and destabilized streambanks (Meehan 1991). This period followed decades (since the 1920s) when management actions such as the construction of valley bottom roads, channel straightening, and log drives had a great direct effect on stream channels (Burnett et al. 2007; Steel et al. 2016). Beschta et al. (1995) reported that "*Land management practices in the interior Columbia… have profoundly impacted forest, grassland, and aquatic ecosystems. Watersheds and forests have been degraded (e.g., ecosystems fragmented, habitats simplified or lost, disturbance regimes altered). At every level of biological organization -- within populations, within assemblages, within species, and across the landscape -- the integrity of biological systems has been severely degraded. This is best seen in the marked reduction in the biological diversity in the region*." The authors further stated that "*By narrowly concentrating on forest health (often a euphemism for tree health, recently referring to carbon cycling), federal land*

managers have embarked on an ambitious attempt to address forest management in ways that risk neglecting watershed health and the ecology of aquatic ecosystems."

One of the primary goals of amending planning documents in the 1990s was to implement new management practices that would support viable native salmonids (Ratner et al. 1997; McHugh et al. 2017). The primary method to improve stream conditions was to limit activities such as timber harvest, road construction, livestock grazing, and other activities near streams that had caused the degradation of streams and riparian areas (Boisjolie et al. 2017; Roper et al. 2018). In addition, there were new policy guidelines to minimize sediment runoff from roads, requirements to conduct watershed scale analysis, identify priority watersheds where aquatic species would have greater protection, and implement stream restoration projects. Concurrent with changes in management policies that were expected to improve streams and riparian areas was a 70% reduction in the quantity of timber harvested from public lands in the Pacific Northwest region (Adams et al. 2006).

The Eastside Screens were implemented in 1994 in order to preserve the relatively few remaining large and old trees, and to protect ecosystem values such as wildlife and stream habitats. Those protections were recently removed by the scientifically controversial decision that the Forest Service implemented when the Undersecretary of the Department of Agriculture signed the Environmental Assessment (EA) Decision Document to remove protections for trees over 21 inches on east side forests in Oregon. Those protections were not in place long enough to restore the large and old trees, and the crucial fish and wildlife habitat they provided for recovery from the past century of logging that had removed the largest and oldest trees in eastern Oregon. There remains a significant deficit of large live and dead trees on the landscape in eastern Oregon as well as a relatively low abundance of the fish and wildlife species that the Eastside Screens were designed to protect and maintain.

Large trees are the foundation of old growth and mature forests, and they have a crucial role in supporting biodiversity, native fish and wildlife including numerous sensitive and Endangered Species Act (ESA) listed species, and clean water (DellaSala and Baker 2020). It is important to retain ALL remaining large trees since they are scarce on a landscape that has experienced decades of high grading timber harvest for large old trees. Large, old trees are also important since they are much more resistant to surviving wildfires. There is a large body of science that shows that increased harvest of large trees results in long-term and irreparable harm to fish and wildlife, ecosystem processes, biodiversity, and water quality. Since the Eastside Screens were implemented in the mid-1990s, the ecological basis for the Screens has not changed.

Since the Eastside Screens were amended, all six eastside forests have proposed projects to cut trees over 21 inches, with some projects including large tree removal in riparian areas. These proposed projects range in size from 35,000 to over 110,000 acres. Thus far three projects, Morgan Nesbit on the Wallowa-Whitman, Ellis on the Umatilla, and South Warner on the Fremont-Winema forests have proposed cutting trees over 21 inches in Riparian Habitat Conservation Areas (RHCAs).

For example, the Ellis project proposes to thin trees up to 9 inches diameter breast height (dbh) in the first 100 feet of the RHCA along fish bearing streams (Category 1), but contains no restrictions on harvest for the next 200 feet to the edge of the RHCA. In Category 2 and 3 streams (perennial and non-fish bearing streams and ponds, lakes and wetlands), harvest is limited for the first 75 feet from the stream but not the remaining 75 feet to the outer edge of the RHCA. Category 4 intermittent streams have even less protection, with restricted harvest only in the first 50 feet from the edge of the stream and no limits to the edge of the RHCA. Another project, Cliff Knox,

proposes logging operations in RHCAs including roadwork and ground-based skidding, and the cutting of trees over 21 inches adjacent to RHCAs.

Even though riparian buffers were established in PACFISH and INFISH to protect riparian areas, streams, and wetlands, the Forest Service has increasingly pursued cutting in RHCAs. The Forest Service has been using silvicultural prescriptions and modifying buffers to eliminate protections for and allow the cutting of large trees that provide critical shade for the streams. The impact of cutting large, mature trees, particularly in mixed conifer forests, old growth, connectivity corridors, and especially in riparian areas, will significantly and directly impact many important functions that old trees provide. Large trees over 21" are important because they support a large variety of fish and wildlife species by providing a multi layered large structural habitat as well as habitat for snag dependent and old growth species, provide shading that preserves clear, cold water for native aquatic species and assists in the improvement of soil health.

II. Riparian areas provide countless benefits for aquatic species.

Riparian areas provide very important ecosystem functions for their associated aquatic environments. Riparian areas, wetlands, seeps, and springs are among the most critical fish and wildlife habitats. Riparian areas provide habitat for over 80% of the native fish and wildlife species in western landscapes. However, riparian areas typically comprise less than 5% and sometimes as little as 1-2% of National Forest lands.

Historically, river systems provided highly complex habitat conditions for a diversity of native salmonids including Chinook salmon, steelhead, bull trout, cutthroat trout, and redband trout populations. Mature forests covered almost 75% of the region's forest types (DellaSala and Baker 2020). Old growth and large mature forests buffered the river system and contributed large quantities of wood to stream channels, forming pools and creating hiding and feeding cover for adult and juvenile fish. Mature trees and streamside riparian vegetation shaded streams, provided connectivity between floodplains and stream channels, and kept water cool for fish production.

Large trees in riparian areas are particularly important, either live or dead, standing or fallen onto the forest floor or into the stream, and are critical to forest and watershed function. In streams, they are referred to as large woody debris (LWD). There is abundant literature on the importance of LWD to the structure, function, and biodiversity of forests and particularly in aquatic ecosystems.

Large trees in riparian areas provide stream-side shading and, when they fall into streams, hiding cover for aquatic species. Large mature trees accrue soil depth, cycle nutrients, mitigate pollution, purify water, release oxygen, and provide habitat for wildlife at levels far superior to logged forests (Mackey et al. 2013, Mackey 2014, Mackey et al. 2014, Brandt et al. 2014).

The bulk of the National Forest System roads were built in the last 50 years, and with a few exceptions, most were constructed for access to timber harvest, particularly along streams and in riparian areas. Given the depletion of large trees over the past century from high grading timber harvest practices, the remaining large trees in riparian areas are all the more important to retain. Large trees provide a far greater benefit than smaller trees since they are critical for forming and retaining high quality pools, they last longer than smaller trees, and are more effective at providing instream habitat and reducing bank erosion.

Forest Service research scientists have repeatedly acknowledged the importance of large old trees for aquatic ecosystems. Hessburg et al. (2020) reported that "*Larger stems with root wads are more effective at creating deep*

plunge pools and side channels than smaller wood pieces because they can deflect greater hydraulic power and they last longer in streams. Smaller stems are often removed by spring flood and other channel reorganizing events...Large trees play a vital role in creating instream structure by adding complexity to stream channels and providing shade, and they are essential to creating high-quality, durable fish habitats…Across a continuum of habitats from the headwaters to the mouth, large wood plays a functional role in the creation of complex habitats for native fish (Fauschet al. 2002, Vannote et al. 1986)." The authors further stated that "Highly complex habitat mosaics reflect a combination of dead trees, log and debris jams, sediment, varying hydraulic power, and stream width (fig. 24). In headwater areas, habitat is often characterized by high-gradient streams. In such environments, large wood moderates flow, providing cold water and micro refugia for fish, salamanders, and other aquatic species (Vannote et al. 1986). Farther downstream, large wood contributes to the complexity of floodplain habitats by slowing water, depositing sediment, and facilitating seasonal flooding. These floodplain environments are highly productive for native fish and are enhanced by the presence of embedded large wood (Jeffres et al. 2008). Large water-adjacent trees often contribute to the complexity of aquatic habitats (Reeves et al. 2018). Large wood slows water, resulting in the deposition of sediment that is then sorted into microhabitats by the water column (Montgomery and Buffington 1997). Instream cover provided by large wood offers critical refuge from predation, particularly for rearing juvenile fishes (Dolloff and Warren 2003). Large wood is also important to the life histories of dozens of species of fish that associate with large wood for cover, spawning, and feeding. Other aquatic organisms such as crayfish freshwater mussels, and turtles also use large wood during part of their life cycles (Dolloff and Warren 2003). Further, large wood with root wads tends to survive longer in the stream channel, providing cover and moderating sediment and flow dynamics more effectively than small wood, which tends to be washed downstream. Shading of stream channels by large riparian trees provides critical thermal regulation and cooling (Poole and Berman 2001), particularly for cold-water dependent fish such as bull trout (Salvelinus confluentus) (Dunham et al. 2011). As climate changes, anticipated thermal stress will further reduce habitat available to native coldwater fish (Falke et al. 2016, Isaak et al. 2017, Rieman et al. 2007). Large trees throughout the river network are important regulators of thermal condition."

Yet, despite these extensive observations on the importance of large old trees to aquatic ecosystems and their importance for fish and other aquatic species, the Eastside Screens amendment removes the protections for large trees in riparian areas.

III. Riparian logging impacts ESA-listed aquatic species—such as Chinook salmon, steelhead, bull trout—and other native fish and aquatic species in many ways, including by impacting nutrient loads, stream temperatures, sediment loads and LWD, all important components for habitat quality.

It is well established that timber harvest and thinning near streams and in riparian areas can harm water quality and fish habitat. An established and growing body of science has documented the negative effects associated with the removal of large, commercial-sized trees. While non-commercial thinning and prescribed burning of fine fuels may only cause a short-term loss of habitat (i.e. a few months or a few years), the impacts from removal of large trees and their canopies, snags and down wood can last decades or longer.

Effects on fish habitat from loss of riparian vegetation include increased stream temperature, loss of cover, increased erosion, a widening and shallowing of the stream channel, and reduction or loss of perennial flow. Degraded habitat is characterized by increased sediment, increased water temperatures, a decline in pool depth, quality and frequency, reduced LWD, increased cutbanks and bank instability, and high width/depth ratios. Water

quantity and quality problems, primarily flow reduction or loss, temperature, sedimentation, and turbidity, limit fish distribution and production (Bottom et al. 1985).

Studies have shown that logging, even selective logging, has increased instream fine sediments (Kreutzweiser et al. 2005, Miserendino and Masi 2010) and increased instream water temperatures (Guenther et al. 2012), and these changes in habitats are found decades after logging.

Most streams on National Forest lands in Eastern Oregon already have high stream temperatures and currently violate state water quality standards for temperature. These high temperatures are a serious and long-term threat to water quality and continue to be a problem due to both past and current land management practices of timber harvest, high road densities and livestock grazing. High stream temperatures, especially in violation of state and Forest Plan stream temperature standards, create chronic and acute lethal conditions for native fish and limit their productivity and survival in areas where they are already stressed by high loads of fine sediments. Even local increases of water temperatures and sediment at the subwatershed or reach scale can cause local extinctions which cannot be recovered (Frissell 2017).

Logging in riparian areas can increase nutrient loads, stream temperature, and sediment to the stream, compromising fish habitat and water quality. Any active management in stream corridors and riparian areas causes a risk of harm to stream ecosystems (Frissell 2017) via the release of nutrients and increases in sediment and stream temperatures.

