WILD
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Comments on Amendments to Land Management Plans to Address Old-Growth Forests Across the National Forest System: Draft Environmental Impact Statement for the Old Growth National Amendment (FRN 65356)

Submitted for the public record via:
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Wild Heritage is a science-based conservation group whose mission is to protect primary forests of all age classes and forest types globally and in North America. Given the scarcity of primary forests in the US (lower 48 states especially), we call for the protection of all remaining primary forests (old growth, complex early seral that has not been logged) in addition to allowing mature forests to restore old-growth characteristics overtime (i.e. proforestation, Moomaw et al. 2019).

We appreciate the opportunity to comment on the Draft Environmental Impact Statement (DEIS) for the National Old Growth Amendment (OGNA) proposed for all 128 national forests. We recognize that this has been a monumental task for the agency as initially directed by President Joe Biden under Executive Order (EO) 14072. However, we have substantive concerns with the analysis and findings that do not provide an adequate range of alternatives, are not based on best available science, will degrade ecological integrity of mature and old-growth forests (MOG), and cause undo harm to their biodiversity values and carbon stores.

Wild Heritage has published numerous peer-reviewed studies on old-growth ecology and its conservation that have national and regional significance in structuring an alternative based on best available science. We summarily find that the DEIS did not following the best available science largely because it ignored requests from the public and scientists to fix the numerous problems in scoping and the agency's inadequate treat analysis, and to provide protection for all of the nation's MOG from logging. Our main concerns with the DEIS are summarized in the following points.

(1) The DEIS does not: (a) provide an adequate range of alternatives nor does it take a hard look at the importance of mature forest protections as well as old growth, (b) must include protection from all forms of logging (thinning or otherwise) in old-growth forests on the Tongass National Forest, and (c) lacks a proper analysis of carbon loss from management actions, and the appropriate recognition of the substantial carbon sink in MOG that will be degraded by the agency's "stewardship" activities. None of the alternatives comply with relevant administrative policies,

including, the Glasgow Leaders' Forest Pledge, the Paris Climate Agreement (Article 5.1), and US global policy on reducing emissions across all sectors, particularly forestry.

(2) Not a single acre of MOG is protected under the DEIS despite requests made by hundreds of scientists in scoping to use this unique opportunity to prohibit the **commercial exchange** of large trees in the nation's older forests. In doing so, the DEIS essentially ignores the overwhelming public and scientific support for strict protections from logging. In fact, logging levels are projected to go up, especially in the Pacific Northwest where MOG is concentrated (Threat Analysis, Figure A8.6-7).

(3) The alternatives would squander a unique opportunity to end degradation of MOG and is therefore inconsistent with the Glasgow Forest Pledge - that is - logging in the DEIS would result in forest degradation as defined by multiple studies (e.g., Rogers et al. 2022, DellaSala et al. in prep - see below).

(4) The DEIS is silent on the 30 x 30 aspects of EO 14008 whereby the agency was directed by the president to begin closing the gap on this target - that is-while the Forest Service barely responded to the intent of EO 14072, it completely ignored the protection direction of EO 14008. Compliance with EO 14008 therefore should have been analyzed.

(5) Does not address the White House road-map on nature-based solutions[1] given nothing in the DEIS protects a single acre of carbon-dense MOG from logging that is the nation's best terrestrial carbon sinks (DellaSala et al. 2022a - mature/old growth analysis).

(6) Inappropriately compares all disturbances as having equivalent degradation effects on ecosystem integrity while downplaying major differences between commercial logging and natural disturbances. The threat analysis is an apples to oranges comparison of natural disturbances vs logging because natural disturbances result in essential successional processes in MOG that produce complex early seral forests with high levels of biodiversity, integrity, and carbon stocks (Swanson et al. 2010), while logging removes legacies, degrades integrity, and releases carbon (Law et al. 2018, Hudiburg et al. 2019, Moomaw and Law 2023). This major difference is not analyzed properly in the DEIS that groups logging together with natural disturbances as if they are equivalent in impacts to ecosystem integrity (we mentioned this repeatedly in scoping and in our comments on the threat assessment). Thus, the agency did not take a hard look at all forms of logging in MOG in relation to degradation as defined in the literature, discussed below, and in our prior comments.

(7) Overstates the efficacy of thinning to reduce the intensity and frequency of insect outbreaks, forest diseases, and wildfires by ignoring published reviews of the substantial co-lateral damages from Forest Service logging and fire suppression actions that are far worse than the beneficial effects of natural disturbances on ecosystem integrity and ecosystem dynamics (DellaSala et al. 2022b - Sisyphus article).

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[1] https://www.whitehouse.gov/briefing-room/statements-releases/2022/11/08/fact-sheet-biden-%E2%81%A0harris-administration-announces-roadmap-for-nature-based-solutions-to-fight-climate-change-strengthen-communities-and-support-local-economies/

(8) The agency did not analyze an alternative that restricts all forms of commercial exchange of large trees even though large trees and their carbon values have been defined and analyzed independently (see below) and sent to the agency during scoping.

For these reasons, we request that the Forest Service develop a preferred alternative that places clear restrictions on the **commercial exchange** of all large trees in MOG nationwide (that includes frequent and infrequent fire systems) and that you include full protections for the Tongass National Forest because it has the highest concentration of old growth in the nation, is the nation's most vital carbon sink (DellaSala et al. 2022c - Tongass article), is potential climate refugia (DellaSala et al. 2015 - NWFP article), and does not need thinning in its older forests. While Alternative 3 includes restrictions on commercial harvest, we prefer that you analyze restrictions on the **commercial exchange of large trees** (defined below) given that the agency can still log commercially under Alternative 3 by defining the purpose and need as something other than a commercial timber harvest.

We summarily disagree with the agency's decision to not select Alternative 3 on grounds that it would limit the application of prescribed fire without commercial removal of large trees (see below). While small tree thinning under limited conditions can reduce the potential for crown damage, small trees play a vital ecosystem role in resilience strategies as they tend to be the survivors of beetle infestations (Six et al. 2014, 2016) and may have important adaptive traits in a warming climate (Baker and Williams 2015).

We also disagree with the notion that the action alternatives constitute "stewardship" of old-growth ecosystems. Removing carbon, degrading wildlife habitat, compacting soils from thinning, and logging large trees in no way, shape, or form is "stewardship." As an example of one of the problems in the agency's notion of stewardship, the Forest Service continues to conduct an inappropriate analysis of carbon stock reductions from its management actions by using the wrong spatial scale of analysis in comparing timber harvest emissions at the project level to the entire US GHGs in many of its EAs. The agency also routinely overstates wood substitution benefits (Harmon 2019), and downplays logging related carbon losses (DellaSala et al. 2022b). In doing so, the Forest Service has not taken a hard look at the cumulative degradation of ecosystem integrity from its proposed management (mainly timber harvest) by downplaying logging emissions and falsely comparing them alongside natural disturbance processes. For these reasons, we request that you conduct a comprehensive carbon life cycle analysis (Hudiburg et al. 2019), compare the alternatives to one another and not the entire US GHGs, and then select the alternative with the lowest emissions.

We now focus our comments on the questions raised by the agency on the DEIS.

Question 1: Does the approach outlined in the DEIS appropriately consider place-based information and current land management direction about old-growth forest management?

None of the alternatives meet this NEPA obligation as they provide too much local discretion, and there is not an adequate range of alternatives to place restrictions on logging in MOG. While the agency's inventory of MOG was an important contribution that recognizes the variability in MOG ecosystems nationwide, the main problem is local discretion.

We request that the Forest Service take a hard look at local discretion vs national direction from historical situations that it likewise struggled with. For instance, prior to the National Roadless Conservation Rule, the agency resisted nationwide prohibitions on road building, asking for local discretion and "flexibility" that was the main reason why roadless areas were declining in the first place. A similar level of resistance to national direction from President Bill Clinton at the time also occurred in the initial rollout of the Northwest Forest Plan, as the agency resisted logging restrictions even though the public and scientists overwhelmingly rejected the local discretion/flexibility argument because the Forest Service needs national guidance in order to follow the intent of policies that place any restrictions on logging. In other words, the agency has a propensity to fit logging into most issues that it is addressing and without national direction will continue to use local discretion to push through logging projects that degrade MOG by calling them "stewardship," "restoration," "resilience," "forest health," etc. In other words, the Forest Service will always find a reason to log by calling it something else and by deflecting criticism from the public and scientists.

In what is a Deja-Vu moment, the agency is now resisting prohibitions on logging in MOG as it continues to weigh alternatives based on "flexibility" and "discretion" that will cause undo harm to the public's values inherent in MOG. Because of historic logging, we are now in a situation where every acre of MOG is critically important as the nation's best climate and biodiversity refugia and the Forest Service has most of those acres (DellaSala et al. 2022a). Thus, there is a public responsibility on the part of the agency to properly steward this limited resource by first and foremost protecting it from timber harvest throughout the national forest system because this is the only disturbance you can realistically control.

Notably, as stated on p. 16 of the DEIS, "None of the alternatives require all areas currently meeting the definition (and associated criteria) of old-growth forest to be retained as such. Standard 2.a (DEIS p. 29) allows vegetation management to occur in areas currently meeting the definition (and associated criteria) of old-growth forest for the purposes of proactive stewardship." We reiterate - this is not stewardship - it's a means to keep timber harvest open via discretionary language at the local level and this threat is reflected in the threat analysis that shows timber harvest actually increasing over decades in MOG (Figures A8.6-7). Simply put, timber harvest is an ongoing cumulative threat and not a stewardship objective.

Thus, we request that all large trees of all species be retained in MOG management units nationwide (frequent and infrequent fire systems) as the main purpose and need. Protecting large trees from logging should be a theme carried through all alternatives that properly defines the agency's stewardship obligations. Immediately, the agency also needs to cancel all timber sales in MOG currently planned or in the pipeline.

Question 2: What would be the impacts if Standard 3 would be updated to read as: "Proactive stewardship in old-growth forests shall not result in commercial timber harvest."

First, we support additional restrictions on commercial harvest within MOG. However, as noted this must include an adequate examination and alternative that is based on "**no commercial exchange**," which would tighten the many loopholes in the DEIS. Strengthening protections for not only old growth but for mature would benefit climate mitigation and biodiversity objectives of the agency's stewardship and ecosystem integrity responsibilities across the national forest system. There is simply no other way to do this and any form of commercial exchange in MOG is damaging to the public's climate and biodiversity values in MOG. We note that the national forests are no longer the nation's wood basket as minimal amounts of timber volume come from national forests (Oswalt et al. 2019[2]). The agency's main multiple use obligation in this situation is to examine the multiple values that would be enhanced by restricting commercial exchange in MOG. Those values that need proper analysis include - carbon retention, wildlife habitat, imperiled species habitat, drinking water, and recreation as among the top ecosystem services uniquely provided by MOG on federal lands (DellaSala et al. 2022a). At a minimum, the agency needs to conduct a proper life cycle carbon accounting (Law et al. 2018, Hudiburg et al. 2019). The agency could still do fuel reduction through limited small tree removals and prescribed fire (see below).

Question 3: Do current standards and guidelines provide enough restrictions to protect current and future old-growth forests from future timber harvest?

Neither current standards nor the DEIS provide adequate protections for MOG and the DEIS does not examine an adequate range of alternatives that restrict the commercial exchange of trees. While the DEIS is under consideration, the Forest Service continues to log in MOG and needs to cancel those sales and any other MOG sales immediately[3]. The threat analysis projects that logging of MOG will continue nationally and in the Pacific NW, despite overwhelming public and scientific support for the opposite as reflected in our prior comments and that defy true notions of "stewardship." Importantly, in the only nationwide analysis of MOG that evaluated MOG protection levels, the Forest Service has protected just 24% of its MOG with over 50 million acres deemed vulnerable to logging (DellaSala et al. 2022a). Thus, the agency's standards and guidelines are summarily too weak to ensure millions of acres of MOG will not be degraded. The only way to ensure that MOG is protected is to terminate the commercial exchange and timber targets in MOG and that was not properly analyzed by the agency.

As mentioned, the Forest Service has not provided an adequate analysis of the carbon stores impacted by ongoing logging under the alternatives. The agency did not analyze an

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[2] This pdf was too large to attach but it's a USFS publication - https://research.fs.usda.gov/treesearch/57903

[3] https://www.climate-forests.org/worth-more-standing

alternative that restricts all forms of logging of large trees even though large trees and their carbon values have been defined in the literature (Birdsey et al. 2023) and that information was provided to the agency in public scoping. Tree diameter distributions are available from FIA and so are their carbon values. Despite the agency having this information from its own inventory, the carbon and biodiversity benefits of protecting large trees in MOG were not adequately examined. Thus, there is little mention of the carbon stores and natural climate solution values of large trees in the DEIS.

We cross reference to comments by Dr. Birdsey (submitted separately and the citations are in his comments) -

> "Mature and old-growth forests with large trees have characteristics that are beneficial for climate change mitigation and other ecosystem values such as biodiversity (Lutz et al. 2018), and represent a significant portion of the CO_2 that needs to be removed from the atmosphere by the land (Lawrence et al. 2022). MOG forests store far more carbon than younger managed forests, and in most cases can continue to accumulate carbon for centuries if not logged or severely disturbed (Birdsey et al. 2023b; Law et al. 2018; Leverett et al. 2020). For example, large trees in MOG forests on federal lands store between 41 and 84 percent of the total biomass carbon stock (Birdsey et al. 2023b; Mildrexler et al. 2020). Furthermore, the largest trees in MOG forests accumulate C faster than smaller trees (Mildrexler et al. 2020; Mildrexler et al. 2023; Stephenson et al. 2014). And older undisturbed MOG forests also continue to pack away carbon annually in their woody debris and soils, which are largely protected from effects of severe disturbance."

Additionally, we strongly disagree with the DEIS assertion of the importance of harvest wood pools (HWP), as the DEIS overstates HWP carbon stores and fails to conduct a proper carbon life cycle analysis. Published literature shows the value of HWP is overstated (Harmon 2019) and that most carbon leaves the forest when logged (Law et al. 2018, Hudiburg et al. 2019, Moomaw and Law 2023). Thus, the agency did not conduct a proper life cycle analysis in overstating HWP carbon stores while understating logging emissions that are up to 10x greater than natural disturbances combined (Harris et al. 2016).

Importantly, the agency's own research has repeatedly demonstrated that older forests with larger trees are more resistant wildfires (Lesmeister et al. 2019, 2021) then logged areas. Other studies have shown protected forests burn in lower fire intensities (Bradley et al. 2016) and logged areas combine with extreme fire weather that contribute to large wildfires (Zald and Dunn 2018). This information was not properly evaluated in the DEIS.

Other Issues

Problems with Alternative 3 assumptions - the Forest Service rejected Alternative 3 on grounds that it would restrict the use of prescribed burning. We disagree with this assertion and ask that the agency evaluate these studies that all show how prescribed fire can be used safely even in dense forests without mechanical removal of large trees. Many of these are the agency's own publications:

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. Available on the USFS website - https://www.fs.usda.gov/psw/publications/knapp/psw_2005_knapp001.pdf

Knapp, E.E., and Keeley, J.E. 2006. Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest. Int. J. Wildland Fire 15: 37–45. Available on the USFS website - https://research.fs.usda.gov/treesearch/41752

Knapp, E.E., Schwilk, D.W., Kane, J.M., Keeley, J.E., 2007. Role of burning on initial understory vegetation response to prescribed fire in a mixed conifer forest. Canadian Journal of Forest Research 37: 11–22. Available on the USFS website - https://research.fs.usda.gov/treesearch/34451

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: 13-25. Available on the USGS website - https://pubs.usgs.gov/publication/70170396

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. USFS website - https://research.fs.usda.gov/treesearch/38347

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. Not an open access journal - https://courses.seas.harvard.edu/climate/eli/Courses/global-change-debates/Sources/Forest-fires/more/North-etal-2015-short-perspective.pdf

> "…fire is usually more efficient, cost-effective, and ecologically beneficial than mechanical treatments."

And here is the abstract from Stephens et al. 2021 on the use of managed wildfire to proactively reduce fuels over large areas with minimally costs:

> "Reducing the risk of large, severe wildfires while also increasing the security of mountain water supplies and enhancing biodiversity are urgent priorities in western US forests. After a century of fire suppression, Yosemite and Sequoia-Kings Canyon National Parks located in California's Sierra Nevada initiated programs to manage wildfires and these areas present a rare opportunity to study the effects of restored fire regimes. Forest cover decreased during the managed wildfire period and meadow and shrubland cover increased, especially in Yosemite's Illilouette Creek basin that experienced a 20% reduction in forest area. These areas now support greater pyrodiversity and consequently greater landscape and species diversity. Soil moisture increased and drought-induced tree mortality decreased, especially in Illilouette where wildfires have been allowed to burn more freely resulting in a 30% increase in summer soil moisture. Modeling suggests that the ecohydrological cobenefits of restoring fire regimes are robust to the projected climatic warming.