A. Nutrients. One important function of riparian areas is nutrient filtering and retention from harvest activities up slope. Any vegetation disturbance from wildfires or timber harvest, but especially logging, frees phosphorus and nitrogen in soils and causes a spike of these elements in streams. Excess nitrogen causes increased growth of aquatic plants and algae and in excessive amounts it can use up dissolved oxygen and block light to deeper waters. Too much nitrogen and phosphorus in the water causes algae to grow quickly and beyond what riparian areas and streams can handle. Large increases in algae harms water quality and aquatic habitats and decreases oxygen that fish and other aquatic life need to survive. In large algal blooms, oxygen is depleted leading to toxicity and even death of large numbers of fish. Sweeney and Newbold (2014) reported that "*The most familiar aspect of streamside forest buffers is their role in creating sufficient space to intercept pollutants created by upland activity before they enter the stream. It is intuitive that wider buffers with more vegetation have greater potential for intercepting, sequestering, degrading, and processing pollutants*." The authors conducted modeling of nitrogen removal and, for a site with average water flux, predicted "*removal efficiency of 48% for a 30-m buffer, increasing to 90% for a 100-m buffer*."

Wetlands, like riparian areas, also serve important ecosystem functions, such as improving water quality by filtering sediments, and nutrients and contaminants from the water column (Environmental Protection Agency 2002). Wetlands are also critically essential habitats for a wide variety of plants and animals, including many federally threatened and endangered species.

B. Stream temperature. Timber harvest, particularly in streamside zones, increases water temperature that can become chronic or acutely lethal to native fish species especially salmonids that are adapted to cold water. Yonce et al. (2021) observed that "*The effects of timber harvest on the thermal regime of streams have been observed globally*". The authors stated that "*Reduction in baseflow, which can occur due to soil compaction during harvest, may also reduce the capacity to absorb increased thermal inputs. Preventing these adverse effects was a motivating*

factor in the development of riparian buffer management practices for forestry. Riparian buffers influence water temperature through shading that reduces direct insolation to streams, and secondary effects on microclimate (air temperature and wind) within the buffer are also important. Additional benefits of buffers include reducing peak storm runoff, maintaining stable baseflow, and potentially filtering out sediment, nutrients, and other pollutant loads from the surrounding area."

Stream temperatures are also increased by the interruption of hillslope drainage patterns. By intercepting surface and subsurface flow, and increasing the channels on the landscape, it alters the magnitude of peak flows and lowers base stream discharge (Furniss et al. 1991). Loss of riparian cover and shading from timber harvest is well known while a third mechanism is the conversion of groundwater to surface water (Williams 1999). When water is changed from subsurface to surface water, as streams degrade, it is exposed to solar heating (Fissekis and Hersh-Burdick 2007; Wonzell et al. 2009). The hyporheic zone is the area under or beside a stream channel or floodplain that contributes water to the stream and has been found to have a significant role in supporting cold water refugia for salmonid fish populations.

Stream temperature is also impacted by the density of the road network in watershed. Increases in stream temperature have been strongly correlated with roads constructed along valley bottoms and next to stream channels and from the associated loss of riparian vegetation and canopy cover adjacent to those roads. Higher stream temperature impacts aquatic species by raising stream temperatures above the tolerable range for rearing, and increases vulnerability to disease, reduces metabolic efficiency, shifts fish species assemblages, and inhibits upstream migration (Beschta et al. 1987; Hicks et al. 1991).

C. Sediment. It is well documented in many studies that elevated sediment occurs as a result of timber harvest and the increase of "temporary" roads that continue to have impacts on the landscape well after the project is completed. PACFISH and INFISH both expounded on the contribution of timber harvest and roads to the degradation of streams and listing of anadromous and inland fish species. Many scientists and reports have affirmed that 200-to-300-foot riparian buffers along streams are minimums to protect aquatic habitats. A review of numerous authors in INFISH reported that "*non-channelized sediment flow rarely travels more than 300 feet and that 200-to-300-foot riparian 'filter strips' are generally effective at protecting streams from sediment from non-channelized flow."* Beschta et al. (1995) reported that "*Analysis of sediment impacts, for example, that accept existing conditions as the baseline are highly inappropriate because these have been increased over natural background levels for 50-100 years in many cases. There is considerable evidence that current conditions are insufficient to maintain viable populations of many native species, including sensitive and declining trout, salmon, and other fishes*." The large influxes and biological impacts of sediment beyond those normally in a stream are well documented, and come from timber harvest, roads construction and grazing. Bowerman et al. (2014) reported that fine sediments reduced percolation of water through salmonid redds (fish nests) and impacted both egg and early life survival. The authors also reported that management actions that restore hydraulic complexity in the form of pool–riffle sequences, point bars, and large wood enhance hyporheic exchange and support higher salmonid survival. May and Lee (2004) also stated that "*increases in coarse sediment supply can be associated with sharp reductions in salmonid habitat and productivity*" and reported that streams with discontinuous flow caused by sediment increases reduced survival by crowding fish into smaller areas with reduced food availability. The additional bedload of both fine sediments and coarser sediment delivered to streams fills in the channel, losing pool depth, channel complexity, and changing the channel profile to a shallow, wide profile (Chin et al 2004; May and Lee 2004).

Increased sediment in streams connected with roads causes increased aggradation of stream beds, filling of pools, enlarged channel widths and widening width-to-depth ratios (Jackson and Beschta 1984; Lisle 1982). Lee et al. (1997) (referenced in Carnefix and Frissell 2009) reported as road density increases, there is a clear decline in pool frequency and frequency of large pools, both of which are essential requirements for high-quality fish habitat. Lee et al. (1997) reported that increasing road densities are correlated with declines in the four non-anadromous salmonid species including bull trout, Westslope cutthroat trout, Yellowstone cutthroat trout, and redband trout. All species are less likely to use streams in highly roaded areas for spawning and rearing, and if found are less likely to be at strong population levels. As pools are filled in by sediment, they support fewer fish, and they suffer higher mortality. Elevated levels of fine sediment also adversely affect salmonid embryo survival (Bjornn and Reiser 1991; Jensen et al. 2009) and have been linked to decreased fry emergence and juvenile densities, loss of winter carrying capacity, and increased predation (Chapman 1988; Everest et al. 1987; Scrivener and Brownlee 1989; Magee et al. 1996; Weaver and Fraley 1993; Young et al. 1991). Furthermore, higher fine sediment load reduces intragravel dissolved oxygen, increases metabolic waste concentrations, decreases intergravel space for aquatic life, and restricts movements of alevins (young fry) (Bjornn and Reiser 1991; Chapman 1988; Everest et al. 1987; Baird et al. 2012).

Sedimentation affects fish habitat quality by increasing the amount of fines and causing embeddedness of gravel and substrate. This in turn reduces spawning habitat by making gravel difficult to lift, oxygenation to incubating eggs, and cover for rearing fish. Turbidity affects fish production by reducing production of aquatic insects and plankton, and foraging efficiency of fish. Sediment fills interstitial spaces between rocks in the substrate, reduces habitable area in streams, and when it exceeds 20 percent of the total area on the substrate, can smother fish and frog eggs and increase mortality (Bjornn and Reiser 1991). Increased turbidity reduces the ability of fish to feed on aquatic insects and reduces aquatic insect and plant production. Many streams throughout eastern Oregon forests have documented sediment embeddedness of greater than 20% and in some cases has high as 45% (USDA Summit Off Highway Vehicle Trail (USDA, Ochoco National Forest SFEIS 2016)).

As another example, the US Fish and Wildlife Service (2010) describes the effects of sediment on ESA-listed bull trout: "*The introduction of sediment in excess of natural amounts can have multiple adverse effects on bull trout and their habitat (Rhodes et al. 1994, pp. 16-21; Berry, Rubinstein, Melzian, and Hill 2003, p. 7). The effect of sediment beyond natural background conditions can be fatal at high levels. Embryo survival and subsequent fry emergence success have been highly correlated to percentage of fine material within the streambed (Shepard et al. 1984, pp. 146, 152). Low levels of sediment may result in sublethal and behavioral effects such as increased activity, stress, and emigration rates; loss or reduction of foraging capability; reduced growth and resistance to disease; physical abrasion; clogging of gills; and interference with orientation in homing and migration (McLeay et al. 1987a, p. 671;Newcombe and MacDonald 1991, pp. 72, 76, 77; Barrett, Grossman, and Rosenfeld 1992, p. 437;Lake and Hinch 1999, p. 865;Bash et al. 2001n, p. 9;Watts et al. 2003, p. 551;Vondracek et al. 2003, p. 1005;Berry, Rubinstein, Melzian, and Hill 2003."*

D. Large Woody Debris. LWD is an important measure of habitat complexity and is important for sediment retention, pool formation and bank stability (Cordova 1995; Stuart et al. 2007). It is also an important feature in the physical and biological structure of a forested stream (McDade et al, 1990). In general, higher native salmonid densities are found in streams with more LWD. LWD adds to stream complexity and stability and provides habitat for a variety of species and age classes in aquatic communities (Lisle 2002). Most RHCAs on the managed portions of National

Forest lands are deficient in LWD from past and present timber harvest. Roper et al. (2019), comparing actively managed and reference (unmanaged) reaches of streams on national forests in eastern Oregon and Washington, and Idaho and Montana, reported that wood frequency, wood volume, and pool frequencies all increased as the percent of the riparian zone that was forested increased.

IV. Logging-associated roadbuilding and road use also causes degradation of water quality and adversely impacts ESA-listed and aquatic species.

The Eastside forests all have high road densities, a legacy of logging operations. Roads act like dry stream beds, and when rains come, they push significant amounts of sediments and polluted water into streams and rivers. This is true whether roads are functionally open, designated open or designated closed - the roads continue to have some of the greatest impacts contributing sediment to streams and aquatic habitats.

The ongoing existence of a dense road network has already stressed the system and is causing significant effects. The construction and use of new roads in riparian areas to facilitate timber harvest will only increase the significant impact that roads are having on riparian areas, wetlands, seeps, and springs and associated fish and wildlife species. The Forest Service is already proposing new road construction, the reopening of old roadbeds and new stream crossings to facilitate timber harvest. These actions will dramatically increase the impact of and the amount of sediment being pushed into the system. These are not minor, short-term impacts but large-scale, long-term impacts to aquatic systems that are already on the brink.

Most national forests have road density standards that were implemented as part of the 2005 Travel Management Rule (USDA 2005). The 2005 Travel Management Rule was adopted to address environmental harm resulting from unregulated motorized use across National Forest Service lands. For example, the Ochoco Forest has a road density standard of $\leq$ 3 mi/mi^2 in general forest (USDA, Forest Service 1989 Ochoco Forest Land and Resource Management Plan), yet in their own analysis of roads in 2003, road densities are as high as 12 mi/mi^2 (USDA Forest Service, Roads Analysis 2003). Another example is the Malheur National Forest where there are road density standards of 1.5 mi/mi^2 in big game summer range and 1 mi/mi2 in big game winter range (USDA Forest Service 2021b, Cliff Knox Project DEIS) yet the open road density in the project area is 3.98 mi/mi2 in the area planned for timber harvest. Since there are many closed and decommissioned roads that are either being driven or still present on the landscape in terms of their effects, the real road density is much higher.

In 2020 and 2021, volunteers with the Great Old Broads for Wilderness conducted surveys of "closed and decommissioned roads" in project areas of the Ochoco Forest. The Black Mountain Vegetation Management project DEIS stated that the existing road density was 2.66 mi/mi^2 only using ML 2-5 open roads (USDA, Forest Service 2018, Black Mountain DEIS). However, the Broads noted that counting ML 1 closed roads of which most were driven, the road density for M 1-5 roads was 3.66 mi/mi^2. The Forest Service failed to enumerate the real open road densities on the landscape. The surveys showed that the density was even higher as it found that 63% of the ML-1 "closed" roads, 33% of the decommissioned roads, and numerous user-created roads had unauthorized vehicular use. The surveys noted that 80-90% of the "closed" roads had little or no barriers to restrict access and most had been driven. In another area of the forest, the proposed Mill Creek project area (a project that proposes the removal of large trees greater than 21 inches), the survey crews found a similar level of closed and decommissioned roads actively driven by the public and many user-created roads.

Road density standards and meeting those standards are important because the effects of roads and motorized trails on the landscape concentrate flow and increase runoff and sediment to streams. The increased hydrologic connectivity of flow and sediment seriously degrades instream habitat for aquatic species including macroinvertebrates (aquatic insects), Columbia spotted frog, and a variety of salmonids including native fish such as Chinook salmon, steelhead, bull trout, and redband trout.

Many authors have reported on the consequences of forest management and the attendant proliferation of roads across the landscape. DellaSala et al. (2011) state that "*the roaded, intensively managed landscapes of the other national forest lands have been closely correlated with heavily sediment-laden streams and dramatic changes in flow regimes (Espinosa et al. 1997; Trombulak and Frissell 2000; Center for Biological Diversity et al. 2001; Coffin 2007; Frissell and Carnefix 2007).*"

Elliot et al. (2011) reported that sediment is the greatest pollutant of forest streams, and in the absence of wildfire, a forest road network is usually the main annual source of sediment in forest watersheds. A major factor that increases erosion is traffic. Roads with heavy traffic generate 4 to 5 times the sediment of roads compared to roads with light traffic (Elliot et al. 2010). Carnefix and Frissell (2009) found that there is not a truly "safe" threshold road density for aquatic species, but instead negative impacts begin with the first road segment in a watershed, and highly significant impacts began at road densities as low as 1 mi/mi^2. Motorized use of unpaved roads is a direct factor in sediment production (Furniss et al. 1991). While several research efforts have attempted to describe and quantify increased sediment production for use of roads, some studies have documented that heavily used roads increase sediment production by 130 times greater than abandoned roads (Reid and Dunne 1984). Other studies have documented that sediment production for roads with traffic deliver 2 to 30 times sediment production compared to unused roads (Luce and Black 2001). Foltz et al. (2009) reported that after Forest Service roads were reopened from being closed or decommissioned, sediment concentrations were significantly higher and were attributed to decreased vegetative cover. In addition, the authors found that 30 years of no traffic and vegetation regrowth was not sufficient to allow recovery of soil infiltration to values similar to an undisturbed forest. In other words, the years of compaction by vehicles effectively and permanently impacted runoff and sedimentation from lack of infiltration. Stream crossings along roads are also a major source of sediment to streams (Furniss et al. 1991).

The small roadless areas that have been left "unmanaged", with a lack of logging and roads, play a critical role in maintaining high-quality water and protecting aquatic ecosystems. The clean water from remnant roadless areas is important to maintain healthy coldwater salmonid fisheries, sustain viable aquatic ecosystems, and help protect threatened species and ecosystems (Abell et al. 2000; Trout Unlimited 2004). Roadless area are an important refugia for many salmon and trout populations, as well as for a diversity of endangered freshwater species (Henjum et al. 1994; Huntington 1998; Trombulak and Frissell 2000; Center for Biological Diversity et al. 2001; Strittholt and DellaSala 2001; Oechsli and Frissell 2002; Strittholt et al. 2004; Petersen 2005). DellaSala et al. (2011) state that "*restoration of salmon and trout fisheries in places with high road densities will likely fail without the pivotal role provided by roadless areas as fishery strongholds*." Further, they state that "*For many major drainages (entire watersheds of major rivers, such as the Columbia River Basin), roadless areas and other wilderness areas represent the last few percentages (typically 1% to 5%) of the landscape with a minimally disturbed, or near natural, hydrology*."

V. <u>The FS falsely relies on PACFISH and INFISH to protect streams and riparian areas. By failing to disclose all activities and consequences and relying on PACFISH and INFISH to protect riparian areas, the Forest Service disregards impacts to native fish habitat and fish populations.</u>

The Decision Notice and Finding of No Significant Impact (USDA 2021a) for removing the 21-inch rule of the Eastside Screens states that "*the direction of INFISH and PACFISH, which provide standards and guidelines to protect water quality, continue to apply*" while the Decision Summary states that *"all management will remain the same within Riparian Habitat Conservation Areas. PACFISH, INFISH, their objectives, goals, standards and guidelines direct management will still apply."* Based on this continued management direction, the FS brazenly concludes that the removal of protections for large trees across the Eastside Forests will have "no effect" on ESA-listed aquatic species.

PACFISH and INFISH were designated with the intent to recover highly degraded streams from past and present management activities of timber harvest, roading, mining, and livestock grazing. Timber management activities were only allowed if they were implemented with the intent to move Riparian Management Objectives (RMOs) to a better condition.

However, in the past decade, all forests east of the Cascades have increasingly pursued timber harvest in riparian areas, often under the guise of "restoration" or "wildfire resiliency." In some cases, forests have created arbitrary designations of a "streamside management zone", "an inner and outer RHCA zone" and a "limited activity buffer" that allow commercial harvest and other logging operations in a portion of the RHCA. In some cases, RHCA buffers themselves are too narrow to prevent impacts to aquatic ecosystems, and this further narrowing of buffers has introduced still more impacts. This has led to continued timber harvest, roading and livestock grazing and the failure to recover degraded streams and riparian areas.

Yet, the EA and Decision Notice for amending the Eastside Screens failed to provide any numerical data on stream conditions and parameters for meeting or violating RMOs from PACFISH and INFISH. All six forests that were covered under the EA to remove the 21-inch rule have highly degraded watershed function, streams and riparian conditions throughout all actively managed areas. The few areas that may meet RMOs are typically found in wilderness, roadless areas, and undeveloped lands. The EA and Decision Notice fail to look at baseline conditions and the cumulative effect of removing the protections for large trees across the broad landscape.

The EA and Decision document to amend the Eastside Screens (USDA 2021a) state that "*Aquatic and riparian species habitats are protected through the guidance of the PACFISH/INFISH strategies and will not change under this amendment" and "Project level analyses will be required to address any site-specific effects that projects may have on riparian and wetland associated species and their habitats*."

However, at the site-specific project level, the Forest Service fails to acknowledge that increased sediment from the large planning areas for timber sales will increase impacts on ESA-listed and sensitive aquatic species. For example, the Ellis Integrated Vegetation Management project on the Umatilla National Forest encompasses a planning area of over 114,000 acres for commercial timber harvest, thinning, and additional roads to conduct treatment activities. While the DEIS acknowledged that watersheds and streams were in very poor degraded conditions, the only data provided were that the expected sediment loads would increase from all action alternatives (USDA 2021c, Ellis DEIS and Ellis Hydrology Report). The projected sediment increases are alarmingly high, and in most of the subwatersheds, sediment is expected to increase anywhere from 100% to an astonishing almost 400% over the existing condition during treatment activities. Over 85 miles of streams in the project area are identified as designated critical habitat for ESA-listed Mid-Columbia River steelhead. The DEIS states that there are existing conditions of highly degraded watersheds and streams with elevated water temperatures and elevated sediment, and the project will result in increases of sediment from soil disturbance and loss of shade from the project. Then the DEIS asserts that "*Alternatives 2 and 5 [which will have the greatest amount of harvest and roads]*

would not hinder attainment of relevant properly functioning indicators pertaining to sediment and roads." In other words, the FS found that despite the huge sediment increases caused by the project's riparian logging and associated roadwork, the project is consistent with the PACFISH management direction.

As discussed above, sediment increases of this magnitude pose significant consequences for aquatic species. High sediment loads and water temperatures have already led to the severe decline of ESA-listed Mid-Columbia steelhead. Clearly in the case of the Ellis Integrated project and other projects, impacts to fish habitat and ESA-listed species will continue to occur, notwithstanding the PACFISH/INFISH management direction. Despite severely degraded riparian and stream habitat conditions and watersheds not in proper functioning condition, and the acknowledgement that timber harvest will dramatically increase sediment, the Forest Service continues to authorize riparian logging activities.

Another example is bull trout in the North Fork of the Malheur River that will be impacted by the Cliff Knox project (USDA 2021b). The Forest Service used a U.S. Fish and Wildlife Service process paper titled "A Framework to Assist in Making Endangered Species Act Determinations of Effect for Individual or Grouped Actions at the Bull Trout Subpopulation Watershed Scale" (USDI FWS 1998) to describe the environmental baseline for the project. The ESA-listed bull trout in this area has a subpopulation of less than 50 adults and are found in an 8-mile segment of designated critical habitat of the Malheur river and tributaries in the project area. The Cliff Knox DEIS cites that "*The Malheur River core area was estimated to have 50-250 individuals; however, the short-term trend was determined to be declining. The threat to the species was considered to be substantial, imminent and the population is at a high risk for extinction (USDI FWS 2008b)."* This high-risk bull trout subpopulation is characterized as in rapid decline or maintaining at alarmingly low numbers and under current management, the subpopulation will not improve with two generations (5 to 10 years). Yet, despite degraded habitat conditions with high water temperatures and sediment loads, the Forest Service downplays the impacts of increased sediment and loss of shade from the project and finds that the project is consistent with the INFISH management direction.

The impacts from riparian logging activities have the potential to increase significantly now that the Forest Service is permitted to cut large trees. As discussed previously, large trees are of outsized importance in terms of the benefits they provide to riparian areas, including provision of LWD, retention of fine sediment, and reductions of temperature. Removal of large trees will deplete already degraded systems. When roads are built in riparian areas and roads are constructed to remove large trees, the cumulative impacts from removing large trees will further aggravate seriously degraded conditions, leading to further declines in ESA-listed fish species. Since many of the ESA-listed fish are in dangerously low numbers, further timber harvest and roading will likely lead to local extinctions. Once gone, they cannot be recovered.

High quality forested riparian habitat for ESA-listed fish species is directly linked to the presence and abundance of large old trees. The combination of shade, soil and bank stability, nutrient cycling, and high-quality fish habitat is dependent on the continued existence of trees in riparian areas, particularly large trees since they have longer retention and durability. Bisson et al. (2003) reported that large trees are important to retain in areas with hydrologic connectivity to streams because they provide longer duration habitat structure in floodplains than small trees. Since large old trees have been depleted for over a century it is important to retain all remaining large trees. Continued removal under the guise of stand improvement is based on a silvicultural construct and not based on the habitat needs of ESA-listed species that are already jeopardized by past logging and roading practices.

In sum, the Forest Service's conclusion that the removal of protections for large trees will have "no effect" on ESA-listed aquatic species, based on the PACFISH/INFISH management direction, is insupportable. PACFISH and INFISH fail to prevent against logging-related impacts, and such impacts are likely to increase in magnitude with the removal of large trees. The continued entry into riparian areas via roads to harvest large trees will further compact and disturb soils, remove trees that are important for shade, sediment retention, nutrient cycling, and water quality, and further harm ESA-listed fish species. Yet the Forest Service is proposing to allow removal of large trees under the guise of restoration and wildfire resiliency contrary to the best available science and facts about large trees. One has only to look and compare wilderness and roadless areas to highly managed forested areas to see the last best chinook, steelhead and trout habitat is in the largely untrammeled areas. The quality of fish habitat and the abundance of ESA species are highly impacted by managed habitats due to the removal of large wood and extensive road systems to remove timber. In my opinion, the loss of the Eastside Screens' protections for large trees is another nail in the future coffin for ESA fish species and will likely lead to their extinction.

VI. Conclusion

Large trees in riparian areas are particularly important for a multitude of reasons. They are critical for a myriad of ecosystem services including filtering and providing clean water, shade to reduce water temperature, nutrient cycling, and future wood recruitment for LWD in streams. LWD provides important functions for sediment retention, hiding cover for aquatic species, a substrate for macroinvertebrates as food sources for fish, pool formation, and bank stability. These are important components for high quality habitat that support ESA-listed and sensitive fish species like Spring Chinook, steelhead, and bull, cutthroat and redband trout. Logging and associated roadbuilding activities adversely impact riparian areas in many ways, and such impacts have continued to occur in the last 25 years despite the PACFISH/INFISH management direction. Allowing the cutting of large trees in and around RHCAs—along with associated roadbuilding activities—will trigger increased impacts for riparian ecosystems and further jeopardize the future existence of ESA-listed fish species.

Sincerely,

/*Amy M. Stuart*/electronic signature

Amy M. Stuart, Fish Biologist

Literature Cited

Abell R.A., et al. 2000. Freshwater Ecoregions of North America: A Conservation Assessment. Washington (DC): Island Press.