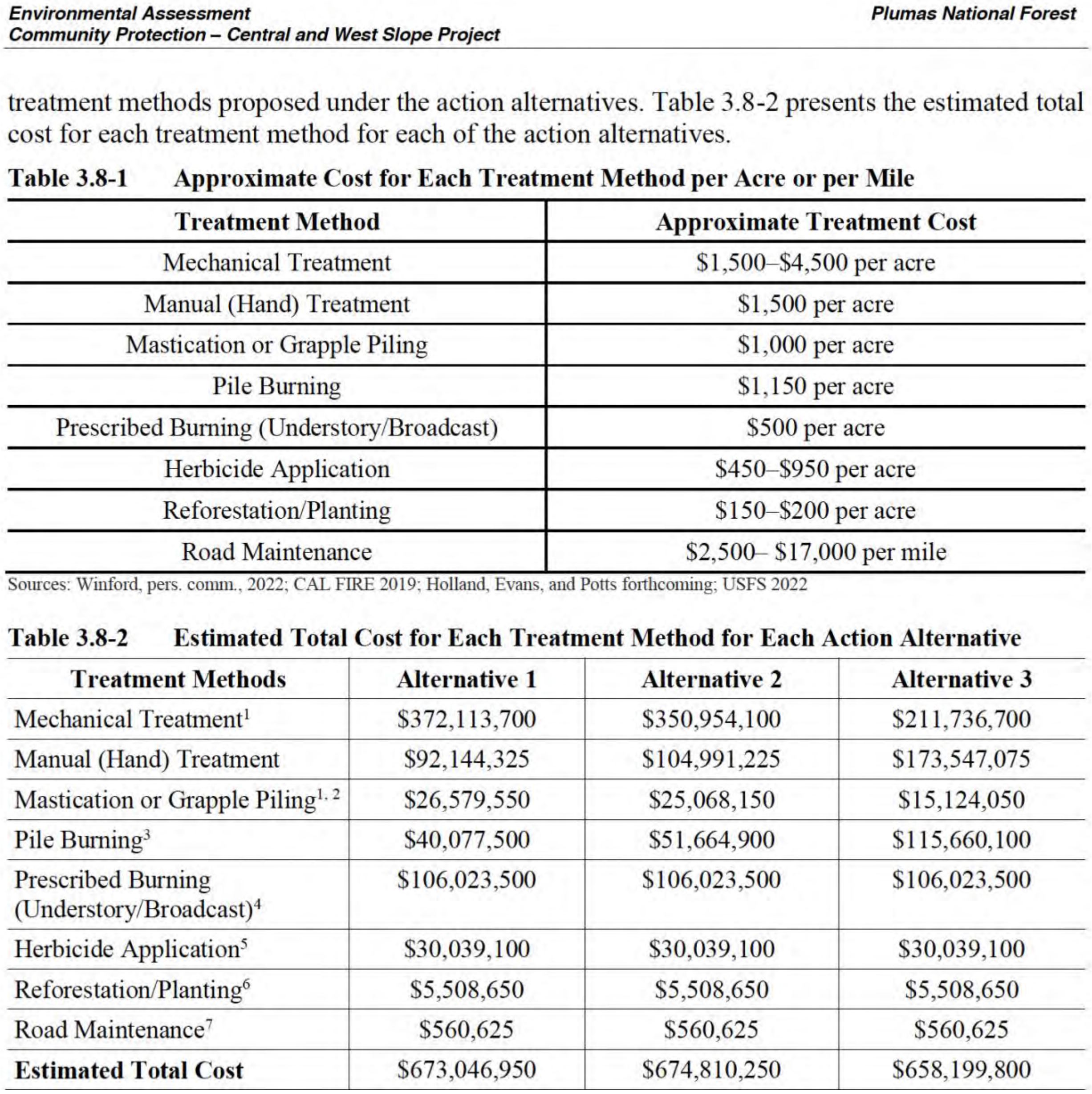
Support will be needed from the highest levels of government and the public to maintain existing programs and expand them to other forested areas."

Despite efforts by the Forest Service to reduce fire intensity to MOG and elsewhere, mechanical efforts will fail for at least these reasons:

(1) Thinning will become increasingly ineffective in a changing climate as top-down fire weather drives large fires that then combine with logged areas to affect vast landscapes (Zald and Dunn 2018) and that cause damage to nearby towns when they escape mainly from fires spilling over from privately logged lands (Downing et al. 2023).
(2) Thinning costs way more than prescribed fire and managed wildfire use (see below) and can be as effective if not more so than thinning that has carbon and ecosystem damage/costs (DellaSala et al. 2022b).
(3) The odds of a thinned site encountering a fire are really small (<1% Schoenaggel et al. 2017) during the period of low fuels, and expanding the scale, intensity, and frequency of thinning to improve the odds come at substantial ecological and carbon costs (DellaSala et al. 2022b).
(4) The agency's treatments are at distances so far removed from towns (more than 1-km from structures in many cases) to be ineffective at wildfire risk reduction to communities (Schoenaggel et al. 2017, DellaSala et al. 2024). Thus, there is no benefit to communities leaving in proximity to national forests when treatments are so far removed from structures.

We believe that the DEIS fails to provide an adequate range of alternatives by overstating mechanical treatments as a pre-requisite for prescribed fire, by not providing sufficient cost comparisons in relation to treatment types (prescribed fire, thinning, wildfire use), nor does it take a hard look at the literature supporting prescribed fire without mechanical treatments.

We submit this cost comparison for the Plumas National Forest as an example of how costly mechanical treatments are compared to prescribed burning only.



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treatment methods proposed under the action alternatives. Table 3.8-2 presents the estimated total cost for each treatment method for each of the action alternatives.

Table 3.8-1 Approximate Cost for Each Treatment Method per Acre or per Mile

Treatment Method	Approximate Treatment Cost
Mechanical Treatment	$1,500–$4,500 per acre
Manual (Hand) Treatment	$1,500 per acre
Mastication or Grapple Piling	$1,000 per acre
Pile Burning	$1,150 per acre
Prescribed Burning (Understory/Broadcast)	$500 per acre
Herbicide Application	$450–$950 per acre
Reforestation/Planting	$150–$200 per acre
Road Maintenance	$2,500– $17,000 per mile

Sources: Winford, pers. comm., 2022; CAL FIRE 2019; Holland, Evans, and Potts forthcoming; USFS 2022

Table 3.8-2 Estimated Total Cost for Each Treatment Method for Each Action Alternative

Treatment Methods	Alternative 1	Alternative 2	Alternative 3
Mechanical Treatment[1]	$372,113,700	$350,954,100	$211,736,700
Manual (Hand) Treatment	$92,144,325	$104,991,225	$173,547,075
Mastication or Grapple Piling[1, 2]	$26,579,550	$25,068,150	$15,124,050
Pile Burning[3]	$40,077,500	$51,664,900	$115,660,100
Prescribed Burning (Understory/Broadcast)[4]	$106,023,500	$106,023,500	$106,023,500
Herbicide Application[5]	$30,039,100	$30,039,100	$30,039,100
Reforestation/Planting[6]	$5,508,650	$5,508,650	$5,508,650
Road Maintenance[7]	$560,625	$560,625	$560,625
Estimated Total Cost	$673,046,950	$674,810,250	$658,199,800

Ecological Integrity vs "Stewardship"

The Forest Service is obligated under the NFMA Rule of 2012 to maintain ecosystem integrity on the national forest system and yet its logging activities are taking the nation in the opposite direction as they are a form of forest degradation.

We provide excerpts from DellaSala et al. in peer review that pertains to the difference between degradation and integrity and integrity should be the agency's touchstone in evaluating whether it is actually stewarding MOG.

Abstract: Forests harbor almost two-thirds of Earth's terrestrial biodiversity and play a crucial role in sequestering and storing carbon that is linked to their ecological integrity and biological diversity functions. Forest degradation—the loss of forest-ecosystem integrity measured by changes to native-species composition, functional processes, and keystone structures—is a major source of emissions and serious cause of biodiversity decline. Addressing this loss is critically important for fulfilling the Paris Climate Agreement and the post 2020 Kunming-Montreal Global Biodiversity Framework. Additionally, most forested countries have signed pledges to end degradation along with deforestation by 2030. However, many countries, particularly in the Global North, fail to fully acknowledge degradation as a problem within their own borders, and no country is on track to meet the Kunming-Montreal pledge. We propose a framework that would enable monitoring degradation of large, old trees to intact landscapes along a continuum of forest-integrity loss relative to reference conditions derived from primary, mature, historic, or semi-natural conditions. Examples of degradation include multiple forms of commercial logging and road building that alter native species composition, structure, and functionality. Case studies from temperate, boreal, and tropical biomes illustrate how expansive the degradation footprint is globally. We highlight an urgent call for countries to better detect and assess the cumulative damages of forest-degradation and to end it as promised.

- Ending forest degradation has been an emerging multilateral policy issue since the formation of the United Nations Forum on Forests in 2000. It was noted as a priority in the United Nations Forest Instrument, and again in the United Nations Strategic Plan for Forests. At the United Nations Climate Change Conference, 145 nations signed the Glasgow Leaders' Declaration on Forests and Land Use ("Glasgow Leaders' Declaration"), which seeks to "facilitate the alignment of financial flows with international goals to reverse forest loss and degradation" by 2030 and commits signatories to halting and reversing deforestation and land degradation by 2030. The Kunming-Montreal Global Biodiversity Framework proposed 23 action-oriented global targets, including ensuring that at least 30 percent of lands and waters are protected and degraded areas are under effective restoration by 2030. In addition, Goal A of this framework emphasized the need to ensure that "integrity, connectivity and resilience of all ecosystems are maintained, enhanced, or restored, substantially increasing the area of natural ecosystems by 2050." Target 1 of this framework also seeks "to bring the loss of areas of high biodiversity importance, including ecosystems of high ecological integrity, close to zero by 2030."
- We define ecological integrity as a measure of the composition, structure, and function of an ecosystem in relation to the system's natural range of variation. This integrity concept integrates different characteristics of an ecosystem that collectively describe its ability to achieve and maintain its optimum operating state in the face of the prevailing environmental drivers and anthropogenic stressors, while continuing to maintain its self-organisation and regeneration capacity (Mackey et al. 2024b). We adopted the approach of Rogers et al. (2022) in identifying foundational elements for ecosystem integrity that include representative structures, processes, native species, and resilience.

- Additionally, ecosystem condition (the relative level of ecosystem integrity) can be based on the state, processes, and changes in the ecosystem, including (1) carbon and nutrient stocks, (2) abiotic physical and chemical states such as water quantity and quality; (3) biotic composition, structure, and function; and (4) landscape diversity and connectivity (Rogers et al. 2022). In this approach, a forest with native species composition, keystone structures (e.g., biological legacies: large, old trees, snags, down wood, native understories), and functional processes (e.g., natural disturbances, food web complexities, pollinators, below ground processes, soil integrity) has high integrity compared to one where anthropogenic disturbance have destabilized these key elements in various degrees. Conversely, we refer to degradation as anthropogenic disturbances that trigger the immediate and long-term deterioration of integrity (Rogers et al. 2022, Mackey et. al. 2024b).

What the agency is proposing in the DEIS is more akin to degradation as defined above then "stewardship" and will compromise ecosystem integrity by the removal of important legacy large trees, compacting soils, drying out understories, releasing carbon, and impacting wildlife habitat (DellaSala et al. 2022b). In sum, that is a form of degradation and not stewardship or integrity. As stated in DellaSala et al. in review, MOG needs to function as the reference condition in assessing integrity vs. degradation. Given that the agency wants to continue logging in MOG, the DEIS is impacting reference conditions needed to determine the efficacy of its forest management practices, is downplaying cumulative impacts of logging in MOG that are glossed over, nor can it claim that what it is doing is stewardship, restoration, or resilience.

To fix the numerous problems in the DEIS, we request that you:

- Develop a new alternative or substantially revise Alternative 3 by prohibiting any removal of commercial materials from all mature and old-growth forests as identified in the agency's mapping of MOG and related published accounts (DellaSala et al. 2022a). This includes the use of prescribed fire in fire-adapted forests without mechanical removal of any large trees and judicious understory removals that while focused on lowering fuel levels must also retain representative small tree densities, native vegetation, soil integrity, soil and understory microclimates, mycorrhizal networks, and biological legacies. That is - see the forest for more than just the trees.
- A revised alternative 3 or new alternative would also restrict post-disturbance "salvage" logging as this form of logging is most degrading to complex early seral forests, successional processes, wildlife habitat, and carbon stocks (Thorn et al. 2018).
- Include in a new alternative or revised alternative 3 the concept of "proforestation" (Moomaw et al. 2019) by allowing mature forests to fully develop old-growth characteristics overtime to begin recovering the greatly depleted old-growth ecosystem and further build carbon stocks.
- Provide an adequate evaluation of the impacts of logging relative to natural disturbances that clearly distinguishes the two using published definitions of degradation and integrity and not some unclear notion of "stewardship," "resilience," "restoration," and "forest health."

- Provide an adequate range of alternatives that is based on the comments provided herein, the omission of data and studies provided in our scoping comments, and that fully restricts all forms of logging within MOG with the exception of some small tree removals in specialized cases.
- Analyze the importance of large trees to carbon stocks, fire resistance, and wildlife habitat and use published sources (e.g., Birdsey et al. 2023) to determine national forest specific diameter limits in large-tree definitions and logging thresholds.
- Analyze how the agency's "stewardship" objectives can best comply with the Paris Climate Agreement (Article 5.1 on natural climate solutions), Glasgow Leaders' Forest Pledge (end degradation as defined herein), and the 2020 Kunming-Montreal Global Biodiversity Framework. Importantly, this should include a comprehensive GAP analysis to identify levels of protection using recognized GAP status codes for each of the MOG types and how best to meet the 30 x 30 directive of EO 14008. None of the alternatives analyzed this and therefore there is not an adequate alternative that truly "conserves" older forests and complies with EO 14072.
- Adopt and analyze a definition of ecosystem integrity that includes the published literature (e.g., Rogers et al. 2022) and not some nebulous notion of stewardship.

In closing, Wild Heritage has presented the Forest Service during scoping and in invited MOG research summits on each of these points raised. However, our information and scoping comments have been ignored in the development of alternatives and thus the DEIS did not take a hard look at the issues raised, did not use the best available science, and provided an inadequate range of alternatives. The Forest Service can and must do better to truly steward the nation's dwindling and best natural climate solution.

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*literature submitted as attached pdfs

frontiers in
ECOLOGY AND EVOLUTION

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Bet-hedging dry-forest resilience to climate-change threats in the western USA based on historical forest structure

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Dry forests are particularly subject to wildfires, insect outbreaks, and droughts that likely will increase with climate change. Efforts to increase resilience of dry forests often focus on removing most small trees to reduce wildfire risk. However, small trees often survive other disturbances and could provide broader forest resilience, but small trees are thought to have been historically rare. We used direct records by land surveyors in the late-1800s along 22,206 km of survey lines in 1.7 million ha of dry forests in the western USA to test this idea. These systematic surveys (45,171 trees) of historical forests reveal that small trees dominated (52–92% of total trees) dry forests. Historical forests also included diverse tree sizes and species, which together provided resilience to several types of disturbances. Current risk to dry forests from insect outbreaks is 5.6 times the risk of higher-severity wildfires, with small trees increasing forest resilience to insect outbreaks. Removal of most small trees to reduce wildfire risk may compromise the bet-hedging resilience, provided by small trees and diverse tree sizes and species, against a broad array of unpredictable future disturbances.

Keywords: dry forests, wildfires, insect outbreaks, droughts, climate change, resilience, land surveys, bet-hedge

INTRODUCTION

Dry forests globally may be particularly vulnerable to climatic change, because their setting is prone to wildfires, insect outbreaks, and droughts; these disturbances may increase, and post-disturbance tree recruitment is often poor. Recruitment limitation in forests is a widespread concern (Clark et al., 1999), particularly where moisture is limiting, as in *Pinus* forests in drier parts of precipitation gradients (Dorman et al., 2013). For example, dry forests of the western USA (Figure S1), which include montane ponderosa pine (*Pinus ponderosa*) forests and dry mixed-conifer forests also with firs (*Abies* spp.) and Douglas-fir (*Pseudotsuga*), can have poor tree recruitment that limits their recovery after fires, insect outbreaks, and droughts. Tree recruitment in dry *P. ponderosa* forests of the western USA over the last century has been poor, concentrated in episodic pluvials (Savage et al., 1996), and spatially variable (Stein, 1988; Roccaforte et al., 2012). Mortality of *P. ponderosa* at their ecotone with lower-elevation woodlands during a 1950s drought (Allen and Breshears, 1998) also indicates vulnerability. Rising temperatures and drought could further reduce tree recruitment in dry forests (Anderson-Teixeira et al., 2013). Climate envelopes of seedlings vs. established trees of *P. ponderosa* suggest general recruitment failure is underway, possibly a precursor to broader range contraction (Bell et al., 2014).