Adams, D.M., R.W. Haynes, and A.J. Daigneault. 2006. Estimated timber harvest by U.S. region and ownership, 1950-2002. Gen. Tech. Rep. PNW-GTR-659. Pacific Northwest Research Station. 72 pp.

Beschta, R.L., C.A. Frissell, R. Gresswell, R. Hauer, J.R. Karr, G. W. D.A. Perry, and J.J. Rhodes. 1995. Wildfire and salvage logging: Recommendations for ecologically sound post-fire salvage management and other post-fire treatments on federal lands in the west. 14 pp.

Beschta, R.L., R.E. Bilby, G.W. Brown, L.B. Holtby and T.D. Hofstra. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. Pp. 191-232, In: Salo and Cundy, eds.

Bisson, P.A.; B.E. Rieman, C. Luce, P.F. Hessburg, J. L. Lee, G.H. Kershner, G.H. Reeves, and R.E. Gresswell. 2003. Fire and aquatic ecosystems of the Western USA: current knowledge and key questions. Forest Ecology and Management 178(1–2): 213–229.

Bjornn, T.C. and D.W. Reiser. 1991. Habitat requirements of salmonids in streams. *In* Meehan, W. (Ed). Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.

Boisjolie, B.A., M.V. Santelmann, R.L. Flitcroft, and S.L. Duncan. 2017. Legal ecotones: A comparative analysis of riparian policy protection in the Oregon Coast Range, USA. Journal of Environmental Management 197 (2017) 206-220.

Bottom, D.L., P.J. Howell, and J.D. Rodgers. 1985. The effects of stream alterations on salmon and trout habitat in Oregon. Oregon Department of Fish and Wildlife, Portland. 70 pp.

Bowerman, T., B.T. Neilson, and P. Budy. 2014. Effects of fine sediment, hyporheic flow, and spawning site characteristics on survival and development of bull trout embryos. Can. J. Fish. Aquatic Sci. 71: 1059–1071.

Brandt, P., D. J. Abson, D. A. DellaSala, R. Feller, and H. von Wehrden. 2014. Multifunctionality and biodiversity: ecosystem services in temperate rainforests of the Pacific Northwest, USA. Biological Conservation 169:362–371.

Burnett, K.M., G.H. Reeves, D.J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. Ecol. Applic. 17:66 – 80.

Carnefix, G. and C. Frissell. 2009. Aquatic and other environmental impacts of roads: the case for road density as indicator or human disturbance and road-density reduction as restoration target; a concise review. Pacific Rivers Council Science Publication 09-001. 9 pp.

Center for Biological Diversity. 2001. Imperiled trout and the importance of roadless areas: A report by the Western Native Trout Campaign. Tucson, AZ: The Center for Biological Diversity, Pacific Rivers Council, Biodiversity Associates.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117(1): 1-21.

Chin, A., D.M. Rohrer, D.A. Marion, and J.A. Clingenpeel. 2004. Effects of all-terrain vehicles on stream dynamics: In: J.M. Guldin (ed.). Ovachita and Ozark Mountains Symposium: Ecosystem Management Research. USDA For. Serv. Gen. Tech. Rep. SRS-74. Pp. 292-296.

Coffin, A.W. 2007. From roadkill to road ecology: A review of the ecological effects of roads. Journal of Transport Geography 15:396–406.

Cordova, J. 1995. Streamside forests, channel constraint, large woody debris characteristics, and pool morphology in low order streams, Blue Mountains, Oregon. M.S. Thesis. Oregon State University. Corvallis, OR. 143 pp.

DellaSala, D.A. and W.L. Baker 2020. Large trees: Oregon's bio-cultural legacy essential to wildlife, clean water, and carbon storage.

DellaSala, D.; J. Karr, and D. Olson. 2011. Roadless areas and clean water. Journal of Soil and Water Conservation, 66(3): 78A-84A. Accessed at: http://.jswconline.org/content/66/3/78A.full.pdf.

Dose, J. J. and B. B. Roper, 1994. Long-Term Changes in Low-Flow Channel Widths Within the South Umpqua Watershed, Oregon. Water Resources Bulletin 30:99-1000.

Elliot, W. J., I. S. Miller, and L. Audin (eds.). 2010. Cumulative watershed effects of fuel management in the western United States. Gen. Tech. Rep. RMRS-GTR-231. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 299 p.

Elliot, W.J., P.R. Robichaud, and R.B. Foltz. 2011. Erosion processes and prediction n NW US forests. International Symposium on Erosion and Landscape Evolution. September 18-21, 2011. Anchorage, Alaska. 8 pp.

Environmental Protection Agency. 2002. Functions and values of wetlands. Office of Water EPA 843-F-01-002c Environmental Protection Office of Wetlands, March 2002; Agency Oceans and Watersheds (4502T). 2 pp.

Espinosa, F.A., Rhodes, J.J., and McCullough, D. A. 1997. The failure of existing plans to protect salmon habitat on the Clearwater National Forest in Idaho. J. Env. Management 49: 205-230.

Everest, F.H., R.L. Beschta, J.S. Scrivener, K.V. Koski, J.R. Sedell and C.J. Cedarholm. 1987. Fine sediment and salmonid production: a paradox. Pp. 98-142, In: J. Colt and R.J. White, eds. Streamside management: forestry and fishery interactions. Contrib. No. 57. Seattle, WA. Institute of For. Res., Univ. WA.

Fissekis, A. and R. Hersh-Burdick. 2007. The physical characteristics of hyporheic Flow. Center for Watershed Sciences. University of California, Davis.

Foltz, R.B., N.S. Copeland, and W.J. Elliot. 2009. Reopening abandoned forest roads in northern Idaho, USA: quantification of runoff, sediment concentration, infiltration, and interrill erosion parameters. J. Environmental Management (Impact Factor: 3.06). 04/2009; 90(8):2542-50.

Frissell, C. 2017. Panel on logging in streamside corridors. John Day, Oregon. https://bluemountainsbiodiversityproject.org/panel-on-logging-in-streamside-corridors-john-day-oregon-2017/.

Frissell, C. and Carnefix, G.; 2007. The Geography of freshwater conservation: roadless areas and critical watersheds for native trout. Wild Trout IX symposium. Accessed at: http://www.blm.gov/or/plans/wopr/pub_comments/paper_documents/Paper_1989- 2023/WOPR_PAPER_01989.120001.pdf.

Furniss, M.J., T.D. Roelofs, and C.S. Yee. 1991. Road construction and maintenance in Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats. American Fisheries Society Special Publication 19:297-323.

Guenther, S., T. Gomi, and R. Moore, R. 2012. Stream and bed temperature variability in a coastal headwater catchment: influences of surface-subsurface interactions and partial-retention forest harvesting. Hydrological Processes, 28: 1238–1249.

Henjum, M. G., J. R. Karr, D. L. Bottom, D. A. Perry, J. C. Bednarz, S. G. Wright, S. A. Beckwitt, and E. Beckwitt. 1994. Interim protection for late-successional forests, fisheries, and watersheds: National forests east of the Cascade crest, Oregon and Washington. Technical Review 94-2, The Wildlife Society, Bethesda, MD.

Hessburg, P.F., S. Charnley, K.L. Wendel, E.M. White, P.H. Singleton, D.W. Peterson, J.E. Halofsky, A.N. Gray, T.A. Spies, R.L. Flitcroft, and R. White. 2020. The 1994 Eastside screens large tree harvest limit: Review of science relevant to forest planning 25 Years later. Gen. Tech. Rep. PNW-GTR-990. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 114 p.

Hicks, B.J., J.D. Hall, P.A. Bisson and J.R. Sedell. 1991. Responses of salmonids to habitat changes. Pp. 483-518, In: W.R. Meehan, ed. Influences of forest and rangeland management on salmonid fishes and their habitat. American Fisheries Society Sp. Publ. 19. Bethesda, MD.

Huntington, C.W. 1998. Streams and salmonid assemblages within roaded and unroaded landscapes in the Clearwater River Sub-basin, Idaho. In Proceedings of the forest-fish conference: Land management practices affecting aquatic ecosystems, eds. M.K. Brewin and D.M.A. Monida. Calgary, AB: Natural Resources Canada, Canada Forest Service, Northern Forest Center.

Hutto, R. L., R. E. Keane, R. L. Sherriff, C. T. Rota, L. A. Eby, and V. A. Saab. 2016. Toward a more ecologically informed view of severe forest fires. Ecosphere 7(2):e01255. 10.1002/ecs2.1255.

Jackson, W.L. and R. L. Beschta. 1984. Influences of sand delivery on the morphology of sand and gravel channels. Water Resources Bulletin 20(4): 527-533.

Jensen, D.W., E. A. Steel, A.H. Fullerton, and G.R. Pess. 2009. Impact of fine sediment on egg-to-fry survival of Pacific salmon: A meta-analysis of published studies. Reviews in Fisheries Science, 17(3):348–359.

Kreutzweiser, D.P., S.S. Capell, and K.P. Good.2005. Effects of fine sediment inputs from a logging road on stream insect communities: A large-scale experimental approach in a Canadian headwater stream. Aquatic Ecology 39(1):55-66. DOI:10.1007/s10452-004-5066-y.

Lee, D.C., J.R. Sedell, B.E. Rieman, R.F. Thurow, J.E. Williams, D. Burns, J.L. Clayton, L. Decker, R. Gresswell, R. House, P. Howell, K.M. Lee, K. Macdonald, J. McIntyre, S. McKinney, T. Noel, J.E. O'Connor, C.K. Overton, D. Perkinson, K. Tu. and P. Van Eimeren. 1997. Broadscale Assessment of Aquatic Species and Habitats. In: An Assessment of Ecosystem Components in the Interior Columbia Basin and Portions of the Klamath and Great Basins, T. M. Quigley and S. J. Arbelbide (Editors). USDA Forest Service Gen. Tech. Rep. PNW-GTR-405, Vol. III, Portland, Oregon, pp. 1057-1713.

Lisle, T.E. 1982. Effects of aggradation and degradation on riffle-pool morphology in natural gravel channels, northwestern California. Water Resources Research. 18:1643-1651.

Luce, B.H. and T.A. Black. 2001. Effects of traffic and ditch maintenance of forest road sediment production. Effects of Traffic and Ditch Maintenance on Forest Road Sediment Production. In Proceedings of the Seventh Federal Interagency Sedimentation Conference, March 25-29, 2001, Reno, Nevada. pp. V67–V74.

Mackey, B., I. Colin Prentice, W. Stelen, J.I. House, D. Lindenmayer, H. Keith and S. Berry. 2013. Untangling the confusion around land carbon science and climate change mitigation policy. Nature Climate Change. Vol. 3:552-557.

Mackey, B. 2014. Counting trees, carbon and climate change. Significance 11, no. 1: 19–23. https://doi.org/10.1111/j.1740-9713.2014.00720.x.

Mackey, B., D.A. DellaSala, C. Kormos, D. Lindenmayer, D, N. Kumpel, B. Zimmerman, S. Hugh, V. Young, S. Foley, K. Arsenis, and J.E.M. Watson. 2014. Policy Options for the World's Primary Forests in Multilateral Environmental Agreements. Cons. Let. doi: 10.1111/conl.12120.

Magee, J.P., T.E. McMahon, and R.F. Thurow. 1996. Variation in spawning habitat of cutthroat trout in a sediment-rich stream basin. Transactions of the American Fisheries Society 125 :768-779.

May, C.L. and D.C. Lee. 2004. The Relationships among In-Channel Sediment Storage, Pool Depth, and Summer Survival of Juvenile Salmonids in Oregon Coast Range Streams. North American Journal of Fisheries Management 24:761–774.

McDade, M.H., Swanson, F.J., McKee, W.A., Franklin, J.F., and Van Sickle, J. 1990. Source distances for coarse woody debris entering small streams in western Oregon and Washington. Can. J. For. Res. 20: 326–330.

McHugh et al. 2017. Linking models across scales to assess the viability and restoration potential of a threatened population of steelhead (*Oncorhynchus mykiss*) in the Middle Fork John Day River, Oregon, USA. Ecological Modelling. 355:24-38.