In contrast, paleoecological research shows that dry forests of the western USA persisted for thousands of years in the face of wildfires, insect outbreaks, and droughts (Jenkins et al., 2011), suggesting recruitment was not generally deficient and historical forests were resilient. However, this persistence appears incongruent with the hypothesis that these dry forests historically had low abundance of seedlings, saplings and small trees (Covington and Moore, 1994; Allen et al., 2002). This hypothesis is based in part on tree-ring reconstructions, which show that large trees were historically dominant in most sampled stands (Williams and Baker, 2012a). However, small trees could have been common, but missed in tree-ring reconstructions because small trees had high mortality rates and may decompose by the time of reconstruction (Allen et al., 2002). Also, tree-ring reconstructions are not located systematically across landscapes and plot-level size-class distributions are often averaged, masking variability (Williams and Baker, 2013). Nonetheless, frequent surface fires were thought to have limited small trees, and some early accounts do suggest low abundance of tree recruitment (Leiberg et al., 1904; Covington and Moore, 1994; Allen et al., 2002). Today, large trees are likely less abundant and small trees more abundant than historically (Covington and Moore, 1994), but our focus is only on historical abundance of small trees, not current abundance. The common hypothesis is that low-severity fires historically limited small trees, so they were a low percentage of total trees and were found across a low percentage of land area.

We use a previously untapped historical source, the General Land Office (GLO) land surveys, which provide spatially extensive direct empirical data on historical tree recruitment (seedlings/saplings, small trees). We use seven study areas that span dry forests of the western USA (Figure S1) to test the hypothesis that dry forests historically had little tree recruitment. We formalize this for the two data sources from the GLO surveys and two components of recruitment abundance: H_1: Small trees were $<20\%$ of total trees, and H_2: Seedlings and saplings (trees < 10 cm diameter) were present on $<20\%$ of forest area.

Past specific estimates of percentages were lacking; we used test values that conservatively represent the hypotheses. Small trees are $\geq$10 cm dbh, with an upper size limit of 30–50 cm, defined for each study area (Williams and Baker, 2012a). We measured and compared recent risks of higher-severity wildfires and insect outbreaks in dry forests, separated into ponderosa pine forests and dry mixed-conifer forests, across the western USA using government data. We reviewed the role of tree recruitment in recovery after these disturbances. We suggest a strategy to maintain the resilience of dry forests to future disturbances, based on our findings.

MATERIALS AND METHODS

Data from the public land survey system, conducted by the U.S. General Land Office, have been widely used in the USA to reconstruct historical vegetation (Schulte and Mladenoff, 2001). Surveys in the study areas were generally done in the late-1800s before widespread expansion of EuroAmerican land uses. The system consists of 9.6 × 9.6 km townships containing thirty-six 1.6 × 1.6 km sections. Surveyors marked quarter corners at the 0.8 km mark and section corners at the 1.6 km mark along section lines. Surveyors were required to record azimuth, distance, species, and diameter of two bearing trees at quarter corners and four trees at section corners. Here we used surveyors' direct estimates of tree diameters. In an accuracy study, we found surveyors estimated diameters with sufficient accuracy to place trees in 10-cm diameter bins (Williams and Baker, 2010). After applying an empirical correction, diameter distributions from bearing trees were 87–88% similar to distributions from plot data (Williams and Baker, 2011), thus are quite accurate. Bearing trees are a statistically valid sample, as they have low bias and error (Williams and Baker, 2010).

We also used section-line data recorded by surveyors. Surveyors in forests were required to record, in order of abundance, the dominant overstory trees and understory plants, often including small trees (seedlings and saplings) and shrubs (Williams and Baker, 2012a). Surveyors also often recorded qualitative estimates of understory tree density. Not all surveyors followed the instructions, thus we limited analysis to the set of surveyors who did so for at least one section-line. The section-line data represent a statistically valid line-intercept estimate of cover (Butler and McDonald, 1983).

To provide data to test hypothesis H_1, we totaled small and large trees in each of the seven study areas and for the composite (**Table 1**, **Figure 1**). Small trees were defined as $\geq$10 cm but $\leq$40 cm, except $\leq$30 cm in the Colorado Front Range, where tree growth is slower (Williams and Baker, 2012a) and $\leq$50 cm in the western Sierra, where tree growth is faster (Baker, 2014).

Table 1 | Study areas, corresponding number of trees and section-line length in forested area, and the percentage of forest section line-length with seedlings and saplings.

Hypotheses and variables	Front range, Colorado[a]	Coconino Plateau, Arizona	Mogollon Plateau, Arizona	Black Mesa, Arizona	Blue Mts., Oregon	Eastern Cascades, Oregon	Western Sierra, California	Total or mean
Dry-forest study area (ha)	65,525	41,214	405,214	151,080	304,709	398,346	329,943	1,696,031[b]
H_1: SMALL TREES WERE < 20% OF TOTAL TREES								
Number of trees	1055	1643	10,848	2741	7496	11,856	9532	45,171[b]
Small-tree diameters used (cm)	$\leq$30	$\leq$40	$\leq$40	$\leq$40	$\leq$40	$\leq$40	$\leq$50	$\leq$30 to 50
Small trees (% of total trees)	91.8	69.5	51.8	81.1	62.0	62.4	60.9	61.6[c]
Chi-square test result[d]	$X^2 = 3404$	$X^2 = 2517$	$X^2 = 6859$	$X^2 = 6403$	$X^2 = 8267$	$X^2 = 13,326$	$X^2 = 9976$	$X^2 = 48,772$
	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
H_2: SEEDLINGS AND SAPLINGS WERE PRESENT ON < 20% OF FOREST AREA								
Section-line length (km)	4004	413	4230	1441	5878	3873	2367	22,206
Seedlings/Saplings present (%)	3.8	43.4	13.3	8.0	34.6	57.4	54.9	29.6
Chi-square test result[f]	$X^2 = 657$	$X^2 = 140$	$X^2 = 119$	$X^2 = 150$	$X^2 = 780$	$X^2 = 3385$	$X^2 = 1780$	$X^2 = 1238$
	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
Seedlings/Saplings dense (%)	0.2	28.8	1.9	-	22.4	30.3	20.0	14.3
Seedlings/sapling pines[e]	0.9	1.4	9.8	7.9	32.7	51.0	42.3	24.8
Seedlings/Sapling firs[e]	0.5	0.0	0.0	0.0	27.1	27.8	39.7	16.4
Seedling/Sapling oaks[e]	0.5	43.3	8.8	7.1	0.0	0.2	42.4	7.6
Seedling/Sapling other trees[e]	2.5	0.4	1.2	2.0	0.3	2.6	25.1	4.0

[a] *Study areas include the Colorado Front Range (Williams and Baker, 2012a), Coconino Plateau, Arizona (Williams and Baker, 2013), Mogollon Plateau and Black Mesa, Arizona and Blue Mountains, Oregon (Williams and Baker, 2012a), Eastern Cascades of Oregon (Baker, 2012), and western Sierra Nevada, California (Baker, 2014).*

[b] *Total.*

[c] *Percentage for the composite across the seven study areas.*

[d] *Degrees of freedom = 1 and N = the number of trees, for all chi-square tests.*

[e] *Seedling/Sapling pines, firs, oaks, and other trees may be overlapping, as a line can have, for example, both pines and firs.*

[f] *Degrees of freedom = 1 and N = the number of 1-km line-lengths, for all chi-square tests.*

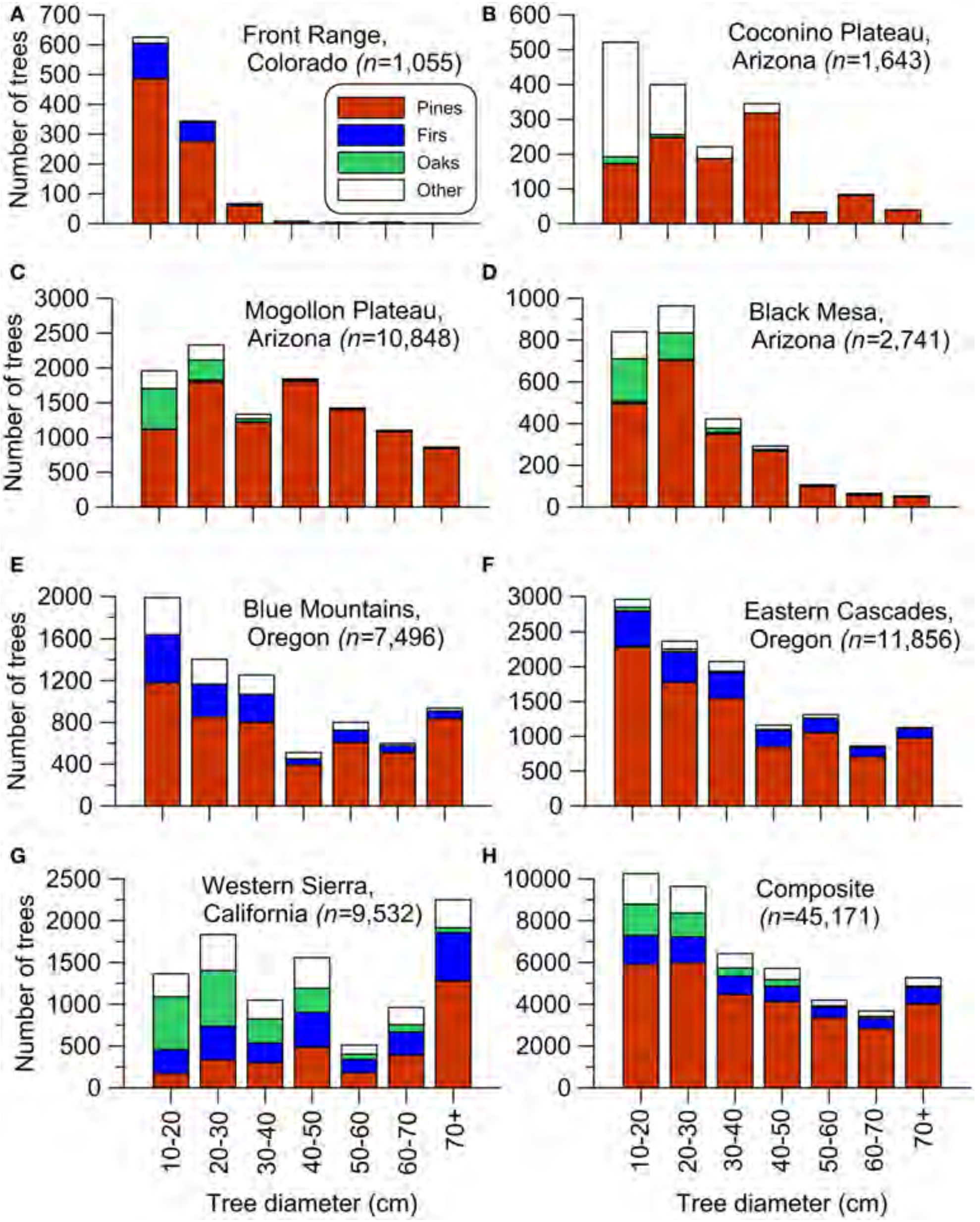

FIGURE 1 | Historical tree size-class distributions for the seven study areas and a composite across all the study areas: (A) Front Range, Colorado, (B) Coconino Plateau, Arizona, (C) Mogollon Plateau, Arizona, (D) Black Mesa, Arizona, (E) Blue Mountains, Oregon, (F) Eastern Cascades, Oregon, (G) Western Sierra, California, (H) The composite of all areas. Distributions use 10-cm bins compatible with the accuracy of diameters measured by the surveyors (Williams and Baker, 2011). Other trees, not found in every area, include *Pinus edulis* and *Juniperus* spp., *Calocedrus decurrens*, *Populus tremuloides*, and *Larix occidentalis*. As in **Table 1**, small trees were defined as trees ≥10 cm but ≤40 cm diameter, except ≤30 cm in Colorado **(A)** and ≤50 cm in California **(G)**.

These diameters generally represent trees that are less than about 140 years old (Bright, 1912; Baker, 2012, 2014; Williams and Baker, 2013). Trees this size today are often thought to have widely established after EuroAmerican settlement because of logging, livestock grazing, and fire exclusion (Covington and Moore, 1994; Allen et al., 2002; Franklin and Johnson, 2012), and thus may be removed in restoration treatments. To test H_1, we used a chi-square goodness-of-fit test of a null hypothesis that small trees were 0.2 of total trees and large trees were 0.8 of total trees. If this null was rejected, we rejected H_1 if small trees were <0.2 of total trees. To control error rates, we Bonferroni-corrected $\alpha = 0.05$, for 8 planned tests, one per study area and one for the composite (**Table 1**, **Figure 1**), to $\alpha = 0.00625$.

To provide data to test H_2, we totaled 1-km section lines for which surveyors recorded understory trees in each of the study areas and for the composite. Similarly, to test H_2, we used a chi-squared goodness-of-fit test of a null hypothesis that the area with seedlings/saplings was 0.2 of the total forested area and the area without seedlings/saplings was 0.8 of the total forested area. If this null was rejected, we then rejected H_2 if seedlings/saplings were found across <0.2 of total forest area. We also Bonferroni-corrected an initial $\alpha = 0.05$ for 8 planned tests.

We used maps of ponderosa pine and dry mixed-conifer forests from Landfire Biophysical Settings (www.landfire.gov). Wildfire area and severity were from raster maps of actual burned area, not fire perimeters, from the Monitoring Trends in Burn Severity (MTBS) program (http://www.mtbs.gov). Insect-caused mortality was from the US Forest Service Forest Health Technology Enterprise Team (http://foresthealth.fs.usda.gov/portal/Flex/IDS). Insect outbreaks were detected using annual aerial surveys. To limit analysis to dry western forests, aerial survey polygons and wildfires were both clipped by the maps of ponderosa pine and dry mixed conifer. The annual sample area varied, but averaged about 9.8 million ha of ponderosa pine and 10.9 million ha of dry mixed-conifer forests (Table S1), about 80% of the 25.8 million ha area of western dry forests.

Comparison of wildfire and insect outbreaks was done for each year both datasets were available. We compared moderate- and high-severity wildfire area, which are the severities with substantial tree mortality, with areas where tree mortality from insects was also substantial, as it was visually detected from aerial surveys. We calculated the rate of wildfire using the fire rotation, which is the number of survey years divided by the fraction of the survey area impacted by fire in those years. The rate of insect outbreaks was determined similarly. Some outbreak areas appeared to overlap in subsequent years and potentially be cumulative. We performed a union and spatial dissolve in GIS to derive a conservative estimate of total area impacted by insect outbreaks over the analysis period. Additional details are in Supplementary Methods.

RESULTS

SMALL TREES HISTORICALLY ABUNDANT AND DOMINANT

Hypothesis H_1 is rejected across all seven study areas and the composite (**Table 1**). Small trees generally dominated historical dry forests, ranging from 51.8 to 91.8% of total trees across the seven study areas and equaling 61.6% of trees in the overall composite (**Table 1**, **Figure 1**). Small trees can be suppressed older individuals, but were predominantly <140 years old (Bright, 1912; Williams and Baker, 2012a). Small trees were somewhat diverse, with pines most abundant, but also firs, oaks and other conifers and hardwoods (**Figure 1**). Hypothesis H_2 is rejected for study areas in California and Oregon, but not in Arizona and Colorado (**Table 1**).

HIGHER RECENT THREAT FROM INSECT OUTBREAKS THAN FROM WILDFIRE

Data from government agencies show that insect outbreaks were recently a more significant threat to dry forests than were moderate- to high-severity wildfires; similar data are not available for droughts. It is conservatively estimated (i.e., consolidating all areas of spatial overlap) that insect outbreaks caused substantial detectable tree mortality in 5,193,752 ha of western dry forests over the 1999–2012 period for which spatial data were available, which is 5.6 times the 934,551 ha impacted by moderate- to high-severity wildfires (Table S1). Mean ratios of insect to fire impact were 4.5 in ponderosa pine and 6.9 in dry mixed-conifer forests (Table S1). At the rates during 1999–2012, it would require 311 years for moderate- to high-severity wildfires to burn once across an area equal to the area of western dry forests, but only 56 years for insect outbreaks to impact this area (Table S1). Rotations for fire varied from 265 years in ponderosa pine to 367 years in dry mixed-conifer forests, and for insects from 53 years in dry mixed-conifer to 59 years in ponderosa pine forests (Table S1).

DISCUSSION

NATURAL DISTURBANCES FOSTERED HISTORICALLY ABUNDANT SMALL TREES AND DIVERSE TREE SIZES

Historical dominance of small trees in dry forests (**Figure 1**) does not support the hypothesis that surface fires generally kept small trees rare. Small trees had successfully recruited and were dominant in all dry-forest areas (**Figure 1**). These small, established trees are given more weight, than smaller, more ephemeral seedlings/saplings, for which evidence is more mixed. Seedlings/saplings were abundant in the majority of areas, except two southwestern landscapes (Black Mesa, Mogollon Plateau) and the Colorado Front Range (**Table 1**). Early scientific sources corroborate limited seedlings/saplings in these areas (Leiberg et al., 1904; Williams and Baker, 2012b). Early foresters emphasized preserving advanced recruitment during logging (Pearson, 1923). Thus, recent high-severity fires do not have unprecedented poor recruitment (Savage and Mast, 2005). Seedling/sapling populations in these landscapes must have fluctuated, since small trees had been able to recruit and dominate all dry forests (**Figure 1**). Particular sequences of fires, droughts, and other disturbances may explain fluctuating seedling/sapling populations (Dugan and Baker, in press), and reinforce the historical role of advanced recruitment.