Meehan, W.R. ed. 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Publication. 622 pp.

Miserendino, L. and Masi, C. 2010. The effects of land use on environmental features and functional organization of macroinvertebrate communities in Patagonian low order streams. Ecological Indicators, 10(2): 311-319.

Oechsli, L., and C. Frissell. 2002. Aquatic Integrity Areas: Upper Missouri River Basin. American Wildlands, The Pacific River Council, Yellowstone to Yukon Conservation Initiative, Bozeman MT.

Ratner, S., R. Lande, and B. B. Roper. 1997. Population viability analysis of spring chinook salmon in the South Umpqua River, Oregon. Conserv. Biol. 11: 879-889.

Reid, L.M. and T. Dunne. 1984. Sediment production From forest road surfaces. Water Resources Research Vol. 20 (11):1753-1761.

Rhodes, J.J., McCullough, D.A., and Espinosa Jr., F.A., 1994. A Coarse Screening Process for Evaluation of the Effects of Land Management Activities on Salmon Spawning and Rearing Habitat in ESA Consultations. CRITFC Tech. Rept. 94-4, Portland, OR.

Roper, B.B., J.M. Capurso, Y. Peroz, and M.K. Young. 2018. Aquatic biodiversity conservation in the context of multiple use management of National Forest System lands. Fisheries, 43, 396–405.

Roper, B.B., W.C. Saunders and J.V. Ojala. 2019. Did changes in western federal land management policies improve salmonid habitat in streams on public lands within the Interior Columbia River Basin? Environ Monit. Assess (2019) 191:574.

Scrivener, J.C. and M.J. Brownlee. 1989. Effects of forest harvesting on spawning and incubation survival of chum and Coho salmon in Carnation Creek, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences. 46:681-696.

Steel, E.A., T.J. Beechie, C.E. Torgerson, and A.H. Fullerton. 2016 Envisioning, Quantifying, and Managing Thermal Regimes on River Networks. BioScience 67(6):506–522.

Strittholt, J.R., and D.A. DellaSala. 2001. Importance of roadless areas in biodiversity conservation in forested ecosystems: Case study of the Klamath Siskiyou ecoregion of the United States. Conservation Biology 15:1742–1754.

Strittholt, J.R., D.A. DellaSala, E. Fernandez, G. Heilman, Jr, and P.A. Frost. 2004. Oregon's legacy Wild Forests: Conservation Value of Oregon's Inventoried Roadless Areas. Corvallis, OR: Conservation Biology Institute, World Wildlife Fund, Oregon Natural Resources Council.

Stuart, A.S., D. Grover, T.K. Nelson, and S.L. Thiesfeld. 2007. Redband trout investigations in the Crooked River Basin. *In* Redband trout: resilience and challenge in a changing landscape. Oregon Chapter, American Fisheries Society, Corvallis. Pp. 77-90.

Sweeney, B.W. and J.D. Newbold. 2014. Streamside forest buffer width needed to protect stream water quality, habitat, and organism: A literature review. Journal of the American Water Resources Association (JAWRA) 50(3): 560-584. DOI: 10.1111/jawr.12203.

Trombulak, S.C., and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

Trout Unlimited (Public Lands Initiative). 2004. Where the Wild Lands are: Oregon; the Importance of Roadless Areas to Oregon's Fish, Wildlife, Hunting and Angling Accessed at: http://www.tu.org/sites/default/files/OR-Where-the-wildands-are.pdf.

USDA, Forest Service. 1989. Final Environmental Impact Statement: Land and Resource Management Plan, Ochoco National Forest and Crooked River National Grassland. U.S.D.A. Forest Service, Pacific Northwest Region (August 1989).

USDA, Forest Service. 1995. Inland Native Fish Strategy Environmental Assessment, Decision Notice and Finding of No Significant Impact, Intermountain, Northern and Pacific Northwest Regions. USDA Forest Service. 2006.

USDA Forest Service and USDI Bureau of Land Management. 1995. Decision notice/decision record for the interim strategies for managing anadromous fish-producing watersheds in eastern Oregon and Washington, Idaho, and portions of California. Washington, DC. PACFISH.

USDA, Forest Service. 2003. Roads Analysis Report Forest-Wide Assessment. Ochoco National Forest, Deschutes National Forest, Crooked River National Grasslands, January 2003.

USDA, Forest Service. 2005. 36 CFR Parts 212, 251, 261, and 295. Travel management; designated routes and areas for motor vehicle use; final rule. Available at http://www.fs.fed.us/recreation/programs/ohv/final.pdf.

USDA, Forest Service. 2018. Black Mountain Vegetation Management Project Draft Environmental Impact Statement. Ochoco National Forest, Paulina Ranger District. 536pp.

USDA, Forest Service. 2021a. Forest Plans Amendment Forest Management Direction for Large Diameter Trees in Eastern Oregon and Southeastern Washington. Environmental Assessment Pacific Northwest Region (R6) Oregon and Washington January 2021. 246 pp.

USDA, Forest Service. 2021b. Cliff Knox Draft Environmental Impact Statement. Malheur National Forest – Prairie City and Emigrant Creek Ranger Districts August 2021. 651 pp.

USDA, Forest Service, 2021c. Ellis Integrated Vegetation Project and Hydrology Report. Umatilla National Forest | Heppner and North Fork John Day Ranger Districts.

US Fish and Wildlife Service. 2010. Biological effects of sediment on bull trout and their habitat – guidance for evaluating effects. Prepared by Jim Muck U.S. Fish and Wildlife Service Washington Fish and Wildlife Office Lacey, WA. 57 pp.

Weaver, T.M. and J.J. Fraley. 1993. A method to measure emergence success of Westslope cutthroat trout fry from varying substrate compositions in a natural stream channel. North American Journal of Fisheries 13:817-822.

Williams, C.D. 1999. Summary of Scientific Findings on Roads and Aquatic Ecosystems. Primary Research and Analysis. Environmental Consultants, Medford, Or. 17 pp.

Wonzell, S., R. Haggerty, and M.N. Gooseff. 2009. Hyporheic Zones and Mountain Streams. Key Findings. USDA Forest Service. Aquatic Ecology and Management. Corvallis, OR. 5 pp.

Yonce, H.N., S. Saumya, J.B. Butcher, T.E. Johnson, S.H. Julius and S.D. LeDuc. 2021. Forest riparian buffers reduce timber harvesting effects on stream temperature, but additional climate adaptation strategies are likely needed under future conditions. Journal of Water and Climate Change 12 (5): 1404–1419.https://doi.org/10.2166/wcc.2020.031

Young, M.K., W.A. Hubert and T.A. Wesche. 1991. Selection of measures of substrate composition to estimate survival to emergence of salmonids and to detect changes in stream substrates. North American Journal of Fisheries Management. 11:339-346.

Amy M. Stuart

13501 NW Grizzly Mountain Rd
Prineville, OR 97754
(541) 447-5448 amystuart63@gmail.com

Education:
M.S. 1980, Wildlife Management, Colorado State University, Ft Collins, CO.
B.S. 1977, Wildlife Biology & Management, Cornell University, Ithaca, NY.

PROFESSIONAL EXPERIENCE:

Oregon Department of Fish and Wildlife (ODFW), 9/2007 to 2/2014, Deschutes Watershed Manager

- Supervised 60 professional and technical staff.
- Managed expenditures of a combined budget of $9 million per biennium for 25 cost centers.
- Implemented fish, wildlife, research and habitat program goals, objectives and priorities.

ODFW 7/1997 to 8/2007, Hydro Power Program Biologist, High Desert Region

- Lead for the High Desert Region for re/licensing and compliance for state and federal FERC licensed hydro projects in the Klamath, Deschutes, Hood and Owyhee basins.
- Lead negotiator and/or technical lead for the Pelton Round Butte Settlement Agreement, Klamath Settlement Agreement, and Powerdale hydro project decommissioning.

ODFW, 1/1990 to 6/997, District Fish Biologist (DB), Supervisory FWB (3 1/2 years) and NRS 3 (4 years), Ochoco District, High Desert Region

- Fish program manager for the Ochoco District (7½ years). Hired, supervised, and conducted performance reviews of 1 permanent, several seasonal employees and 3 high school interns.
- Collected and analyzed fish population abundance and distribution, species composition, and harvest; evaluate hatchery stocking, harvest regulations; implement habitat protection/restoration.

ODFW, 2/1988 to 12/1989, Assistant District Fish Biologist II, Ochoco District, High Desert Region

- Implemented the fish management program. Sole fish biologist and assumed lead responsibility; ½ time Ochoco National Forest Fish Biologist: advised fish issues for timber sales and range allotments; conducted fish, habitat surveys and habitat projects. Authored bull trout plan at Lake Billy Chinook.

ODFW, January 1986 to January 1988, Fish Habitat Biologist II, BPA Program, John Day, NE Region

- Implemented habitat program using restoration techniques to improve fish and wildlife habitat: bank stabilization and habitat projects. Implemented contracts and landowner lease agreements. Prepared annual reports. Developed, supervised and administered budgets, personnel, equipment, and ODFW staff.

1977-1986. ODFW Ocean Salmon, US Forest Service, US Army Corps of Engineers, Colorado Mined Land Reclamation, and private timber cruiser.

PUBLICATIONS

Stuart, A.M., D. Grover, T.K. Nelson, and S.L. Thiesfeld. 2007. Redband trout investigations in the Crooked River. Redband Trout: Resilience and Challenge in a Changing Landscape, Oregon Chapter, American Fisheries Society.

Stuart, A.M., S.L. Thiesfeld, D.E. Ratliff, T.T. Fies, and R.M. Hooton. 1997. Changes in management of bull trout in the Metolius River - from trash fish to trophy. Proceedings of the Friends of the Bull Trout Conference, May 1994. Bull Trout Task Force, Calgary, Alberta.

Stuart, A.M, S.L. Thiesfeld, T.K. Nelson, and T. Shrader. 1996. Crooked River Basin Fish Management Plan. Oregon Department of Fish and Wildlife, Portland, OR. May 1996.

Stuart, A. 1977. Flora and fauna of Craters of the Moon National Monument. In Volcanism of the Eastern Snake River Plain, Idaho: A Comparative Planetary Geology Guidebook, pp. 228-232. Edited by Greeley and King. National Aeronautics and Space Administration, Washington, D.C.

Co-Authored:

Ratliff, D.E., et al. 1999. Alternatives for renewing fish passage at Pelton Round Butte hydroelectric project, Madras, Oregon: 3d Public Draft. Interagency Fisheries Technical Subcommittee. Portland General Electric Company. Portland, Oregon.

Ratliff, D. E., et al. 1997. Changes in attitude toward bull trout at Lake Billy Chinook, Oregon. Proc. Friends of the Bull Trout Conference, May 1994. Bull Trout Task Force, Calgary, Alberta.

Ratliff, D.E., et al. 1996. Distribution, life history, abundance, harvest, and limiting factors of bull trout in the Metolius River and Lake Billy Chinook, Oregon, 1984-1994. ODFW, Portland, Oregon.

Riehle, M., et al. 1997. Progress report of the multi-agency study of bull trout (Salvelinus confluentus) in the Metolius River system, Oregon. Proc. Friends of the Bull Trout Conference, May 1994. Bull Trout Task Force, Calgary, Alberta.

Thiesfeld, S.L., et al. 1995. Angler surveys on Lake Billy Chinook, Oregon, 1990-1993. Oregon Department of Fish and Wildlife, Information Report 95-1, Portland, Or.

Thiesfeld, S.L., et al. 1996. Migration patterns of adult bull trout in the Metolius River and Lake Billy Chinook, Oregon. Oregon Department of Fish and Wildlife, Information Report 96-1, Portland.