Dominance of small trees, and even ephemeral seedling/sapling populations in most areas, indicates more imperfect limitation of tree recruitment by historical low-severity fires than previously thought. Other disturbances, including droughts, insect outbreaks, and more severe fires likely killed canopy trees and increased tree recruitment, particularly if followed by pluvials (Savage et al., 1996; Dugan and Baker, in press). The Colorado Front Range and Black Mesa (Williams and Baker, 2012a) had the greatest dominance of small trees (**Figures 1A,D**), and our reconstructions showed these areas had more higher-severity fires (Williams and Baker, 2012a,b). Historical abundance of small trees and importance of higher-severity fires in structuring tree populations across dry-forest landscapes are supported by an independent dataset of tree ages (Odion et al., 2014). Higher-severity fires likely interacted with other disturbances to produce diverse tree sizes that were together more resilient to disturbance than would have been the case if only low-severity fires had occurred and large trees had dominated. Historical dominance by small trees and diverse trees sizes are consistent with long-term persistence and resilience of dry forests after disturbances (Jenkins et al., 2011).

ABUNDANT SMALL TREES AND DIVERSE TREE SIZES CONFER RESILIENCE IN MODERN FORESTS

Modern observations also document key, but contrasting roles for advance recruitment and surviving larger trees in forest resilience after fires, insect outbreaks, and droughts. Higher-severity fires may be followed by variable recruitment, including poor recruitment, lags in recruitment, or abundant recruitment in some areas (Roccaforte et al., 2012), with large, surviving trees and proximity to them important (Bonnet et al., 2005; Haire and McGarigal, 2010).

About a dozen bark-beetles, that kill trees over large areas of dry forests in the western USA, are the major outbreak insects (Bentz et al., 2010; Weed et al., 2013). In this case, larger trees are differentially susceptible, which often leaves smaller surviving trees as the key source of post-outbreak recruitment. Vulnerability of larger trees to bark beetles is related to greater food resources (Raffa et al., 2008). In a 1970s outbreak of mountain pine beetle (*Dendroctonus ponderosae*) in ponderosa pine in Colorado, tree survival was substantially higher for trees <20 cm diameter (McCambridge et al., 1982). Similarly, western pine beetles (*Dendroctonous brevicomi*s) kill relatively few trees <40 cm (Miller and Keen, 1960). However, *Ips* in Arizona preferentially kill smaller trees (Negrón et al., 2009). Nonetheless, advance recruitment generally dominates post-outbreak recruitment. After spruce beetle (DeRose and Long, 2010) and mountain pine beetle outbreaks (Astrup et al., 2008), small trees present before outbreaks dominated post-outbreak recruitment. Since these small trees were more diverse than pre-outbreak canopy trees, post-outbreak forests may have greater resilience to future outbreaks (Diskin et al., 2011; Kayes and Tinker, 2012).

Drought often also differentially kills the largest, oldest trees, with less mortality in small and mid-sized trees (Allen et al., 2010), thus also leaving advance recruitment. Drought effects on tree mortality can be widespread and affect forests for centuries (Allen et al., 2010). Drought also influences the occurrence of wildfires, insect outbreaks, and regional tree mortality (Allen et al., 2010), thus it is difficult to parse the impacts of drought alone.

The upshot is that both small trees and surviving larger trees and a diversity of tree species provide resilience to disturbances. Surviving larger trees are particularly important after higher-severity fires and abundant small trees are particularly important after insect outbreaks and droughts.

RESTORING AND MAINTAINING THE BET-HEDGING RESILIENCE OF HISTORICAL FORESTS

Current restoration strategies that seek to increase forest resilience focus predominately on impacts from severe wildfires, but bark-beetle outbreaks and other insects affected 5.6 times the area of western dry forests impacted by moderate- to high-severity fires over the most recent 14-year period (1999–2012). Current rates of moderate- and high-severity fire, with a combined rotation of 311 years (Table S1), would likely not prevent recovery of old-growth forests in the interlude between fires, but rates of insect outbreaks, with a rotation of 56 years (Table S1), could prevent recovery of most older dry forests. Previous research, using the same data sources, in a more limited and lower-elevation area in the southwestern United States, found that beetle-outbreaks affected 2.5–4 times as much area as moderate- to severe wildfires (Williams et al., 2010). Both wildfires (Dennison et al., 2014) and beetle-outbreaks (Bentz et al., 2010; Weed et al., 2013) are increasing in parts of the western United States. Future outcomes are uncertain and complex, however, as beetle-outbreaks can affect wildfire probability (Simard et al., 2011), and as tree mortality occurs, both beetle outbreaks and wildfires could become self-limited (Williams et al., 2010).

Ecological restoration of public dry forests in the western USA is increasingly a goal, because these forests were altered by unsustainable logging, livestock grazing, and fire exclusion that allowed abundant small trees to recruit (Covington and Moore, 1994). Retaining older trees, while removing most small trees up to ages or sizes of trees recruited since EuroAmerican settlement (Figure S2A), is thus often a restoration focus (Covington and Moore, 1994; Allen et al., 2002; Abella et al., 2006; Franklin and Johnson, 2012). Typical upper tree age and size limits are 120–150 years old or 30–50 cm diameter (Abella et al., 2006; Franklin and Johnson, 2012).

We show here, however, that these small trees were the tree sizes historically dominant in these forests (**Figure 1**, **Table 1**), thus removing most small trees so they are no longer dominant is not ecological restoration. There are also efforts underway to increase resilience of forests to droughts by removing most small trees and lowering stand density. However, stand density does not appear to play a major role in level of tree mortality from drought (Ganey and Vojta, 2011). Thus, strategies to reduce most small trees are neither restorative nor very effective.

We suggest diverse historical tree sizes and abundant and dominant small trees long provided bet hedging in dry-forest landscapes subject to unpredictable disturbances. These forests can be more effectively restored and their resiliency to future disturbances increased by maintaining or restoring the historical abundance, dominance, and diversity of small trees, while also restoring large trees depleted by logging (Figure S2B). This can be achieved with historically congruent diversities of forest structures across landscapes, based on GLO and other spatial reconstructions. This bet-hedging landscape approach to ecological restoration is consistent with long-term persistence of historical forests, the high current threat from insects, and would likely confer more resilience to disturbances, that may all increase in the future, than would just retaining larger or older trees across large areas.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fevo.2014.00088/abstract

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Assessing carbon stocks and accumulation potential of mature forests and larger trees in U.S. federal lands

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Mature and old-growth forests (collectively "mature") and larger trees are important carbon sinks that are declining worldwide. Information on the carbon value of mature forests and larger trees in the United States has policy relevance for complying with President Joe Biden's Executive Order 14072 directing federal agencies to define and conduct an inventory of them for conservation purposes. Specific metrics related to maturity can help land managers define and maintain present and future carbon stocks at the tree and forest stand level, while making an important contribution to the nation's goal of net-zero greenhouse gas emissions by 2050. We present a systematic method to define and assess the status of mature forests and larger trees on federal lands in the United States that if protected from logging could maintain substantial carbon stocks and accumulation potential, along with myriad climate and ecological co-benefits. We based the onset of forest maturity on the age at which a forest stand achieves peak net primary productivity. We based our definition of larger trees on the median tree diameter associated with the tree age that defines the beginning of stand maturity to provide a practical way for managers to identify larger trees that could be protected in different forest ecosystems. The average age of peak net primary productivity ranged from 35 to 75 years, with some specific forest types extending this range. Typical diameter thresholds that separate smaller from larger trees ranged from 4 to 18 inches (10–46 cm) among individual forest types, with larger diameter thresholds found in the Western forests. In assessing these maturity metrics, we found that the unprotected carbon stock in larger trees in mature stands ranged from 36 to 68% of the total carbon in all trees in a representative selection of 11 National Forests. The unprotected annual carbon accumulation in live above-ground biomass of larger trees in mature stands ranged from 12 to 60% of the total accumulation in all trees. The potential impact of avoiding emissions from harvesting large trees in mature forests is thus significant and would require a policy shift to include protection of carbon stocks and future carbon accumulation as an additional land management objective on federal forest lands.

KEYWORDS

carbon stock, climate change, large trees, mature forests, national forest lands

1. Introduction

Nature-based climate solutions are needed to meet anticipated national targets associated with the Paris Climate Agreement which establishes a global framework to avoid dangerous climate change by limiting warming to less than 2°C (United Nations, 2015). In the United States, the Biden administration announced a "roadmap" for nature-based solutions during the COP27 climate summit (White House, 2022a). Reducing carbon dioxide (CO_2) emissions and increasing CO_2 removals from the atmosphere using forests are considered to be the most significant of terrestrial natural climate solutions globally and in the U.S. (Griscom et al., 2017; Fargione et al., 2018).

Protecting mature forests to achieve their potential to reduce greenhouse gases is controversial in part because it restricts logging (Law and Harmon, 2011; Moomaw et al., 2020). Forests in the later stages of seral development (mature and old-growth, DellaSala et al., 2022a) and the large trees within them (Stephenson et al., 2014; Mildrexler et al., 2020) play an outsized role in the accumulation and long-term storage of atmospheric carbon, and consequently enabling their protection where lacking has been recognized as an effective nature-based climate solution (Griscom et al., 2017). Notably, President Joe Biden issued an executive order (White House, 2022b) recognizing the climate value of mature and old-growth forests and directed federal officials to define and inventory them on Federal lands and develop policies for their conservation. Thus, providing techniques for defining when forests qualify as mature and quantifying their relative carbon content and storage potential has high policy relevance.

This undertaking supports the nation's goal of achieving net-zero greenhouse gas emissions by 2050 and to conserve 30% of the nation's land by 2030 (White House, 2021). Protecting older, larger trees and mature forests would also help reverse the global degradation of older forests that have diverse ecological values (Lindenmayer et al., 2012), and facilitate the continued growth of mid-sized trees toward maturity (Moomaw et al., 2019). Mature forests provide refugia for many imperiled species (Buotte et al., 2020; DellaSala et al., 2022a), store disproportionate amounts of above-ground carbon in forests (Stephenson et al., 2014; Lutz et al., 2018; Mildrexler et al., 2020), and historically constitute a large volume of valuable timber (Johnson and Swanson, 2009). These values often conflict with one another resulting in contentious policy debates about land management objectives and best practices, particularly on federal lands in the U.S. where much of the remaining mature forest area resides according to national forest inventory data (Bolsinger and Waddell, 1993; DellaSala et al., 2022a). Recent studies of land values reveal that the importance of mature forests for ecosystem integrity and non-timber ecosystem services far exceeds their value for timber products (Watson et al., 2018; Gilhen-Baker et al., 2022).

Some researchers argue that it is necessary to log larger trees in fire-suppressed forests in the western U.S. to restore fire regimes, reduce biomass, and minimize emissions from wildfires (Kirschbaum, 2003; Hessburg et al., 2020; Johnston et al., 2021). However, these assertions have been challenged (Stephenson et al., 2014; Lutz et al., 2018; Mildrexler et al., 2020; DellaSala et al., 2022b) in part because removing larger trees from forests having high carbon stocks creates a significant "carbon debt" that can take decades or centuries to repay (Moomaw et al., 2019; Law et al., 2022).

It follows that our objectives are to (1) present an approach to defining larger trees and mature forests on federal lands; (2) estimate the current carbon stock and annual carbon accumulation in larger trees in mature forests across a representative selection of national forests, and (3) estimate the carbon stock and accumulation left unprotected by current binding designations.

We do not identify the proportion of mature forest area and carbon stocks that could be classified more specifically as "old growth." Defining old-growth in a consistent way across the diversity of temperate forests is challenging since existing definitions are based on structural, successional, and biogeochemical factors that are unique for individual forest types and researcher's interests (Wirth et al., 2009). Our characterization of mature forests has ecological and policy relevance for restoring old-growth characteristics over time, pursuant to the presidential executive order as well (DellaSala et al., 2022a). Thus, we determined that this paper would be more broadly focused on mature forests rather than old-growth forests.

2. Materials and methods

2.1. Approach

Our approach requires addressing two components: (1) individual trees referred to as the "larger" trees in a forest; and (2) mature forest stand development represented by stand age. This method for identifying larger trees in mature stands—and the related assessment of above-ground live carbon stocks and annual carbon accumulation—is intended to be broadly applicable and readily implementable independent of how mature stands are defined. We settled on defining stand maturity with respect to the age of maximum Net Primary Productivity (NPP), which is estimated as the annual net quantity of carbon removed from the atmosphere and stored in biomass (see section 2.2 for definitions of key terms). NPP was calculated by combining 4 terms: Annual accumulation of live biomass, annual mortality of above-ground and below-ground biomass, foliage turnover to soil, and fine root turnover in soil (He et al., 2012). Live biomass and annual mortality were estimated from the Forest Inventory and Analysis (FIA) database. Foliage and fine root turnover were estimated using maps of leaf area index (LAI) and forest age to derive LAI-age relationships for different forest types. These relationships were then used to derive foliage and fine root turnover estimates using species-specific trait data (He et al., 2012).

This is a particularly appropriate approach to maturity in the context of how forests help temper climate change. Our integrating method of associating the median tree diameter with age is intended to be applicable to other definitions of stand maturity, including simple ones applied across the landscape without regard to specific stand characteristics, for example a uniform age cutoff.

2.2. Key definitions and data source

Net Primary Productivity (NPP)—The difference between the amount of carbon produced through photosynthesis and the amount of energy that is used for respiration. Estimate is based on the net increment of tree and understory biomass, leaf production, and fine root turnover (He et al., 2012).

Biomass—The carbon stored in live trees greater than 1 inch (2.54 cm) diameter at breast height (dbh), including stump, bole, bark, branches, and foliage.

Carbon stock—The carbon stored in live biomass at a point in time, unless otherwise defined to include additional ecosystem components, in units of megagrams (Mg) or teragrams (Tg) of carbon (C).

Carbon accumulation—The net change in carbon stock of live tree biomass over a period of time, in units of megagrams (Mg) or teragrams (Tg) of carbon (C), per hectare (ha^{-1}) and/or or per year (yr^{-1}).

Metric ton—In the literature, the term metric ton (Mt or tonne) is often used instead of megagram.

Definitions of other terms commonly used in this paper are included in the **supplementary material**.

To apply our method to each national forest, recent FIA data collected by the U.S. Forest Service were queried using the EVALIDator online query system (USDA Forest Service, 2022). The sampling approach and estimation methods of forest inventory variables in the FIA database follow documented procedures (**Supplementary material**; Bechtold and Patterson, 2005). Our analysis is focused on above-ground carbon in live-trees, though some representative data are also presented about all ecosystem C pools to show the full potential of protecting carbon stocks on selected national forests.

2.3. Study area

The study area includes 11 individual national forests or small groups of national forests in the conterminous U.S. (**Table 1** and **Figure 1**), selected to represent the geographic diversity of U.S. forests and to have at least one forest in each USFS region. Forests with similar characteristics within a region were grouped if preliminary analysis determined that there were insufficient sample data to develop the biomass distributions for a single forest by main forest types.

2.4. Defining larger trees and mature forests

We combine two key indicators—stand age and tree diameter—in a way that could be used by land managers to assess maturity for informing management practices, in contrast to basing maturity and management on either tree diameter or stand age alone as in some previous studies (Mildrexler et al., 2020; Johnston et al., 2021). Mature forests are defined as stands with ages exceeding that at which accumulation of carbon in biomass peaks as indicated by NPP. We considered FIA sample plots to represent stands of relatively uniform condition. The sampled areas and trees are partitioned into uniform domains during field sampling and data processing if more than one stand condition falls within the sampling area. For this study, a new term "Culmination of Net Primary Productivity" (CNPP) is used to describe the age at which NPP reaches a maximum carbon accumulation rate. Physiologically, peak productivity occurs approximately at the age when the growing space in the

TABLE 1 National Forests, sampling dates, and number of sample plots used in our study.

National Forest	FIA sampling dates	Number of sample plots
Gifford Pinchot, WA	2008–2019	626
Malheur, OR	2011–2019	758
Black Hills, SD	2013–2019	348
Chequamegon-Nicolet, WI	2013–2019	559
Green Mountain, VT and White Mountain, NH	2013–2019	580
Appalachian National Forests[1]	2013–2020	982
White River, CO	2010–2019	291
Flathead, MT	2010–2019	341
Arizona National Forests[2]	2010–2019	849
Central California National Forests[3]	2011–2019	410
Arkansas National Forests[4]	2017–2021	427

[1] Pisgah (NC), Nantahala (NC), Cherokee (TN), Monongahela (WV), Jefferson (VA), George Washington (VA).

[2] Coconino, Prescott, Tonto, Sitgreaves, AZ.

[3] Eldorado, Stanislaus, and Sierra, CA.

[4] Oachita, Ozark-St. Francis, AR.

ecosystem is fully covered by leaf area—i.e., tree canopy closure reaches 100%. After this age, NPP either stays constant or declines gradually, depending on tree species composition, and other environmental factors such as nutrient availability (Kutsch et al., 2009; He et al., 2012). Previous analyses of FIA data indicate that peak NPP occurs at a relatively young stage of stand succession, roughly 25—50 years following stand establishment (**Figure 2**; He et al., 2012; Dugan et al., 2017; Birdsey et al., 2019). Foresters have a similar metric, referred to as the "culmination of mean annual increment" (CMAI), that is based on estimated net volume increment (i.e., volume growth minus mortality) as a function of age, rather than net productivity as a function of age, which is more relevant to assessing forests potential to reduce greenhouse gases. CMAI is calculated in the same way as CNPP, except that the mean annual increment variable is net volume increment instead of net primary productivity.

Larger trees are then defined as having a diameter at breast height (dbh) that is equal to or greater than the median diameter in forest stands at or near the age of stand-level CNPP. A range of ages around the age of CNPP, taken to be the CNPP age plus or minus one age class (30-year bin size), was used in order to have sufficient FIA sampling plots (generally 100 or more) to develop a tree diameter distribution for individual forest types. Then the median diameter of the distribution is used as the lower diameter threshold of maturity for the population of trees in the CNPP age class.

Our approach involves clustering (post-stratifying) sample plots by forest type and stand age class, and individual sample trees by tree diameter class, and then calculating estimates for the clusters (populations) as groups. Because most clusters include a wide distribution of tree diameters, there can be larger trees present in stands having ages below CNPP age, and *vice versa*, stands with ages above CNPP age can have trees with diameters below the lower diameter limit. The definitions of mature stands and associated larger trees in this study is conceptually consistent with stages of maturity derived from classifying FIA sample plots (Stanke et al., 2020; USDA Forest Service, 2022) and from an approach involving spatial data (DellaSala et al., 2022a). **Table 2** compares the terminology and approaches of each.

To estimate the area of mature stands based on sample plot characterization, we used the FIA stand-size variable coded as "large diameter" (column 2 of **Table 2**) because our method is not based on stand-scale variables alone but rather a crosswalk

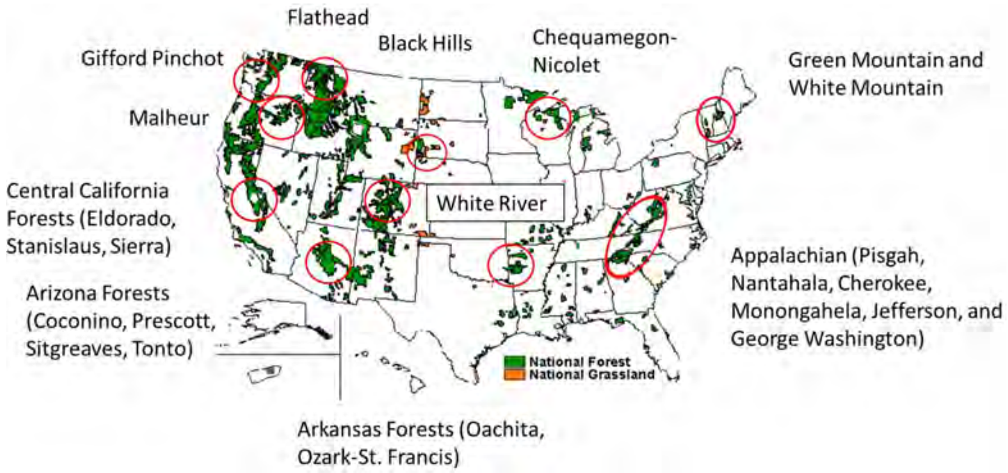

FIGURE 1
Approximate locations of 11 National Forests in our study area.

of stand and tree population variables. Large diameter stands are defined by FIA as those with more than 50 percent of the stocking in medium and large diameter trees, and with the stocking of large diameter trees equal to or greater than the stocking of medium and small diameter trees.

2.5. Estimation of carbon stock and accumulation in living biomass

We used the age-to-diameter crosswalk to estimate live above-ground carbon stocks and annual carbon accumulation for larger trees in forests above the CNPP threshold. We focused on live above-ground biomass since it is typically the largest of the C pools (except for soil in some cases) and is the most dynamic in terms of how carbon stocks and accumulation change with age or tree size (Domke et al., 2021). The estimated carbon in biomass of trees or stands is taken directly from the FIA database and is based on measurements of dbh and height. The current standard FIA approach to estimating biomass from tree measurements uses the component ratio method (Woodall et al., 2011). Unless stated otherwise, we use the term "carbon" to refer to carbon in live-tree biomass, not the carbon in all ecosystem carbon pools. Live-tree biomass includes the main stem or bole of the tree, rough or rotten sections of the bole, tree bark, branches, and leaves.

Estimation of the carbon accumulation rate is based on remeasurement of the same grid of sample points and trees at intervals ranging from 5 to 10 years depending on the state, with generally shorter remeasurement cycles in the eastern U.S. compared with the western U.S. (Table 1). Carbon in live-tree biomass was estimated at the beginning and end of the time period, and carbon accumulation was calculated as change in carbon over the period divided by the number of years.

The uncertainty of estimates of carbon stock and carbon accumulation was taken directly from the FIA data retrieval system that reports sampling error with 67% confidence, which we multiplied by 1.96 to report estimates with 95% confidence. These uncertainty estimates do not include the uncertainty of using biomass equations to estimate

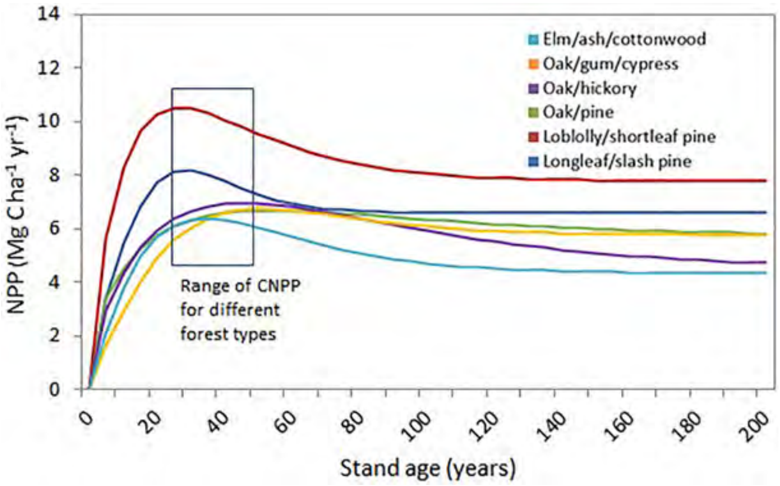

FIGURE 2
Net primary productivity (NPP) for selected forest types in the South (He et al., 2012). Culmination of NPP (CNPP) occurs at the stand age having the greatest annual increment rate, typically at or just after the tree canopy closes. Younger stands are those with ages less than CNPP. Older stands have ages greater than CNPP. CNPP is highly variable among forest types and geographic regions—in this example, from ages 23 to 45. The He et al. (2012) paper includes detailed uncertainty analyses of these and other NPP curves.

TABLE 2 Successional stages of forest maturity or stand structure as defined by several studies.

Maturity or structural stage	FIA stand-size[1]	Stanke et al. (2020)[1]	DellaSala et al. (2022a)[2]	This study[3]
1	Small diameter	Pole	Young	Young
2	Medium diameter	Mature	Intermediate	Mature
3	Large diameter	Late	Mature/Old-growth	

Classifications across the rows are similar but not identical.
[1] Stand structural stage is classified based on the relative basal area of canopy stems in various size classes.
[2] Forest maturity model based on three spatial data layers of forest cover, height, and above-ground living biomass for all landownerships.
[3] Based on culmination of net primary productivity (CNPP) and median stand diameter at CNPP. Late succession or old-growth not distinguished from mature.

tree carbon from diameter and height measurements or from wood density.

2.6. Domains and filters

We filtered the data to include only sample plots that were classified in the database as belonging to the national forest or group of forests being analyzed. For estimating CNPP, we screened out sample plots if they showed evidence of logging or natural disturbance. The remaining "undisturbed" stands, however, could still include some tree mortality and loss of live biomass associated with aging and succession, or small-scale disturbances. All plots including those disturbed or harvested were included in final estimates of the carbon stock and accumulation for the whole forest or for reserved and unreserved areas within the National Forest. Reserved and unreserved areas were defined by the FIA database variable "reserved class." The classification of reserved is not the same as land defined as "protected" by the USGS GAP analysis project (USGS, 2019). Reserved land is withdrawn by law(s) prohibiting the management of land for the production of wood products, though tree harvesting may occur to support other management objectives. We use the classification "unreserved" as a proxy for forest areas that are lacking protection from timber harvest, while acknowledging that this definition of unreserved land may not be consistent with other definitions of unprotected land.

2.7. Model outputs

Estimates of carbon stock and accumulation are presented separately for reserved and unreserved forest areas since the target for future management policies may focus on carbon stocks of older forests in areas that could be logged in the future. Some additional details regarding definitions and calculation protocols are available in the **Supplementary material**.

3. Results

3.1. National forest characteristics

Individual forests and groups of forests range in forest area from about 0.4 to 2.0 million hectares (M ha), and the total area of all forests analyzed is about 8.9 M ha (**Table 3**). The carbon stock in above-ground biomass ranges from 9 to 113 million megagrams (Mg). There is a wide range of average C density, with the lowest amount of 21 Mg ha^{-1} in Arizona National Forests, and the highest amount of 166 Mg ha^{-1} in the Gifford Pinchot National Forest in Washington. The total carbon in the forest ecosystems, which includes above- and below-ground biomass, dead wood, litter, and soil, is from 2 to 5 times the amount of carbon in above-ground biomass alone (Domke et al., 2021). All but one of the national forests studied (the Black Hills National Forest in South Dakota) experienced an increase in above-ground carbon over the

TABLE 3 Biomass carbon stock and accumulation for all live-trees greater than 1 inch (2.54 cm), for each National Forest or group of forests studied.

National Forest	Total forest area (ha)	Total biomass C stock (Mg)	Total biomass C accumulation[1] (Mg yr^{-1})	Average C density (Mg ha^{-1})	Average C accumulation[2] (Mg $ha^{-1}yr^{-1}$)
Gifford Pinchot	508,502	84,233,113	878,348	166	1.73
Malheur	584,951	23,566,550	234,124	40	0.40
Black Hills	394,508	9,130,825	−32,622	23	−0.08
Chequamegon-Nicolet	583,050	30,777,312	607,023	53	1.04
Green and White Mountains	478,285	35,572,874	299,164	74	0.63
Appalachian Forests	1,216,520	112,798,380	1,122,302	93	0.92
White River	685,869	30,887,524	N/D	45	N/D
Flathead	906,902	39,688,676	N/D	44	N/D
Arizona Forests	2,083,049	43,194,094	N/D	21	N/D
Central California Forests	996,197	86,238,281	125,730	87	0.13
Arkansas Forests	454,986	64,714,071	1,498,668	142	3.29
Total	8,892,819	560,801,700	4,732,737	63	0.91

[1] Change in carbon stock over approximately the last 10 years.

[2] Average of national forests with available growth data from FIA database.

"N/D" means data were not available.

remeasurement period, ranging from 0.13 (Central California) to 3.29 (Arkansas) Mg $ha^{-1}yr^{-1}$. All of the national forests were affected by disturbances—the most common being fire, insects and logging—though the areas and mix of disturbance types that occurred and the areas undisturbed are highly variable among the forests (**Supplementary Table 1**). Natural disturbances can result in significant tree mortality and transfer of carbon from live to dead trees, and gradual net emissions over several decades especially if the disturbances are of high severity (Birdsey et al., 2019). In the case of logging disturbances, emissions are significant both in the near term and over time, even when accounting for the amount of carbon in the harvested live trees that is initially transferred to the long-term harvested wood product pool (Hudiburg et al., 2019).

3.2. Culmination of net primary productivity and diameter limits

The estimated CNPP ages range from 35 to 75 years among the 11 National Forests with an average age of 50 years (**Table 4**) and are highly variable by forest type within each forest (**Supplementary Table 2**). Productivity at CNPP ranges from <1.0 to about 4.0 MgC $ha^{-1}yr^{-1}$, which is higher than the average productivity among all age classes since it represents the peak value. Typically, the productivity values after CNPP age decline at a variable rate by region and forest type (**Figure 2**). The estimates of CNPP age may be affected by sparse data points for some age classes, different stand disturbance histories, and other factors that influence tree growth rates over time such as climate and topography. In this study, the age at CNPP is used to define the lower age threshold for mature forests.

Determining the age threshold associated with CNPP involves examining the distribution of biomass by diameter (dbh) class for the stand-age class window around the age of CNPP. In most cases, there is a clearly defined peak of biomass at the median diameter of the distribution (**Supplementary Figure 1**). Because of the diversity of stand conditions associated with CNPP across the landscape, as well as uneven aged stand conditions, there are rather wide distributions of tree sizes associated with any particular CNPP (**Supplementary Figure 1**). Since the FIA stand-age data we used were compiled into diameter classes of 2 inches (5 cm), we used the upper end of the range to define the diameter threshold. Typically, there is more carbon stored in the population of trees with diameters at and near the diameter at CNPP, though these trees can grow to much larger sizes as indicated by the upper end of the diameter distributions. For the national forests in this study, the diameter limits ranged from a low of 4 inches (10 cm) for Douglas-fir in the Flathead National Forest to a high of 18 inches (46 cm) for two forest types in the Central California National Forests (**Supplementary Table 2**). Combining CNPP with median diameter in a cross-tabulation results in identifying the carbon stocks in larger trees in mature forests for each national forest, highlighted in yellow in the example table (**Supplementary Table 3**).

TABLE 4 Average age and tree diameter at culmination of net primary production (CNPP), all forest types combined on 11 National Forests in our study area.

National Forest	Average CNPP age (Years)	Diameter threshold (Inches/cm)
Gifford Pinchot	45	13/33
Malheur	45	12/30
Black Hills	75	14/36
Chequamegon-Nicolet	45	9/23
Green and White Mountains	35	12/30
Appalachian Forests	35	11/28
White River	55	6/15
Flathead	45	8/20
Arizona Forests	75	12/30
Central California Forests	50	16/41
Arkansas Forests	40	10/25
Average of all Forests	50	11/28

Tree diameters represent the lower age bound of mature forests (i.e., age at CNPP). Detailed ages and tree diameters by forest type are shown in supplementary Table 2.

3.3. Comparison of CNPP and CMAI

Evaluation of forest inventory data indicated that CNPP and CMAI occur at about the same age (**Supplementary Figure 2**). Some older studies based on different data, mainly from volume growth and yield studies, associate CMAI with a greater age (e.g., McArdle, 1930). This difference is likely caused by several factors such as management intensity, temporal changes in productivity from environmental changes, and sampling protocols.

3.4. Carbon stocks and accumulation of larger trees in mature stands

The total C stock and C accumulation of larger trees in stands older than age at CNPP compared with all trees and stands is highly variable among the different forests analyzed (**Table 5**). Likewise, sampling errors are highly variable, reflecting the total areas classified as mature and therefore the number of FIA sample plots therein. Sampling errors for C accumulation estimates are significantly higher than for C stocks, mainly because the variability of accumulation rates among sample plots is higher than the variability of stock estimates.

TABLE 5 Estimated area, carbon stock, carbon accumulation, and sampling errors for larger trees in mature stands within individual National Forests based on most recent forest inventory data (Table 1).

National Forest	Area (ha)	C Stock (Mg)	C stock sampling error[1] (%)	Net C accumulation (Mg yr^{-1})	Net C accumulation sampling error[1] (%)	C stock[2] (% of total NF)	Net C accumulation[2] (% of total NF)
Gifford Pinchot	440,005	68,148,420	5.5	380,998	22.7	80.9	43.4
Malheur	471,439	16,886,265	7.1	165,949	19.1	71.7	70.9
Black Hills	215,379	3,711,144	14.6	−15,167	82.2	40.6	−46.5
Chequamegon-Nicolet	303,176	20,625,499	6.9	281,034	11.9	67.0	46.3
Green and White Mountains	301,884	15,786,690	7.9	60,593	141.7	44.4	20.3
Appalachian	1,033,833	83,571,980	6.2	675,970	15.3	74.1	60.2
White River	390,370	26,038,059	13.1	N/D	N/D	84.3	N/D
Flathead	507,053	27,841,625	13.6	N/D	N/D	70.2	N/D
Arizona National Forests	1,738,672	36,254,717	11.2	N/D	N/D	83.9	N/D
Central California National Forests	821,991	65,973,313	8.8	−66,370	52.2	76.5	−52.8
Arkansas National Forests	384,972	41,808,132	6.3	619,759	13.5	64.6	41.4
Total/mean	6,608,774	406,645,844	[redacted]	2,102,766	[redacted]	72.5	44.4

[1] With 95% confidence.

[2] Calculated by dividing values by those in Table 3. The percentages of carbon stocks and accumulation of larger trees in mature stands compared with all forests are also shown (last 2 columns). Larger trees in mature stands are the subset of the forest population composed of trees greater than the median dbh associated with CNPP in stands greater than CNPP age (Figure 2). Areas of mature forests estimated by a proxy variable "stand-size class" from FIA (see methods).