Presentations

* Deschutes River Conservancy. 2008. The Pelton Round Butte Project: Fish Passage Plan and Reintroduction Objectives. Madras, Or.
* Oregon Chapter American Fisheries Society (OR AFS). 2007. The Pelton Round Butte Story: Quest for Success: Using Models and Science to build Successful Fish Passage at the Pelton Round Butte Project. Eugene, Or.
* Briefing to several federal, state and tribal agencies. 2005. Historic and potential restoration of anadromous fish to the Upper Klamath basin. Medford, Oregon.
* Cal-Neva-Humboldt Chapter, AFS. 2004. Relicensing the Klamath: An Opportunity for Restoration? Redding, Ca.
* Western Association of Fish and Wildlife Agencies. 2000. FERC Relicensing Process. Redmond, Or.
* Oregon Chapter American Fisheries Society. 1999. Hydro Relicensing in the State of Oregon, the Good, the Bad, and the Ugly. Sunriver, Or.

Numerous presentations to the Oregon Fish and Wildlife Commission and conservation groups for 20 years on a variety of topics including the Crooked River Basin Fish Management Plan, Annual Fishing Regulations, Hydro Relicensing, anadromous fish reintroduction and several projects in the Hood, Klamath, John Day and Deschutes basins.





Jonathan J. Rhodes
Hydrologist
2330 SE Taylor St •• Portland, OR 97214 •• 503.709.7007

April 28, 2022

Oliver Stiefel
Staff Attorney, Crag Law Center
3141 E Burnside Street
Portland, OR 97214

Re: Review and evaluation of how the removal of trees greater than 21" dbh will significantly and persistently harm aquatic systems on USFS lands east of the Cascades.

Dear Mr. Stiefel,

I am a hydrologist with more than 35 years of experience, with a B.S. in hydrology from University of Arizona, a M.S. in hydrology and hydrogeology from University of Nevada-Reno and I finished all required academic work toward a Ph.D. in forest hydrology at the University of Washington. Since 2001, I worked as a consulting hydrologist for a variety of clients, including county and tribal governments in Oregon, Washington, and Idaho. Prior to that I worked for more than 12.5 years at the Columbia River Inter-Tribal Fish Commission (CRITFC), where I served as Senior Scientist-Hydrologist. My professional experience includes work with tribal, federal, state, county, and city governments, universities, and non-profit groups in eight western states. A copy of my curriculum vitae is attached.

Most of my work has focused on the effects of current and proposed uses of land and water on water quality, streams and habitats for native trout and salmon. I am quite familiar with the management direction in PACFISH and INFISH, including how the USFS has implemented activities on its lands in Eastern Oregon and Washington. Our work at the CRITFC provided much of the foundation of PACFISH. I am also quite familiar with riparian and stream conditions on these USFS lands.

I have co-authored numerous papers on the effects of logging (including thinning), roads, and other activities on watersheds and aquatic systems published in peer-reviewed scholarly

journals. I've served as a peer-reviewer for scholarly forestry and fishery journals, including the North American Journal of Fisheries and the Open Forest Science Journal, as well as the Proceedings of Forest-Fish Conference: Land Management Affecting Aquatic Ecosystems.

My evaluation of how the removal of trees greater than 21" dbh will significantly and persistently harm aquatic systems on USFS lands east of the Cascades is based on my education and experience. It is also based on my considerable experience with forest removal activities on those lands implemented under PACFISH, INFISH and other USFS management direction. **The allowance to log larger trees in Inland USFS lands will cause significant long-term harm to already highly degraded aquatic systems and imperiled fish.**

There are several reasons that aquatic systems and imperiled fish will be harmed by the allowance to remove larger trees. Most significantly, this loss of larger trees will contribute to the loss of downed large woody debris (LWD) in streams and riparian habitats. This will persistently degrade fish habitats and riparian functionality.

The allowance for removal of larger trees is likely to occur within Riparian Habitat Conservation Areas (RHCAs) established under PACFISH and INFISH, based on my reviews of numerous forest removal activities (hereinafter: "logging") implemented in the more than two decades since the adoption of PACFISH and INFISH on numerous inland National Forests. These projects have commonly involved logging within designated RHCAs, despite the guidelines and standards contained in PACFISH and INFISH.

A significant number of these larger trees in RHCAs, if left unmolested by the depredation from logging, would ultimately be recruited into streams via various means (windthrow, bank erosion, death from old age, etc), providing instream LWD. Larger trees within a given distance from streams in RHCAs are more likely to land in streams other factors being equal. Notably, larger trees are farther along the trajectory to age-related mortality, which is a significant LWD recruitment factor.

The loss of larger trees in and near RHCAs also contributes to long-term LWD losses from adjacent trees in RHCAs. This is because, when larger trees fall, they often knock down other trees that provide LWD to streams and riparian areas. Thus, logging of larger trees is likely to ultimately reduce instream LWD in perennial streams via several means.

The removal of larger trees outside of RHCAs on non-fish-bearing non-perennial streams will also reduce LWD levels in these streams. This is because the widths of RHCAs along these streams are not adequate to retain unimpaired levels of LWD recruitment, even if all trees in these RHCAs are retained. The full retention of all trees within one site potential tree height from streams is required to ultimately provide unimpaired levels of LWD recruitment (Rhodes et al., 1994), but RHCA widths on non-perennial streams without fish are much narrower than that under PACFISH and INFISH.

The loss of LWD in streams is extremely significant for several reasons. LWD is vital to the survival and production of imperiled salmonids and the functionality of riparian ecosystems.

As we noted in Karr et al., (2004): "…there is no debate about the key role that large trees play in aquatic systems…"

LWD is the primary pool-forming element in salmonid habitats (Buffington et al., 2002; Pollock and Beechie, 2014). Pools, particularly, large, deep pools, are essential to salmonid production and survival. They provide essential refugia and rearing and resting habitats (McIntosh et al., 2002). Instream LWD provides cover, a vital aspect of pool quality affecting salmonid production and survival (Pollock and Beechie, 2014). It also aids in moderating water temperature (Pollock and Beechie, 2014).

The largest pieces of LWD, which can only come from larger trees, are the most effective agent of pool formation. Larger LWD pieces serve as critical anchors for LWD jams which are important pool forming agents (Buffington et al., 2002) that are particularly important to aquatic systems due to multiple benefits they convey (Pollok and Beechie, 2014). The effectiveness of LWD in pool formation tends to increase with the size of LWD (Buffington et al., 2002). These larger pieces of LWD also have the greatest longevity in stream channels and provide longer duration of instream functionality. Larger trees are older, thus, the recovery time from LWD lost due to logging increases as the size of tree logged increases. The loss of LWD is an extremely persistent impact, lasting more than a century in areas where trees are able to grow back after removal (Rhodes et al., 1994; McIntosh et al., 2000).

Loss of LWD from large tree logging negatively impacts salmonids. Available data indicate that salmonid production increases as LWD increases (Rhodes et al., 1994).

LWD loss contributes to the loss of pool quality, volume, and frequency (McIntosh et al., 2000; Pollock and Beechie, 2014). Salmonid numbers tend to increase with pool volume, quality, and frequency (Rhodes et al., 1994). Pool loss reduces the production capability of salmonid habitat (Rhodes et al., 1994). Thus, the loss of LWD from larger trees incurs long-term significant impacts on salmonids and their habitats (McIntosh et al., 2004; Pollock and Beechie, 2014). The loss of salmonid survival and production caused by loss of larger LWD in streams is not reversible and is irretrievable.

LWD aids in reducing channel erosion and buffering sediment inputs by providing sediment storage in headwater streams (Rhodes et al., 1994). This is an important function even in non-perennial streams because these streams comprise the vast majority of the stream network and provide most of the sediment to salmonid habitats.

LWD provides important sources of organic matter and nutrients in soils, which are vital to the long-term maintenance and protection of soil productivity (USFS and USBLM, 1997a; Karr et al., 2004). Soil productivity is critical to forest vegetation and a host of forest functions.

LWD in riparian areas aids in limiting stream damage from livestock grazing. This is not trivial, because livestock grazing is a major source of damage to salmonid habitats in the affected area (USFS and USBLM, 1997a; b). LWD helps to limit this damage by impeding livestock access to streams. The largest pieces of downed LWD in riparian areas provide the most effective impediment to livestock access to streams.

Any loss of LWD is significant due to its importance to stream habitats and salmonids coupled with their existing conditions. Pool loss in salmonid habitats has been extensive and severe over the past several decades in logged and roaded watersheds draining USFS lands in the interior Columbia basin (USFS and USBLM, 1997a; McIntosh et al., 2000). LWD loss has been a major contributing cause of this pool loss. The loss of pools and LWD has been repeatedly implicated as a significant factor in the widespread decline in the range and numbers of salmonid populations (Rhodes et al., 1994; McIntosh et al., 2000; Pollock and Beechie, 2014). Past logging and roading has greatly depleted existing LWD sources in many riparian areas throughout the affected region. This is extremely significant because one of most important roles of riparian forests with respect to aquatic biodiversity is production of LWD from large trees big enough to anchor wood jams and form pools (Pollock and Beechie, 2014). Instream LWD levels are widely depleted, and the allowance to log larger trees will exacerbate this long-term aquatic affliction. Salmonid populations throughout the affected area are imperiled (USFS and USBLM, 1997a). Additional degradation due to LWD loss contributes to the likelihood of increased extirpation of these populations and is inimical to the recovery of these salmonid populations. The time needed to recover from the loss of LWD caused by large tree logging is on the order of century or more. For these combined reasons, the loss of any sources of LWD from larger trees is ecologically significant.

It is extremely unlikely that the removal of larger trees in riparian areas would convey any potential benefits to aquatic systems. Logging in riparian areas under the rubric of "thinning" has been shown to reduce LWD (Pollock and Beechie, 2014). Similarly, such logging has been repeatedly shown to be highly unlikely to alter fire behavior, because it is extremely unlikely that fire will encounter treated areas during the short period of time that fuels have been temporarily reduced by treatments aimed at fuel reduction (Rhodes and Baker, 2008; Price et al., 2015).

My decades of experience with forest management activities on lands implemented under PACFISH and INFISH amply demonstrate that riparian logging has often been approved under the guise of restoring forest structure and/or fire behavior. While PACFISH and INFISH contain subjective direction that projects are not to retard or prevent attainment of riparian management objectives, in practice, this has not meant that that riparian logging is prohibited, or that negative impacts from such logging have not occurred. Instead, riparian logging activities approved under PACFISH and INFISH have frequently impacted aquatic ecosystem functions. This trend will continue, based on the track record of the USFS over the more than two decades since the adoption of PACFISH and INFISH. In my professional opinion, based on abundant scientific information, these impacts will be more severe and long-lasting now that large tree logging is allowed.

Please don't hesitate to contact me with any questions or follow-up related to any aspect of this work.

Sincerely,

Jonathan J. Rhodes
Hydrologist

Literature Cited

Buffington, J.M., Lisle, T.E., Woodsmith, R.D., and Hilton, S., 2002. Controls on the size and occurrence of pools in coarse-grained forest rivers. River Res. Applications, 18: 507-531.

Karr, J.R., Rhodes, J.J., and five others, 2004. Postfire salvage logging's effects on aquatic ecosystems in the American West. BioScience, 54: 1029-1033.

McIntosh, B.A. and four others, 2000. Historical changes in pool habitats in the Columbia River Basin. Ecological Applications, 10: 1478-1496.

Pollock, M. M. and Beechie, T. J., 2014. Does Riparian Forest Restoration Thinning Enhance Biodiversity? The Ecological Importance of Large Wood. JAWRA, 50: 543-559.

Price, O.F., Pausas, J.G., and five others, 2015. Global patterns in fire leverage: the response of annual area burnt to previous fire. International Journal of Wildland Fire, 24: 297-306.

Rhodes, J.J., McCullough, D.A., and Espinosa Jr., F.A., 1994. A Coarse Screening Process for Evaluation of the Effects of Land Management Activities on Salmon Spawning and Rearing Habitat in ESA Consultations. CRITFC Tech. Rept. 94-4, Portland, Or.

Rhodes, J. J., and Baker, W. L., (2008). Fire probability, fuel treatment effectiveness and ecological tradeoffs in western US public forests. The Open Forest Science Journal, 1(1).

USFS and USBLM, 1997a. The Assessment of Ecosystem Components in the Interior Columbia Basin and Portions of the Klamath and Great Basins, Volumes I-IV. PNW-GTR-405, USFS, Walla Walla Washington.