"N/D" means data were not available.

Of the 11 forests, the C stock of larger trees in mature stands ranged from 41 to 84 percent of the total C stock of the forests, whereas C accumulation ranged from −53 to 71 percent of the total C accumulation. This difference between changes in C stock and C accumulation reflects several underlying causes: (1) younger forests can have higher NPP rates than mature forests as illustrated in Figure 2; (2) increasing mortality as forests grow older because some trees die from overcrowding or insects and diseases; and (3) disturbances such as severe wildfire that kill significant numbers of trees can reduce NPP, in some cases to a negative number.

3.5. Carbon stocks and accumulation in mature stands and larger trees in unreserved forest areas

The methodology described above can be further refined to separate out unreserved areas that could be designated for protection of carbon stocks and accumulation on national forest lands. In the 11 forests analyzed, unreserved C stocks of larger trees from all tree species in mature stands ranged from 36 to 69 percent of total C stocks (Table 6 and Supplementary Table 4). Unreserved C accumulation of such trees in mature forests ranged from 12 to 60 percent of total C accumulation, not including the Black Hills national forest where the unreserved C accumulation was negative because of logging and natural disturbances (primarily insects). Typically, one or a few species comprise the main part of unprotected stocks and accumulation. Generally, the percentage of unreserved C accumulation is less than the percentage of unreserved C stock because the growth rates of mature forests are somewhat lower than younger forests.

3.6. Potential protected carbon stocks with variable diameter and age limits

The final stage of the analysis estimated the amount of C in unreserved areas above variable diameter and age limits for logging (Supplementary Table 5). These data further illustrate the functionality and flexibility of the age to diameter association that we developed for policy makers and land managers. The impact of selecting either the diameter limit or the age limit, or both, is highly dependent on the distribution of the estimated C stocks by these factors. For example, the diameter limit for Gifford Pinchot at a stand age of 80 years (20 inches; 51 cm dbh) would protect 57% of the total above-ground C, and the age limit of 80 years would protect 79% of the total above-ground C. In contrast, the diameter limit for Chequamegon–Nicolet at a stand age of 80 years (13 inches; 33 cm dbh) would protect only 27% of the total above-ground C, and the age limit of 80 years would protect only 48% of the total above-ground C. Each of the studied forests has a unique pattern of unreserved C based on diameter or age limits.

4. Discussion

4.1. Summary of results

The average age of maximum carbon accumulation (CNPP) ranged from 35 to 75 years for all forest types combined (Table 4), and the ranges were wider for individual forest types (Supplementary Table 2). Many factors contribute to determining the CNPP age (e.g., tree species, competition, site productivity, and climate). The lowest CNPP ages were estimated for the eastern forests in the southern and northern Appalachian regions, while the highest CNPP ages were found in the West. Typical diameter thresholds that separate smaller from larger trees (based on CNPP age) ranged from 6 to 16 inches (15–41 cm), with larger diameter thresholds found in the Western forests. The unprotected carbon stock of larger trees in mature stands ranged from 4 to 74 million MgC (Table 6), representing between 36.0 and 68.3 percent of the total carbon in the forest biomass. Forests with the highest percentage of unprotected carbon stock in larger trees in mature forest stands included Gifford Pinchot, Malheur, Chequamegon–Nicolet, and Appalachian National Forests. The unprotected carbon accumulation of larger trees in mature stands ranged widely from 11.5 to 60.2 percent of the total carbon accumulation in biomass, with one forest (Black Hills) showing a reduction in biomass.

4.2. Diameter and age thresholds

Our approach to establishing mature forest definitions and diameter thresholds for larger trees is rooted in a crosswalk of stand age and tree diameter that integrates two variables used to describe mature forests and trees. Both tree diameter and stand age have been used independently in the past to identify the lower bounds of maturity and provide guidance for on-the-ground tree and forest management decision rules (Mildrexler et al., 2020; Johnston et al., 2021). The two variables complement each other because although age is a good indicator of stand maturity, it can sometimes be difficult to determine a precise stand age in the field especially for stands of multi-aged trees, whereas tree diameter is an easily and accurately measured variable in any forestry operation. While our approach lacks complexity, it can form the foundation for more detailed analyses needed to guide on-the-ground management decisions.

Our approach is based on the application of FIA data, a standard source of detailed field inventory data for all forests of the U.S. that is readily available to the public and continuously updated. There are sufficient sample plots to evaluate most

TABLE 6 Carbon stocks and accumulation in larger trees in mature stands in unreserved forest areas, all forest types, within 11 National Forests in our study.

National Forest	Unreserved C stock		Unreserved C increment	
	Mg	% of total C[1]	Mg yr^{-1}	% of total C increment[1]
Gifford Pinchot	57,074,409	67.8	378,553	43.1
Malheur	16,103,923	68.3	108,878	53.7
Black Hills	3,625,966	39.7	−22,597	−69.3
Chequamegon-Nicolet	19,949,333	64.8	271,540	44.7
Green and White Mountains	12,794,081	36.0	60,821	20.3
Appalachian	74,359,965	65.9	675,969	60.2
White River	17,767,821	57.5	N/D	N/D
Flathead	18,383,736	46.3	N/D	N/D
Arizona National Forests	23,540,573	54.5	N/D	N/D
Central California National Forests	51,225,061	59.4	14,483	11.5
Arkansas National Forests	40,184,951	62.1	747,726	49.9
Total	335,009,819	59.7	2,235,373	47.2

[1] Calculated by dividing values by those in Table 3. Percentages of total forest C stock and accumulation are included. Detailed estimates by forest type are in supplementary Table 4.

National Forests individually or in groups, and different forests or regions can be compared or aggregated using consistent and high-quality data. Furthermore, FIA data have become a standard for many other forest analysis tools and greenhouse gas registries (Hoover et al., 2014), so consistency across platforms is also feasible. Finally, there are developments underway to integrate FIA-based ground data analysis with other approaches based on remote sensing and mapping to support policy and land management (Dugan et al., 2017; Harris et al., 2021; Hurtt et al., 2022), which is the objective of future research building directly on this study and related work (DellaSala et al., 2022a).

Moreover, using CNPP as the threshold for stand maturity is an extension of and a refinement on prior work. The concept of CNPP is closely related to CMAI, which has been used for many decades to describe the point at which tree volume increment is greatest in the maturation of a forest stand for assessing return on investment in forestry operations (e.g., Assmann, 1970; Curtis, 1994) but more recently has been proposed as a way to identify the minimum age of ecosystem maturity for protection efforts (Kerr, 2020). Published CMAI estimates are often derived from managed forests and plantations, which limits their applicability to low-intensity management regimes. Also, CNPP is more closely related than volume to the carbon variables of interest (C and CO_2) for analyses of climate mitigation potential by the forest sector to reduce emissions or remove atmospheric CO_2. Considering the uncertainties of establishing the exact age for forests that did not originate as tree plantations, CNPP and CMAI often occur at similar ages in the life of forests, that is, at or very near the age of crown closure and the onset of tree physiological maturity (Burns and Honkala, 1990; Groover, 2017).

4.3. Uncertainty and data limitations

Most forests or groups of forests studied had sufficient sample plots to keep uncertainty of carbon estimates (described in methods) within 15% of the estimated values (**Tables 1**, **5**). In contrast, the uncertainties of carbon accumulation estimates were significantly larger and more variable, ranging from 13 to 142% of the estimated values (**Table 5**). Although the same number of sample plots were available for both estimates, the variability of C accumulation estimates was much higher in some cases, most likely because C accumulation has higher interannual variability if affected by natural disturbances, tree mortality, and tree growth rates that can vary from year to year. Although the reported uncertainty is related to sample size and variability of the tree populations studied, there is additional uncertainty associated with the biomass models used to estimate above-ground biomass carbon. The error of biomass models typically ranges from about 10–15% for large forest areas, with 95% confidence (US Environmental Protection Agency, 2021).

Our ecosystem C estimates only include above-ground live biomass in trees greater than one-inch (2.4 cm) dbh. C pools in standing and down dead wood, understory vegetation including tree seedlings, litter on the forest floor, and soil C account for significantly more C that could double or quadruple the amount of estimated C stock depending on the geographic location of the forest and other land characteristics such as physiography and soil depth (Domke et al., 2021; US Environmental Protection Agency, 2021). Above-ground live biomass is typically the most dynamic of the C pools in forests, though in some cases, particularly related to logging and natural disturbance, the dead wood and litter C pools may change significantly over short periods of time (Domke et al., 2021).

Forest age is an important variable used to estimate when NPP reaches a maximum value (CNPP) above which forests are considered mature. However, forest age (or time since disturbance) can be difficult to determine especially for uneven- or multi-aged forests and is based on coring trees and counting tree rings from just a few sample trees on a sample plot in the FIA sampling protocol. It is likely that the sample trees that are cored do not represent the population of larger and older trees on a sample plot, meaning that the assigned age could be biased to younger ages (Stevens et al., 2016). In some cases, the NPP curve is rather flat at and around the age of CNPP, making it difficult to identify the precise age associated with CNPP. Despite these issues, age is an easily understood metric that is closely related to forest maturity, and the approach of identifying the median diameter associated with CNPP using a 30-year window of age classes helps to mask the uncertainty of using age as a critical step in the methodology.

4.4. Policy and management implications

Recent policy goals target "net zero" emissions for all sectors by 2050 to arrest the global climate emergency. Since net zero cannot be achieved by reducing fossil fuel emissions alone (United Nations, 2015; Griscom et al., 2017), the potential of nature-based climate solutions to contribute to this larger goal is the subject of legislation and executive orders in the U.S. The approach and methodology developed here are designed to inform policy makers about federally managed mature forests and their large and vulnerable C stocks and high rates of accumulation of carbon from the atmosphere. Some recent legislation and executive orders specifically call for increased analysis of the current and potential role of mature forests and large trees (White House, 2021, 2022b; U.S. Congress, 2022). The approach and methods presented here provide options for policy makers to consider as the specific land management rules are implemented by agencies for national forest lands.

Our study further corroborates that large areas of mature federal forests are significant carbon sinks that lack protection. Results indicate that 10 of the 11 forests analyzed were carbon sinks over the last decade or so, with the largest sinks occurring in the Eastern U.S. Forests with less disturbance and/or younger age-class distributions had greater increases in above-ground carbon per area than forests with higher rates of disturbance and/or older age-class distributions. These observations reflect multiple factors: the past history of management, trends in incidence and severity of recent natural disturbances and logging, and the inherent age at which the productivity of different forest types begins to level-off or decline. We also note an important distinction that rates of carbon accumulation tend to be higher in younger forests while the largest amounts of stored carbon are found in mature forests. Protecting these carbon sinks and avoiding losses of carbon from logging would require a policy shift to focus more on the potential role of federal forests in climate mitigation (DellaSala et al., 2022a). Such a shift requires considering how both natural disturbances (exacerbated by climate change) and harvesting are emitting carbon stored in larger trees across federal forest lands. In this context, it is notable that national and regional estimates of emissions from logging (direct plus lifecycle emissions) are 5–10 times greater than direct emissions from natural disturbances (wildfire, insects, and wind combined) (Harris et al., 2016; Law et al., 2018).

For operational land management practices, it is often easier to apply a diameter limit in timber operations by species than an age limit by forest type, because as noted previously it can be challenging to determine a precise stand age, whereas measuring tree diameter is simple and accurate [although see DellaSala et al. (2022a) for an alternate approach to stand maturity without age or dbh determinations]. The diameter limits derived here are based on stand age at CNPP and so have that element of maturity embedded in their determination. And, as noted, this approach can be used regardless of the age selected. For some forest types, stand level characterization is obscured by their frequent association with selective logging and/or natural disturbances like wildfire, making larger trees the more appropriate component for defining maturity.

The results presented here by region and forest type reveal that there is a wide variation in CNPP age and associated tree diameters reflecting variation in forest type/composition, climate, competition for resources and soil moisture, disturbance dynamics, site productivity, and geographic region. This variability needs to be considered in developing policies and management practices. It is also important to consider risks of loss to stored C from natural disturbances, and other values of forests that are tied to land management objectives, which may or may not be compatible with increasing C stocks and accumulation.

We developed an approach to assess mature forests and their current carbon stock and accumulation benefits, and applied the methods to 11 different case studies of individual or groups of National Forests that can inform implementing the president's executive order. This method can be applied regardless of how mature stands are defined (e.g., it is readily applicable to age thresholds above CNPP). And this ground-based estimation approach can be linked with remote sensing and mapping approaches (e.g., DellaSala et al., 2022a) to provide a geographic view of forest maturity as well as protected status beyond the reserved/unreserved designation available in the FIA database.

This work can also be extended to more clearly identify that subset of mature forests that are truly old-growth, and estimate the associated carbon stocks and accumulation. As forests get older, they tend to have very large and increasing carbon stocks, making them especially valuable as carbon reserves (DellaSala et al., 2022a; Law et al., 2022). Even when threatened by natural disturbances or climate change, there is substantial evidence that old-growth forests can continue to maintain or increase carbon stocks (Stephenson et al., 2014; Law et al., 2018; Lesmeister et al., 2021; Begović et al., 2022). Building upon our definition of mature forests, future research could further inform management decisions by more clearly and consistently identifying those mature forests that are truly old-growth or that potentially could become old-growth, and estimating their carbon stocks and accumulation.

5. Conclusion

Our study presents a framework for in-depth analysis and management of larger trees and mature forests on federal lands. The integration of basic data about stand age, tree diameter, biomass carbon dynamics, and reserved status comprises the main elements of the methodology. After applying the methods to 11 national forests, we found that the unprotected carbon stock in larger trees in mature stands ranged from 36 to 68% of the total carbon in tree biomass. The unprotected annual carbon accumulation in tree biomass of larger trees in mature stands ranged from 12 to 60% of the total accumulation in all trees. The potential climate impact of avoiding emissions from logging larger trees and mature forests is thus significant. Key discussion points focused on uncertainty, policy implications, and land management practices. This work is highly relevant to emerging policies regarding climate change, nature-based climate solutions, and mature forests including the role of larger trees.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: https://www.fia.fs.usda.gov/tools-data/.

Author contributions

RB led the research along with GR and DD. All authors contributed to the writing.

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Conflict of interest

GR and CR were employed by Natural Resources Defense Council, Inc.

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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.1074508/full#supplementary-material

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Does increased forest protection correspond to higher fire severity in frequent-fire forests of the western United States?

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Abstract. There is a widespread view among land managers and others that the protected status of many forestlands in the western United States corresponds with higher fire severity levels due to historical restrictions on logging that contribute to greater amounts of biomass and fuel loading in less intensively managed areas, particularly after decades of fire suppression. This view has led to recent proposals—both administrative and legislative—to reduce or eliminate forest protections and increase some forms of logging based on the belief that restrictions on active management have increased fire severity. We investigated the relationship between protected status and fire severity using the Random Forests algorithm applied to 1500 fires affecting 9.5 million hectares between 1984 and 2014 in pine (*Pinus ponderosa*, *Pinus jeffreyi*) and mixed-conifer forests of western United States, accounting for key topographic and climate variables. We found forests with higher levels of protection had lower severity values even though they are generally identified as having the highest overall levels of biomass and fuel loading. Our results suggest a need to reconsider current overly simplistic assumptions about the relationship between forest protection and fire severity in fire management and policy.

Key words: biodiversity; climate; fire frequency; fire severity; fire suppression; Gap Analysis Program levels; logging; protected areas.

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INTRODUCTION

It is a widely held assumption among federal land management agencies and others that a lack of active forest management of some federal forestlands—especially within relatively frequent-fire forest types such as ponderosa pine (*Pinus ponderosa*) and mixed conifers—is associated with higher levels of fire severity when wildland fires occur (USDA Forest Service 2004, 2014, 2015, 2016). This prevailing forest/fire management hypothesis assumes that forests with higher levels of protection, and therefore less logging, will burn more intensely due to higher fuel loads and forest density. Recommendations have been made to increase logging as fuel reduction and decrease forest protections before wildland fire can be more extensively reintroduced on the landscape after decades of fire suppression (USDA Forest Service 2004, 2014, 2015, 2016). The concern follows that, in the absence of such a shift in forest management, fires are burning too severely and may adversely affect forest resilience (North et al. 2009, 2015, Stephens et al. 2013, 2015, Hessburg 2016). Nearly every fire season, the United States Congress introduces forest management legislation based on this view and aimed at increasing mechanical fuel treatments via intensive logging and weakened forest protections.

However, the fundamental premise for this fire management strategy has not been rigorously tested across broad regions. We broadly assessed the influence of forest protection levels on fire severity in pine and mixed-conifer forests of the western United States with relatively frequent-fire regimes to test this assumption. We used vegetation burn severity data from all fires >405 ha over a three-decade period, 1984–2014, in forests with varying levels of protection.