USFS and USBLM (Bureau of Land Management), 1997b. The DEIS for the "Eastside" Planning Area. USDA Forest Service, Walla Walla, Washington

Curriculum Vitae: Jonathan J. Rhodes
Hydrologist

EDUCATION

1989: Doctoral candidacy degree in forest hydrology at the Univ. of Wash. Completed all requirements but dissertation.

1985: M.S. in Hydrology and Hydrogeology at the Univ. of Nev.-Reno. Thesis topic: The influence of seasonal stream runoff patterns on water quality.

1981: B.S. in Hydrology and Water Resources at the Univ. of Ariz.

PROFESSIONAL HISTORY

Sept. 2001 -- present. Principal Hydrologist, Planeto Azul Hydrology. Main duties: Analysis of water and land use effects on streams and aquatic resources, including native salmonids and their habitats; diagnosis of watershed and stream conditions; stream monitoring; development of programmatic and site-specific watershed and stream protection measures; project management. Some projects (and clients): Analysis of potential effects of groundwater pumping on streamflow (Conf. Tribes of the Umatilla Indian Reservation, OR); diagnosis of watershed and stream conditions in an urbanized watershed (West Multnomah Soil and Water Conservation District, OR); analysis of data on sediment effects on ESA-listed salmon in the South Fork Stillaguamish River, WA (Snohomish County, WA).

Aug. 1990 -- Sept. 2001. Consulting hydrologist for non-profit organizations. Past projects (and clients) include: hydrologic characterization of remnant marsh proposed as urban wildlife refuge/greenspace (Multnomah Co. Parks Dept, OR); review of aquatic effects of: quarry expansion (Friends of Forest Park, OR), urban construction (homeowners consortium, W. Linn, OR); forest manipulations on streamflow (Pacific Rivers Council).

Apr. 1989 -- Sept. 2001. Senior Fishery Scientist-Hydrologist, Columbia River Inter-Tribal Fish Commission. Main duties: Administration and implementation of projects monitoring channel change from land use; development of programmatic and site-specific land management plans to ensure protection of watershed integrity, water quality and aquatic resources; development of restoration plans for watersheds degraded by grazing, roads, logging, and mining; design of plans for monitoring watershed and stream erosion, sedimentation, water quality, and habitat conditions; review of land management plans for adequacy of protection of aquatic resources; field evaluation of watershed and channel conditions throughout the Columbia Basin; expert witness testimony; development of technical recommendations for policy staff for protection of natal habitat for anadromous fish; review of state and federal aquatic resource monitoring plans; report and proposal writing; and, participation in various state and federal technical work groups.

Aug. '84 -- Apr. '89. Research assistant, College of Forestry, Univ. of Wash. Main duties: analysis and interpretation of water quality-quantity data; technical report writing; design and maintenance of water chemistry and quantity monitoring network in a coastal forested watershed; training in data acquisition techniques; public presentation of findings.

July -- Oct. 1987 and May -- Oct. 1988. Consulting hydrologist, Tahoe Regional Planning Association, CA and NV. Main duties: field delineation and mapping of riparian zones, wetlands, and erosion-prone areas.

June -- Sept. 1985 and July 1986. Research assistant, Dept. of Geophysics, Univ of Wash. Main duties: operation of field station for glacier research on Mt. Olympus, Wash.; measurement of snow and glacier melt rates; mapping of supra- and extra- glacial streams contributing to basal sub-glacial flow rates on surging and non-surging glaciers in the Alaska Range, Alaska.

Jan. 1984. Consultant with C.M. Skau, Reno, NV. Main duties: field evaluation of logging roads for erosion potential and sedimentation risk; recommendations for placement of future roads to minimize erosion and sediment delivery to fish-bearing streams in coastal Northern California.

Oct. 1983 -- June 1984. Hydrologic Tech., USGS, Carson City, NV. Main duties: aid in development and calibration of predictive water quality model for the Truckee River; statistical analysis of water quality data; identification and quantification of non-point sources of nutrients to Truckee River, NV.

Aug. 1981 -- Sept. 1983. Research Assistant, Univ. of Nev.-Reno. Main duties: design and installation of instrument network to monitor water chemistry and quantity in a small, forested alpine watershed in the Sierra Nevada; water quality sampling; data interpretation and management; preparation of reports, grant proposals, and publications, computer programming for data reduction and storage; mapping of geology, soils and runoff-producing areas; and, training of field technicians.

Feb. -- May 1981. Water Quality Intern, Pima Assoc. of Gov'ts., Tucson, AZ. Main duties: water quality sampling of agricultural production wells; mapping of groundwater levels; and, coordination of sampling efforts.

PROFESSIONAL SERVICE

May 2009 – present. Peer Reviewer for the scholarly journal, Open Forest Science Journal, for papers related to hydrology and forest and watershed responses to disturbance.

Feb. 2010. Invited Guest Lecturer, Lewis and Clark School of Law course on public lands law:
"PACFISH and INFISH and Imperiled Salmonids on Public Lands" Portland, OR.

Feb. 2009. Invited Guest Lecturer, Lewis and Clark School of Law course on public lands law:
"PACFISH and INFISH and Imperiled Salmonids on Public Lands" Portland, OR.

Feb. 2008. Invited Guest Lecturer, Lewis and Clark School of Law course on public lands law:
"PACFISH and INFISH and Imperiled Salmonids on Public Lands" Portland, OR.

Mar. 2007. Invited Panel Speaker, International Environmental Law Conference: "Fuel Treatments & Thinning: Its Impacts and Low Priority Relative to Other Needed Restoration Measures," Univ. of OR, Eugene, OR.

Mar. 2007. Invited Panel Speaker, International Environmental Law Conference: "The Impacts of Livestock Grazing on Water Quality and Trout Habitats," Univ. of OR, Eugene, OR.

Feb. 2005. Invited Guest Lecturer, Lewis and Clark School of Law course on public lands law:
"Postfire Watershed Management on Western Public Lands" Portland, OR.

Mar. 2004. Invited Panel Speaker, International Environmental Law Conference: "Postfire Watershed Restoration," Univ. of OR, Eugene, OR.

April 2002. Invited Speaker, Restoring Public Lands Conference: Reclaiming the Concept of Forest Restoration, "Watersheds and Fisheries: Restoration Needs for Trout Habitats," Univ. of CO, Boulder, CO

Mar 2002. Invited Panel Speaker, International Environmental Law Conference: "Soils, Impacts and Effects on Trout Habitat," Univ. of OR, Eugene, OR

Mar. 2001. Invited Panel Speaker, International Environmental Law Conference: "NFMA and Salmon Habitat Protection," Univ. of OR, Eugene, OR.

May 2000. Invited speaker, 5th National Tribal Conf. on Environmental Management: "Federal Land Management's Effects on Critical Habitat for Endangered Salmon," Lincoln City, OR

July 1998-2000. Peer Reviewer for the scholarly journal, N. Amer. J. Fish, for papers related to the sedimentation of fish habitat in response to erosion from land uses and fire.

Feb. 1998. Invited Speaker, Oregon AFS Annual meeting: "Adaptive management: Is it really adaptive?" Sunriver, OR

May 1996-2000. Guest lecturer, Oregon State Univ. graduate course on riparian and wetland ecology, Corvallis, OR

Apr.-May 1996. Peer-reviewer for Proceedings of Forest-Fish Conference: Land Management Affecting Aquatic Ecosystems, Proc. Forest-Fish Conf., May 1-4, 1996, Calgary, Alberta, Canada. Nat. Resour. Can., Can. For. Serv. Nort. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-356.

Apr. 1995. Invited speaker, Pacific Rivers Council Workshop on Watershed Analysis and Salvage Logging, Wenatchee, Wash.

Apr. 1995. Invited speaker, Oregon State Univ. Dept of Fisheries and Wildlife Seminar, Corvallis, OR

Apr. 1995. Invited speaker, American Fisheries Society North Pacific International Chapter, Annual Meeting, Vancouver B.C., Can.

Mar. 1995. Invited speaker, American Fisheries Society Idaho Chapter Annual Meeting, Boise, ID.

Nov. 1994. Invited speaker, President's Council on Sustainable Development Workshop, Yakima, WA.

Sept. 1994. Invited speaker, Oregon Water Resources Research Institute Streambank Restoration Conference: "Biological Methods to Stabilize Streambanks--From Theory to Practice," Portland, OR.

Mar.-April, 1994. Peer-reviewer for Henjum et al., 1994. Interim Protection for Late Successional Forests, Fisheries, and Watersheds: National Forests East of The Cascade Crest, Oregon and Washington. The Wildlife Soc., Bethesda, MD.

Jan. 1993-Sept. 1995. Member, Oregon Department of Environmental Quality's (ODEQ) Technical Advisory Committee for Triennial Review of the State Water Temperature Standard.

Mar. 1993. Invited speaker, Northwest Scientific Association Symposium: "Cumulative Effects of Land

Management Practices on Anadromous Salmonids," La Grande, OR.

Aug. 1992 - Sept. 1992. Member, Ad Hoc Consultant Selection Committee for Portland Water Bureau Study of Future Water Supply Needs.

May 1992. Invited Speaker, US Forest Service, Pacific Northwest Region, Regional Workshop on Monitoring Soil and Water Resources, Bend, OR.

May 1992. Invited Speaker, Northern Arizona University, School of Forestry, Graduate Seminar Series, Flagstaff, AZ.

Jan. 1991 - Mar. 1995. Member, Technical Work Group: Upper Grande Ronde River Anadromous Fish Habitat Protection, Restoration and Monitoring Plan.

Aug. 1989 - Feb. 1990. Member, Technical Advisory Committee to ODEQ for development of definitions for level of beneficial use impairment by nonpoint sources.

May 1989 - Jan. 1991.Member, Nonpoint Source Technical Advisory Committee to Idaho Department of Environmental Quality: Coordinated Nonpoint Source Monitoring Program For Idaho.

PUBLICATIONS
Peer-Reviewed:

Rhodes, J.J., C.M. Skau, and W.M. Melgin, 1984. Nitrate-nitrogen flux in a forested watershed -- Lake Tahoe, USA. In: Recent Investigations in the Zone of Aeration, Proc. of Inter. Symp., Munich, West Germany, 1984, P. Udluft, B. Merkel, and K. Prosl (Eds), pp. 671-680.

Rhodes, J.J., 1985. A Reconnaissance of Hydrologic Transport of Nitrate in An Undisturbed Forested Watershed Near Lake Tahoe. M.S. thesis, Univ. of Nev. Reno, 254 pp.

Rhodes, J.J., C.M. Skau, and J.C. Brown, 1985. An areally intensive approach to hydrologic nutrient transport in forested watersheds. In: The Forest-Atmosphere Interaction, B.A. Hutchison and B.B. Hicks (Eds), pp. 255-270.

Rhodes, J.J., C.M. Skau, D. Greenlee, and D.L. Brown, 1985. Quantification of nitrate uptake by riparian forests and wetlands in an undisturbed headwaters watershed. US Forest Service Gen. Tech. Rept. RM-120.

Rhodes, J.J., C.M. Skau, and D. Greenlee, 1986. The role of snowcover on diurnal nitrate concentration patterns in streamflow from a forested watershed in the Sierra Nevada, Nevada, USA. In: Proc. of AWRA Symposium: Cold Regions Hydrology, Fairbanks Alaska, 1986, D.L. Kane (Editor), pp. 157-166.

Rhodes, J.J., R.L. Armstrong, and S.G. Warren, 1987. Mode of formation of "ablation hollows" controlled by dirt content of snow. J. Glaciology, **33**: 135-139.

Edmonds, R.L., T.B. Thomas, and J.J. Rhodes, 1991. Canopy and soil modification of precipitation chemistry in a temperate rain forest. Soil Soc. of Amer. J., **55**: 1685-1693.