Study area

Pine and mixed-conifer forests at low/mid-elevations, where historical fires were relatively frequent, are broadly distributed across several ecoregions in the western United States (Fig. 1; Appendix S1: Table S1). Although ponderosa pine often dominates these forests, they can also include Jeffrey pine (*Pinus jeffreyi*), which in places intermix with, and are similar to, ponderosa pine forests, and Madrean pine–oak (*Quercus* spp.) forests with a diversity of pines. Mixed-conifer forests at low/mid-elevations are also broadly distributed across multiple ecoregions (Fig. 1). They can include additional pines (e.g., lodgepole pine, *Pinus contorta*; sugar pine, *Pinus lambertiana*), true firs (*Abies* spp.), Douglas-fir (*Pseudotsuga menzeisii*), and incense-cedar (*Calocedrus decurrens*).

Methods

We used Gap Analysis Program (GAP) protection classes (USGS 2012), as described below, to determine whether areas with the most protection (i.e., GAP1 and GAP2) had a tendency to burn more severely than areas where intensive management is allowed (i.e., GAP3 and GAP4). We compared satellite-derived burn severity data for 1500 fires affecting 9.5 million hectares from years for which there were available data (1984–2014) among four different forest protection levels (Fig. 1), accounting for variation in topography and climate. We analyzed fires within relatively frequent-fire forest types comprised of pine and mixed-conifer forests mainly because these are the predominant forest types at low to mid-elevations in the western United States, there is a large data set on fire occurrence, and they have been a major concern of land managers for some time due to decades of fire suppression. We defined geographic extent of forest types from the Biophysical Settings data set (BpS) (Rollins 2009; *public communication*, http://www.landfire.gov) that derived forest maps from satellite imagery and represents plant communities based on NatureServe's Ecological Systems classification. Baker (2015) noted that some previous work found ~65% classification accuracy of this system with regard to specific forest types and, accordingly, he analyzed groups of related forest types in order to improve accuracy. We followed his approach (see Appendix S1: Table S1). The categories selected from the Biophysical Settings map were ponderosa/Jeffrey pine and mixed-conifer forest types with relatively frequent-fire regimes (e.g., Swetnam and Baisan 1996, Taylor and Skinner 1998, Schoennagel et al. 2004, Stephens and Collins 2004, Sherriff et al. 2014), compared to other forest types with different fire regimes such as high-elevation forests and many coastal forests not studied herein. Forest types in our study totaled 29.2 million hectares (Fig. 1; Appendix S1: Table S1). We used the BpS data to capture areas that were classified as forests before fire, because postfire vegetation maps can potentially show these same areas as temporarily changed to other vegetation types. We sampled our response and predictor variables on an evenly spaced 90 × 90 m grid within these forest types using ArcMap 10.3 (ESRI 2014). This created a data set of 5,580,435 independent observations from which we drew our random samples to create our models. The 90-m spacing was chosen because it was the smallest spacing of points that was computationally practical with which to operate.

Fires

The Monitoring Trends in Burn Severity project (MTBS, *public communication*, http://www.mtbs.gov) is a U.S. Department of Interior and Department of Agriculture-sponsored program that has compiled burn severity data from satellite imagery, which became available in 1984, for fires >405 ha, and was current up to 2014 (Eidenshink et al. 2007). The MTBS Web site allows bulk download of spatial products that include two closely related indices of burn severity: differenced normalized burn ratio (dNBR) (Key and Benson 2006) and relative differenced normalized burn ratio (RdNBR) (Miller and Thode 2007). Both indices are calculated from Landsat TM and ETM satellite imagery of reflected light from the earth's surface at infrared wavelengths from before and after fire to

Fig. 1. Pine and mixed-conifer forests, fires, and ecoregions analyzed in this study.

measure associated changes in vegetation cover and soil characteristics. We defined burn severity with the RdNBR index because it adjusts for prefire conditions at each pixel and provides a more consistent measure of burn severity than dNBR when studying broad geographic regions with many different vegetation types (Miller et al. 2009*a*, Norton et al. 2009). RdNBR values typically range from negative 500 to 1500 with values further away from zero representing greater change from prefire conditions. Negative values represent vegetation growth and positive values increasing levels of overstory vegetation mortality. The RdNBR values could be used to classify fires into discrete burn severity classes of low, medium, and high but this was not performed in our study, as we desired to have a continuous response variable in our models.

We intersected forest sampling points with fire perimeters downloaded from MTBS to determine fires that occurred in our analysis area, and censored fires with <100 sampling points (81 ha). The remaining points represented sampling locations from 2069 fires (Fig. 1). We extracted RdNBR values at each sampling point as our response variable as well as predictor variables that included topography, geography, climate, and GAP status. These sampling points were used to investigate the relationship between forest protection levels and burn severity (Appendix S1: Tables S2 and S3). We chose topographic and climatic variables based on previous studies that quantified the relationship between burn severity, topography, and climate (Dillon et al. 2011, Kane et al. 2015).

Topographic and climatic data

To account for the effects of topographic and climatic variability, we derived several topographic indices (Appendix S1: Table S2) from seamless elevation data (*public communication*, http://www.landfire.gov/topographic.php) downscaled to 90-m^2 spatial resolution due to computational limits when intersecting sampling points. These indices capture categories of topography, including percentage slope, surface complexity, slope position, and several temperature and moisture metrics derived from aspect and slope position. We used the Geomorphometry and Gradient Metrics Toolbox version 2.0 (*public communication*, http://evansmurphy.wix.com/evansspatial) to compute these metrics. We also computed several temperature and precipitation variables (Appendix S1: Table S3) by downloading climatic conditions for each month from 1984 to 2014 from the PRISM climate group (*public communication*, http://prism.oregonstate.edu). Climate grids record precipitation and minimum, mean, and maximum temperature at a 4-km grid scale created by interpolating data from over 10,000 weather stations. To determine the departure from average conditions, we subtracted each climate grid by its 30-yr mean monthly value. These "30-yr Normals" data sets were also downloaded from the PRISM Web site and reflected the mean values from the most recent full decades (1981–2010). We determined mean seasonal values with summer defined as the mean of July, August, and September of the year before a given fire; fall being the mean of October, November, and December of the previous year; winter the mean of January, February, and March of the current year of a given fire; and spring the mean of April, May, and June of the current year.

Protected area status and ecoregion classification

We used the Protected Areas Database of the United States (PAD-US; USGS 2012) to determine forest protection status, which is the U.S. official inventory of protected open space. The PAD-US includes all federal and most State conservation lands and classifies these areas with a GAP ranking code (see map at: http://gis1.usgs.gov/csas/gap/viewer/padus/Map.aspx). The GAP status code (herein referred to interchangeably as GAP class or protection status) is a metric of management to conserve biodiversity with four relative categories. GAP1 is protected lands managed for biodiversity where disturbance events (e.g., fires) are generally allowed to proceed naturally. These lands include national parks, wilderness areas, and national wildlife refuges. GAP2 is protected lands managed for biodiversity where disturbance events are often suppressed. They include state parks and national monuments, as well as a small number of wilderness areas and national parks with different management from GAP1. GAP3 is lands managed for multiple uses and are subjected to logging. Most of these areas consist of non-wilderness USDA Forest Service and U.S. Department of Interior Bureau of Land Management lands as well as state trust lands. GAP4 is lands with no mandate for protection such as tribal, military, and private lands. GAP status is relevant to the intensity of both current and past managements.

We made one modification to GAP levels by converting Inventoried Roadless Areas (IRAs) from the 2001 Roadless Area Conservation Rule (S_USA.RoadlessArea_2001, *public communication*, http://data.fs.usda.gov/geodata/edw/datasets.php) to GAP2 unless these areas already were defined as GAP1. We considered most IRAs as GAP2 given they are prone to policy changes and because they allow for certain limited types of logging (e.g., removal of predominately small trees for fuel reduction in some circumstances).

However, we note that very little logging has occurred within IRAs since the Roadless Rule, although there occasionally have been proposals to log portions of some IRAs pre- and postfire, and fire suppression often occurs.

We modified level III ecoregions (U.S. Environmental Protection Agency (EPA) 2013) to create areas of similar climate and geography (Fig. 1). We did this by extracting ecoregions and combining adjacent provinces in our study region.

Random Forests analysis

We investigated the relationship between protection status and burn severity using the data-mining algorithm Random Forests (RF) (Breiman 2001) with the "randomForestSRC" add-in package (Ishwaran and Kogalur 2016) in R (R Core Team 2013). This algorithm is an extension of classification and regression trees (CART) (Breiman et al. 1984) that recursively partitions observations into groups based on binary rule splits of the predictor variables. The main advantage of using RF in our study is that it can work with spatially autocorrelated data (Cutler et al. 2007). It can also model complex, nonlinear relationships among variables, makes no assumption of variable distributions (Kane et al. 2015), and produces accurate predictions without overfitting the available data (Breiman 2001).

Our independent observations were a random subset of our 5.5 million points, from which we drew three random samples of 25,000 points each. Each sample consisted of 500 fires randomly selected without replacement from the pool of 2069 fires. Fifty points were then randomly selected within each of the 500 fires. Our dependent variables were all continuous (Appendix S1: Tables S2 and S3) except for the main variable of interest, protected area status, which included the four GAP levels. The three observation samples were used to create three RF model runs, each consisting of 1000 regression trees. We conducted three RF model runs to assess whether our random samples of 25,000 points produced fairly consistent results.

The RF algorithm samples approximately 66% of the data to build the regression trees, and the remaining data are used for validation and to assess variable importance. We used this validation sample to determine the amount of variance explained and variable importance. The algorithm also produces individual variable importance measures by calculating differences in prediction mean-square-error before and after randomly permuting each dependent variable's values. Variable importance is a measure of how much each variable contributes to the model's overall predicative accuracy.

Unlike linear models, RF does not produce regression coefficients to examine how a change in a predictor variable affects the response variable. The analogy to this in RF is the partial dependence plot which is a graphical depiction of how the response will change with a single predictor while averaging out the effects of the other predictors, such as the climatic and topographic variables (Cutler et al. 2007). We used this approach, in addition to using RF to determine overall variable importance as described above, in order to determine the effect of GAP status, in particular, on fire severity, while averaging out effects of climate and topography.

Mixed-effects analysis

We performed a linear mixed-effects analysis using the "nlme" add-on package in R (Pinheiro et al. 2015). We used a random intercept model and identified year of fire ($n = 31$) and ecoregion ($n = 10$) as random effects. Similar to our RF models, our independent observations were a random subset of our 5.5 million points but for these models we drew three random samples of 50,000 points each. Each sample consisted of 500 fires randomly selected without replacement, and within each of those fires, 100 points were randomly selected. Our dependent variables were the same used in our RF models, and we log-transformed the non-normal variables of slope, surface roughness, and topographic radiation aspect index. We removed dependent variables that were correlated with each other (Pearson's $r > 0.5$), retaining 21 of 45 candidate dependent variables, and centered these on their means. Model reduction was performed in a stepwise process using bidirectional elimination with Bayesian information criterion selection criterion.

Spatial autocorrelation analysis

Spatial autocorrelation (SA) is the measure of similarity between pairs of observations in relationship to the distance between them. Ecological variables are inherently autocorrelated because

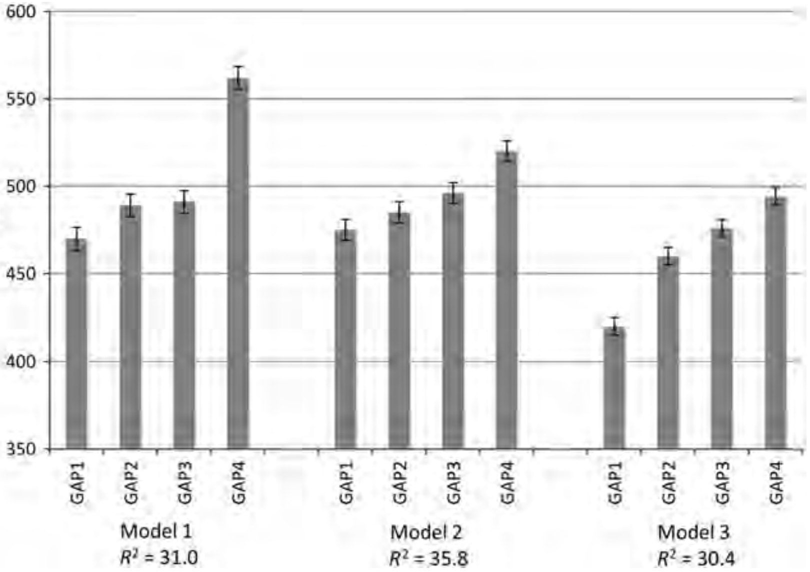

Fig. 2. Random Forests partial dependence of protection status vs. RdNBR burn severity for each model (n = 25,000). The variance explained is shown as pseudo R^2.

landscape attributes that are closer together are often more similar than those that are far apart.

We assessed the SA in the Pearson residuals with inspection of Moran's I autocorrelation index using the "APE" package add-in in R (Paradis et al. 2004) after removing points that shared the same x and y coordinates. Moran's I is an index that ranges from −1 to 1 with the sign of the values indicating strength and direction of SA. Values close to zero are considered to have a random spatial pattern. Our mixed-effects models all had a Moran's I values statistically different from 0 at the 95% confidence level ($P < 0.001$) so we included a spatial correlation structure in our model using the "nlme" package in R. Of Gaussian, exponential, linear, and spherical spatial correlation structures, we determined that the exponential structure produced the lowest Akaike's information criterion (AIC). Despite these additions, our second measurements still found relatively small, but significant, autocorrelation (Moran's I for model runs 1, 2, 3 = 0.10, 0.08, 0.10, all $P < 0.001$).

Results

With regard to ranking of variables in the model runs, variable importance plots from the three RF model runs show that protection status was consistently ranked as one of the 10 most important of the 45 variables in explaining burn severity (Appendix S1: Table S4). The most important variable explaining burn severity was ecoregion for models 1 and 2 and maximum temperature from the previous fall for model 3.

With regard to the GAP status variable in particular, after averaging out the effects of climatic and topographic variables, the RF partial dependence plots show an increasing trend of fire severity with decreasing protection status (Fig. 2). Fires in GAP4 had mean RdNBR values greater than two standard errors higher than all other GAP levels. Fires in GAP3 had mean RdNBR values two standard errors higher than GAP1 in all model runs. GAP3 differences with GAP2 were less pronounced with only one model showing differences greater than two standard errors. Fires in GAP1 were consistently the least severe, being two standard errors less than GAP3 in all model runs and two standard errors less than GAP2 in two of three model runs.

Our mixed-effects models validated these findings with similar results (Fig. 3, Appendix S1: Table S5). Like our RF models, our linear mixed-effects models showed GAP4 fires to have significantly higher RdNBR values and GAP1 fires to have significantly lower RdNBR values when compared to all other GAP classes. Fires in GAP

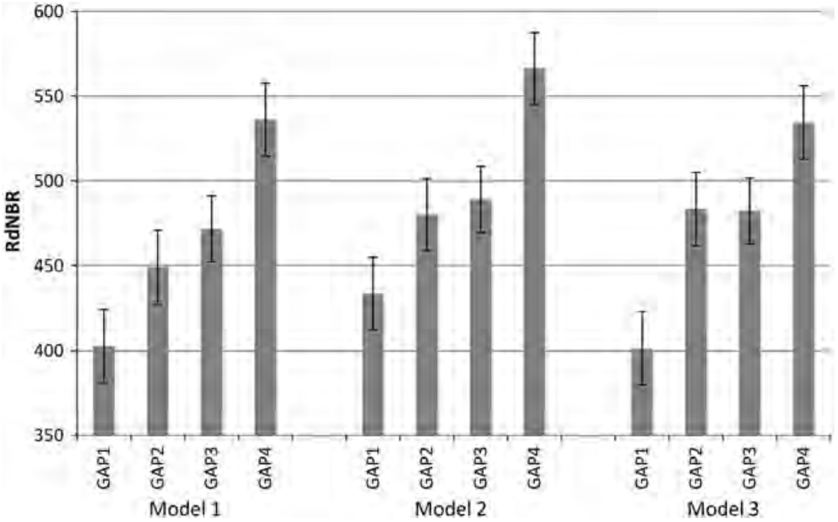

Fig. 3. Linear mixed effects models of protection status vs. RdNBR burn severity (n = 50,000).

status levels 2 and 3 were not significantly different in the mixed-effects models. Although the level of autocorrelation was significant, it was small in our model (Moran's I ~0.1) and not enough to account for such a substantial difference in burn severity among protection classes.

Discussion

Protected forests burn at lower severities

We found no evidence to support the prevailing forest/fire management hypothesis that higher levels of forest protections are associated with more severe fires based on the RF and linear mixed-effects modeling approaches. On the contrary, using over three decades of fire severity data from relatively frequent-fire pine and mixed-conifer forests throughout the western United States, we found support for the opposite conclusion—burn severity tended to be higher in areas with lower levels of protection status (more intense management), after accounting for topographic and climatic conditions in all three model runs. Thus, we rejected the prevailing forest management view that areas with higher protection levels burn most severely during wildfires.