Rhodes, J.J., McCullough, D.A., and Espinosa Jr., F.A., 1994. A Coarse Screening Process for Evaluation of the Effects of Land Management Activities on Salmon Spawning and Rearing Habitat in ESA Consultations. CRITFC Tech. Rept. 94-4, Portland, OR http://www.critfc.org/tech/94-4report.htm

Rhodes, J.J. 1995. A Comparison and Evaluation of Existing Land Management Plans Affecting Spawning and Rearing Habitat of Snake River Basin Salmon Species Listed Under the Endangered Species Act. CRITFC Tech. Rept. 95-4, Portland, OR http://www.critfc.org/tech/95-4report.htm

Rhodes, J.J. 1996. Description and Evaluation of Some Available Models for Estimating the Effects of Land Management Plans on Sediment Delivery, Channel Substrate, and Water Temperature, CRITFC, Portland, OR

Espinosa, F.A., Rhodes, J.J., and McCullough, D. A. 1997. The failure of existing plans to protect salmon habitat on the Clearwater National Forest in Idaho. J. Env. Management **49**: 205-230.

Rhodes, J.J., and Purser, M.D., 1998. Overwinter sedimentation of clean gravels in simulated redds in the upper Grande Ronde River and nearby streams in northeastern Oregon, USA: Implications for the survival of threatened spring chinook salmon, Forest-Fish Conference: Land Management Affecting Aquatic Ecosystems, Proc. Forest-Fish Conf., May 1-4, 1996, Calgary, Alberta, Canada. Nat. Resour. Can., Can. For. Serv. Nort. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-356, pp: 403-412.

Beschta, R.L., Rhodes, J.J., Kauffman, J.B., Gresswell, R.E, Minshall, G.W., Karr, J.R, Perry, D.A., Hauer, F.R., and Frissell, C.A., 2004. Postfire Management on Forested Public Lands of the Western USA. Cons. Bio., 18: 957-967.

Karr, J.R., Rhodes, J.J., Minshall, G.W., Hauer, F.R., Beschta, R.L., Frissell,C.A. Perry, D.A, 2004. Postfire Salvage Logging's Effects on Aquatic Ecosystems in the American West. BioScience, 54: 1029-1033.

Rhodes, J.J. and Odion, D.C., 2004. Comment Letter: Evaluation of the Efficacy of Forest Manipulations Still Needed. BioScience, 54: 980.

Rhodes, J.J., 2005. Comment on "Modeling of the interactions between forest vegetation, disturbances, and sediment yields" by Erkan Istanbulluoglu et al. J. Geophys. Res. Earth Surf., Vol. 110, No. F1, F01012 10.1029/2004JF000240

Rhodes, J.J., 2007. The Watershed Impacts of Forest Treatments to Reduce Fuels and Modify Fire Behavior. Pacific Rivers Council, Eugene, OR

Rhodes, J.J. and Baker, W.L., 2008. Fire probability, fuel treatment effectiveness and ecological tradeoffs in western U.S. public forests. Open Forest Science Journal, 1: 1-7.

Lewis, J., Rhodes, J.J., and Bradley, C. 2018. Turbidity responses from timber harvesting, wildfire, and post-fire logging in the Battle Creek watershed, Northern California. Env. Mgmt, 1-17.

Technical Reports:

1986. Annual Report on Watershed Studies at Olympic National Park. College of Forestry, Univ. of Wash., Seattle, Wash. (Co-authors: R.L. Edmonds, T.B. Thomas, T.W. Cundy)

1987. Annual Report on Watershed Studies at Olympic National Park. College of Forestry, Univ. of Wash., Seattle, Wash. (Co-authors: R.L. Edmonds, T.B. Thomas, T.W. Cundy)

1988. Annual Report on Watershed Studies at Olympic National Park. College of Forestry, Univ. of Wash., Seattle, Wash. (Co-authors: R.L. Edmonds, T.B. Thomas, T.W. Cundy)

1989. Annual Report on Watershed Studies at Olympic National Park. College of Forestry, Univ. of Wash., Seattle, Wash. (Co-authors: R.L. Edmonds, T.B. Thomas, T.W. Cundy)

1990. Coordinated Nonpoint Source Monitoring Program For Idaho. Idaho Dept. of Environmental Quality, Boise, Idaho. (Co-authors: B. Clark, D. McGreer, W. Reid, T. Burton, W. Low, I. Urnovitz, D. McCullough, T. Litke)

1992. The Upper Grande Ronde River Anadromous Fish Habitat Protection, Restoration and Monitoring Plan. Wallowa-Whitman National Forest, Baker, OR (Co-authors: M. Purser, P. Boehne, R.E. Gill, R.L. Beschta, J.R. Sedell, B. McIntosh, J. Zakel, J.W. Anderson, D. Bryson, S. Howes, R. George).

1992. Salmon Recovery Program for the Columbia River Basin: An Advisory Report for the US Congress, Col. Riv. Inter-Tribal Fish Comm., Portland, OR (Co-authors: P.R. Mundy, D.A. McCullough, M.L. Cuenco, T.W. Backman, D. Dompier, P. O'Toole, S. Whitman, E. Larson, B. Watson, G. James).

1993. A comprehensive approach to restoring habitat conditions needed to protect threatened salmon species in a severely degraded river--The Upper Grande Ronde River Anadromous Fish Habitat Protection, Restoration and Monitoring Plan. USFS Gen. Tech. Rept RM-226, pp. 175-179. (Co-authors: J.W. Anderson, R.L. Beschta, P. Boehne, D. Bryson, R.E. Gill, S. Howes, B. McIntosh, M.D. Purser and J. Zakel).

1993. Dante's Video Guide to Habitat Conditions for Wild Spring Chinook Salmon, Steelhead and Bull Trout in the John Day Basin, Oregon. (Video) Presented at AFS National Meeting, Portland, Or, Aug. 29-31. (Co-authors: R. Taylor and M. Purser).

1995. Wildfire and Salvage Logging: Recommendations for Ecologically Sound Post-Fire Salvage Logging and Other Post-Fire Treatments on Federal Lands in the West. Pacific Rivers Council, Portland, OR (Co-authors: R. Beschta, C. Frissell, R. Gresswell, R. Hauer, J. Karr, G. Minshall, D. Perry).

1998. Adaptive management: Is it really adaptive? Abstracts: Oregon AFS Annual Meeting, Feb. 11-13, 1998, p. 31.

1998. Thinning For Increased Water Yield in the Sierra Nevada: Free Lunch or Pie in the Sky? Pacific Rivers Council, Eugene, OR. (Co-author: M. Purser)

1999. Annual Project Report: Watershed Evaluation and Aquatic Habitat Response to Recent Storms. Bonneville Power Administration (BPA), Portland, OR. (Co-author: C. Huntington)

1999. Annual Project Report: Monitoring Fine Sediment in Salmon Habitat in John Day and Grande Ronde Rivers. BPA, Portland, OR (Co-author: M. Purser)

2000. Annual Project Report: Watershed Evaluation and Aquatic Habitat Response to Recent Storms. BPA, Portland, OR. (Co-author: C. Huntington)

2000. Annual Project Report: Monitoring Fine Sediment in Salmon Habitat in John Day and Grande Ronde Rivers. (Co-author: M. J. Greene)

2001. Annual Project Report: Monitoring Fine Sediment in Salmon Habitat in John Day and Grande Ronde Rivers. BPA, Portland, OR. (Co-author: M. J. Greene)

2001. Imperiled Western Trout and the Importance of Roadless Areas. Western Native Trout Campaign, Center for Biological Diversity, Tucson, Az. (Co-authors: J. Kessler, C. Bradley, and J. Wood)

2002. Tryon Creek Watershed: Overview of Existing Conditions, Data Gaps, and Recommendations for the Protection and Restoration of Aquatic Resources. West Multnomah Soil and Water Conservation District, Portland, OR

2002. An Analysis of Trout and Salmon Status and Conservation Values of Potential Wilderness Candidates in Idaho and Eastern Washington. Western Native Trout Campaign, Center for Biological Diversity, Tucson, AZ. (Co-authors: C. Bradley, J. Kessler, C. Frissell)

2003. Stream and Fish Habitat Conditions in Tryon Creek: Their Likely Causes and Ramifications for Salmonids. Proceedings of Urban Ecology and Conservation Symposium, January 24, 2003, Portland, OR. Portland State University, Environmental Sciences and Resources, Portland, OR

2008. Primary Sources of Fine Sediment in the South Fork Stillaguamish River. Interim progress report for Washington State Salmon Recovery Funding Board, Olympia, WA. Snohomish County Public Works Surface Water Management, Everett, WA. (Co-authors: M. Purser, B. Gaddis, S. Britton, T. Coburn, and M. Rustay)

2009. Primary Sources of Fine Sediment in the South Fork Stillaguamish River. Project completion report for Washington State Salmon Recovery Funding Board, Olympia, WA. Snohomish County Public Works Surface Water Management, Everett, WA. (Co-authors: M. Purser, B. Gaddis)

2015. The High Costs and Low Benefits of Attempting to Increase Water Yield by Forest Removal in the Sierra Nevada. 108 pp. Environment Now, 12400 Wilshire Blvd, Suite 650, Los Angeles, CA 90025. (Co-author: CA. Frissell)

Semi-Technical Publications:

1993. Dam the analysis--heal streams instead. The Assoc. of Forest Service Employees for Env. Ethics Inner Voice, **5**(6): 1, 4-5.

1994. Invited Preface to Northwest Science Special Issue--Environmental History of River Basins in Eastern Oregon and Washington. Northwest Sci., **68**.

PROJECT MANAGEMENT

1993-1996. Technical Assistance Contract with NMFS to produce technical guidance for ESA consultations for effects of land management on critical habitat for Columbia basin salmon. Main duties: Primary Investigator; primary author of peer-reviewed reports including proposed guidelines for salmon habitat effects assessment (Rhodes et al., 1994), evaluation of land management plans' protection of critical salmon habitat (Rhodes, 1995), and evaluation of models for estimating land management effects on salmon habitat (Rhodes, 1996); available scientific literature review; budget tracking; project coordination. Total budget: $230,000.

1998-2000. Watershed Evaluation and Aquatic Habitat Response to Recent Storms. Main duties: Primary Investigator; design and implementation of monitoring methods, coordination of technical staff in 10 watersheds with differing levels of grazing and logging in 3 subbasins in Idaho, Washington, and Oregon; technical training; data analysis; contract administration; proposal development; report preparation; budget development and tracking; coordination with grantor representatives. Total budget: $164,000.

1998-2000. Evaluation of Effects of Grazing on Rate of Salmon Habitat Recovery. Main duties: Primary Investigator; design and implementation of monitoring methods, training of field technician; data analysis and synthesis; proposal development; preparation of progress reports; budget development and tracking; coordination with grantor representatives. Total budget: $73,000.

1998-2001. Monitoring Fine Sediment Levels in Salmon Habitat in Grande Ronde and John Day Rivers. Main duties: Primary Investigator; design and implementation of methods for monitoring fine sediment levels in four rivers; field technician training; data analysis and synthesis; subcontract administration; proposal development; progress and technical report preparation; budget development and tracking; coordination with grantor representatives. Total budget: $128,000.

2001-2002. Western Native Trout Campaign, Aquatic Scientist and Coordinator. Main duties: Oversight and assurance of scientific integrity of all reports and work products; coordinate conservation efforts among campaign member organizations and other groups working to protect and restore trout habitats and populations; budget tracking; technical and progress report preparation.

HONORS AND AWARDS

1996. Leadership and Excellence. Col. River Inter-Tribal Fish Comm., Portland, OR

1991. Employee of the Year. Col. River Inter-Tribal Fish Comm., Portland, OR

1984. Academic Recruitment Scholarship for Outstanding Graduate Prospect. Univ. of Wash, Seattle, Wash.

1982. Maxey Award -- Outstanding Graduate Student Paper in Hydrology. Univ. of Nev.-Reno.

1980. Winslow and Myron Reuben Scholarship for Outstanding Undergraduate in the Earth Sciences. Univ. of Ariz., Tucson, Az.

ADDITIONAL TRAINING

1993. USFWS Water Temperature Modeling via SNTEMP

1991. USFWS Introduction to IFIM Investigations