Protection classes are relevant not only to recent or current forest management practices but also to past management. Millions of hectares of land have been protected from logging since the 1964 Wilderness Act and the 2001 Roadless Rule, but these areas are typically categorized as such due to a lack of historical road building and associated logging across patches >2000 ha, while GAP3 lands, for instance, such as National Forests lands under "multiple use management," have generally experienced some form of logging activity over the last 80 yr.

We expect that the effects of historic logging from nearly a century ago to gradually lessen over time, as succession and natural disturbance processes reestablish structural and compositional complexity, but it was beyond the scope of this study to attempt to assess the relative role of recent vs. historical logging. Similarly, industrial fire suppression programs that intensified in the 1940s influenced fire extent across forest protection classes. While more recent let-burn policies have been applied in GAP1 and GAP2 forests in some circumstances, evidence indicates that protected forests nevertheless remain in a substantial fire deficit, relative to the prefire suppression era (Odion et al. 2014, 2016, Parks et al. 2015). Thus, we believe it is unlikely that recent decisions to allow some backcountry fires to burn, largely unimpeded, account for much of the differences in fire severity among protection classes that we found, simply because such let-burn policies have not been extensive enough to remedy the ongoing fire deficit.

While forests in different protection classes can vary in elevation, with protected forests often occupying higher elevations, our results indicate that protection class itself produced notable differences in fire severity after averaging out the effects of elevation and climate (see Fig. 2 and *Results* above). In our study, GAP1 forests were 284 m on average higher in elevation than GAP4 forests, while GAP1 forests experienced lower fire severity. This is the opposite of expectations if elevation was a key influence because higher elevation forests are associated with higher fire severity (see, e.g., Schoennagel et al. 2004, Sherriff et al. 2014). We note that we are not the first to determine that increased fire severity often occurs in forests with an active logging history (Countryman 1956, Odion et al. 2004).

Prevailing forest–fire management perspectives vs. alternative views

An extension of the prevailing forest/fire management hypothesis is that biomass and fuels increase with increasing time after fire (due to suppression), leading to such intense fires that the most long-unburned forests will experience predominantly severe fire behavior (e.g., see USDA Forest Service 2004, Agee and Skinner 2005, Spies et al. 2006, Miller et al. 2009*b*, Miller and Safford 2012, Stephens et al. 2013, Lydersen et al. 2014, Dennison et al. 2014, Hessburg 2016). However, this was not the case for the most long-unburned forests in two ecoregions in which this question has been previously investigated—the Sierra Nevada of California and the Klamath-Siskiyou of northern California and southwest Oregon. In these ecoregions, the most long-unburned forests experienced mostly low/moderate-severity fire (Odion et al. 2004, Odion and Hanson 2006, Miller et al. 2012, van Wagtendonk et al. 2012). Some of these researchers have hypothesized that as forests mature, the overstory canopy results in cooling shade that allows surface fuels to stay moister longer into fire season (Odion and Hanson 2006, 2008). This effect may also lead to a reduction in pyrogenic native shrubs and other understory vegetation that can carry fire, due to insufficient sunlight reaching the understory (Odion et al. 2004, 2010).

Another fundamental assumption is that current fires are becoming too large and severe compared to recent historical time lines (Agee and Skinner 2005, Spies et al. 2006, Miller et al. 2009*b*, Miller and Safford 2012, Stephens et al. 2013, Lydersen et al. 2014, Dennison et al. 2014, Hessburg 2016). However, others have shown that this is not the case for most western forest types. For instance, using the MTBS (www.mtbs.gov) data set, Picotte et al. (2016) found that most vegetation groups in the conterminous United States exhibited no detectable change in area burned or fire severity from 1984 to 2010. Similarly, Hanson et al. (2009) found no increase in rates of high-severity fire from 1984 to 2005 in dry forests within the range of the northern spotted owl (*Strix occidentalis caurina*) based on the MTBS data set. Using reference data and records of high-severity fire, Baker (2015) found no significant upward trends in fire severity from 1984 to 2012 across all dry western forest regions (25.5 million ha), nearly all of which instead were too low or were within the range of historical rates. Parks et al. (2015) modeled area burned as a function of climatic variables in western forests and non-forest types, documenting most forested areas had experienced a fire deficit (observed vs. expected) during 1984 to 2012 that was likely due to fire suppression.

Whether fires are increasing or not depends to a large extent on the baseline chosen for comparisons (i.e., shifting baseline perspective, Whitlock et al. 2015). For instance, using time lines predating the fire suppression era, researchers have documented no significant increases in high-severity fire for dry forests across the West (Williams and Baker 2012*a*, Odion et al. 2014) or for specific regions (Williams and Baker 2012*b*, Sherriff et al. 2014, Tepley and Veblen 2015). Future trends, with climate change and increasing temperatures, may be less simple than previously believed, due to shifts in pyrogenic understory vegetation (Parks et al. 2016).

This is more than just a matter of academic debate, as most forest management policies assume that fire, particularly high-severity fire, is increasing, is in excess of recent historical baselines, and needs to be reduced in size, intensity, and occurrence over large landscapes to prevent widespread ecosystem damages (policy examples include USDA Forest Service 2002, Healthy Forests Restoration Act 2003, USDA Forest Service 2009, HR 167: Wildfire Disaster Funding Act 2015). However, large fires (landscape scale or the so-called megafires) produce myriad ecosystem benefits underappreciated by most land managers and decision-makers (DellaSala and Hanson 2015*a*, DellaSala et al. 2015). High-severity fire patches, in particular, provide a pulse of "biological legacies" (e.g., snags, down logs, and native shrub patches) essential for complex early seral associates (e.g., many bird species) that link seral stages from new forest to old growth (Swanson et al. 2011, Donato et al. 2012, DellaSala et al. 2014, Hanson 2014, 2015, DellaSala and Hanson 2015*a*). Complex early seral forests are most often logged after fire, which, along with aggressive fire suppression, exacerbates their rarity and heightens their conservation importance (Swanson et al. 2011, DellaSala et al. 2014, 2015, Hanson 2014).

Limitations

One limitation of our study is that, due to the coarseness of the management intensity variables that we used (i.e., GAP status), we cannot rule out whether low intensities of management decreased the occurrence of high-severity fire in some circumstances. However, the relationship between forest density/fuel, mechanical fuel treatment, and fire severity is complex. For instance, thinning without subsequent prescribed fire has little effect on fire severity (see Kalies and Yocum Kent 2016) and, in some cases, can increase fire severity (Raymond and Peterson 2005, Ager et al. 2007, Wimberly et al. 2009) and tree mortality (see, e.g., Stephens and Moghaddas 2005, Stephens 2009: Figure 6)—the effects depend on the improbable co-occurrence of reduced fuels (generally a short time line, within a decade or so) and wildfire activity (Rhodes and Baker 2008) and can be over-ridden by extreme fire weather (Bessie and Johnson 1995, Hély et al. 2001, Schoennagel et al. 2004, Lydersen et al. 2014). Empirical data from actual fires also indicate that postfire logging can increase fire severity in reburns (Thompson et al. 2007), despite removal of woody biomass (tree trunks) described by land managers as forest fuels (Peterson et al. 2015). While our study did not specifically test for these effects, such active forest management practices are common on GAP3 and GAP4 lands. Recognizing these limitations, researchers have stressed the need for managers to strive for coexistence with fire by prioritizing fuel reduction nearest homes and allowing more fires to occur unimpeded in the backcountry (Moritz 2014, DellaSala et al. 2015, Dunn and Bailey 2016, Moritz and Knowles 2016).

Follow-up research at finer scales is needed to determine management emphasis and history in relation to fire severity. However, we believe our findings are robust at the subcontinental and ecoregional scales.

CONCLUSIONS

In general, our findings—that forests with the highest levels of protection from logging tend to burn least severely—suggest a need for managers and policymakers to rethink current forest and fire management direction, particularly proposals that seek to weaken forest protections or suspend environmental laws ostensibly to facilitate a more extensive and industrial forest–fire management regime. Such approaches would likely achieve the opposite of their intended consequences and would degrade complex early seral forests (DellaSala et al. 2015). We suggest that the results of our study counsel in favor of increased protection for federal forestlands without the concern that this may lead to more severe fires.

Allowing wildfires to burn under safe conditions is an effective restoration tool for achieving landscape heterogeneity and biodiversity conservation objectives in regions where high levels of biodiversity are associated with mixed-intensity fires (i.e., "pyrodiversity begets biodiversity," see DellaSala and Hanson 2015*b*). Managers concerned about fires can close and decommission roads that contribute to human-caused fire ignitions and treat fire-prone tree plantations where fires have been shown to burn uncharacteristically severe (Odion et al. 2004). Prioritizing fuel treatments to flammable vegetation adjacent to homes along with specific measures that reduce fire risks to home structures are precautionary steps for allowing more fires to proceed safely in the backcountry (Moritz 2014, DellaSala et al. 2015, Moritz and Knowles 2016).

Managing for wildfire benefits as we suggest is also consistent with recent national forest policies such as 2012 National Forest Management Act planning rule that emphasizes maintaining and restoring ecological integrity across the national forest system and because complex early forests can only be produced by natural disturbance events not mimicked by mechanical fuel reduction or clear-cut logging (Swanson et al. 2011, DellaSala et al. 2014). Thus, managers wishing to maintain biodiversity in fire-adapted forests should appropriately weigh the benefits of wildfires against the ecological costs of mechanical fuel reduction and fire suppression (Ingalsbee and Raja 2015) and should consider expansion of protected forest areas as a means of maintaining natural ecosystem processes like wildland fire.

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SUPPORTING INFORMATION

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Review

Building on Two Decades of Ecosystem Management and Biodiversity Conservation under the Northwest Forest Plan, USA

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Abstract: The 1994 Northwest Forest Plan (NWFP) shifted federal lands management from a focus on timber production to ecosystem management and biodiversity conservation. The plan established a network of conservation reserves and an ecosystem management strategy on ~10 million hectares from northern California to Washington State, USA, within the range of the federally threatened northern spotted owl (*Strix occidentalis caurina*). Several subsequent assessments—and 20 years of data from monitoring programs established under the plan—have demonstrated the effectiveness of this reserve network and ecosystem management approach in making progress toward attaining many of the plan's conservation and ecosystem management goals. This paper (1) showcases the fundamental conservation biology and ecosystem management principles underpinning the NWFP as a case study for managers interested in large-landscape conservation; and (2) recommends improvements to the plan's strategy in response to unprecedented climate change and land-use threats. Twenty years into plan implementation, however, the U.S. Forest Service and Bureau of Land Management, under pressure for increased timber harvest, are retreating from conservation measures. We believe that federal agencies should instead build on the NWFP to ensure continuing success in the Pacific Northwest. We urge federal land managers to (1) protect all remaining late-successional/old-growth forests; (2) identify climate refugia for at-risk species; (3) maintain or increase stream buffers and landscape connectivity; (4) decommission and repair failing roads to improve water quality; (5) reduce fire risk in fire-prone tree plantations; and (6) prevent logging after fires in areas of high conservation value. In many respects, the NWFP is instructive for managers considering similar large-scale conservation efforts.

Keywords: biodiversity; climate change; ecological integrity; ecosystem management; global forest model; Northwest Forest Plan; northern spotted owl

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1. Introduction

The 1994 Northwest Forest Plan (NWFP) ushered in ecosystem management and biodiversity conservation on nearly 10 million ha of federal lands within the range of the federally threatened northern spotted owl (*Strix occidentalis caurina*) from northern California to Washington State, mostly along the western slopes of the Cascade Mountains, USA (Figure 1). The plan was prepared in response to a region wide legal injunction on logging of spotted owl habitat (older forests) issued in 1991 by U.S. District Court Judge William Dwyer. After reviewing the NWFP, Judge Dwyer ruled that the plan was the "*bare minimum*" (emphasis added) necessary for the Bureau of Land Management (BLM) and the U.S. Forest Service to comply with relevant statutes (see http://www.justice.gov/enrd/3258.htm; accessed on 29 July 2015). The plan's conservation framework and unprecedented monitoring of forest and aquatic conditions along with at-risk species (those with declining populations) offer important lessons for managers interested in large-scale conservation and ecosystem management [1]. Thus, our objectives are to: (1) showcase the plan's fundamental conservation biology and ecosystem management principles as a regional case study for large-scale forest planning; and (2) build on the plan's conservation approach to provide a robust strategy for forest biodiversity in the context of unprecedented climate change, increasing land-use stressors, and new forest and climate science and policies.

At the time of the NWFP development, President Bill Clinton sought to end decades of conflict over old-growth logging by directing 10 federal agencies responsible for forest management, fisheries, wildlife, tribal relations, and national parks to work together and with scientists on a region wide forest plan that would be "scientifically sound, ecologically credible, and legally responsible." The plan was crafted to ensure the long-term viability of "our forests, our wildlife, and our waterways," and to "produce a predictable and sustainable level of timber sales and non-timber resources that will not degrade or destroy the environment." A multi-disciplinary team of scientists known as the Forest Ecosystem Management Assessment Team [2] was tasked with identifying management alternatives that would meet the requirements of applicable laws and regulations, including the Endangered Species Act, the National Forest Management Act, the Federal Land Policy Management Act, the Clean Water Act, and the National Environmental Policy Act.

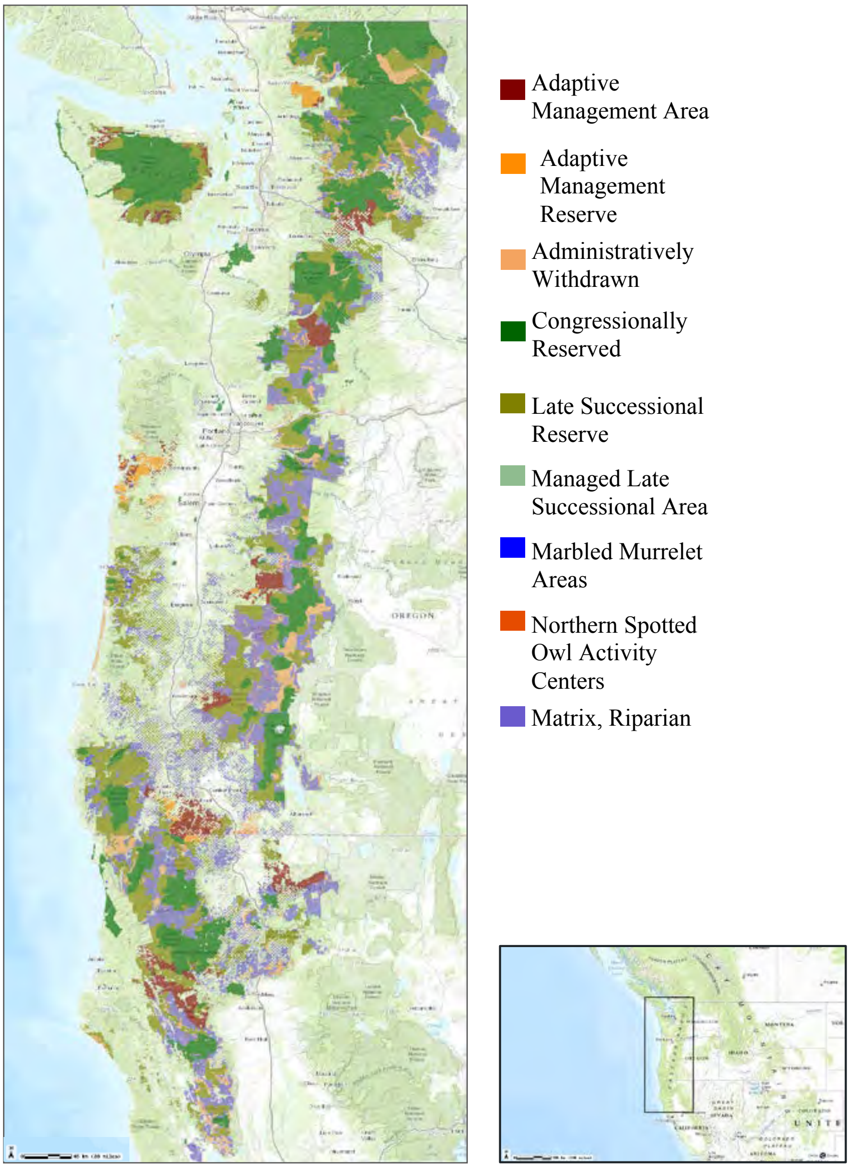

Figure 1. Land-use allocations within the Northwest Forest Plan (NWFP) area: Congressionally reserved—2.93 million ha (30%); Late Successional Reserves (LSRs)—2.96 million ha (30%); Managed Late Successional Reserves—40,880 ha (1%); Adaptive Management Areas—608,720 ha (6%); Administratively Withdrawn 590,840 ha (6%); Riparian Reserves—1.1 million ha (11%); and Matrix—1.6 million ha (16%). Figure created using Data Basin (www.databasin.org; accessed on 29 July 2015) and NWFP data layers [3].

The NWFP amended resource management plans for 19 national forests and seven BLM planning districts with 80% of those lands dedicated to some form of conservation (Figure 1). This increased level of protection and improved management standards were necessary because for many decades federal lands were managed without proper regard for water quality, fish and wildlife viability, and ecosystem integrity. Overcutting of older forests and rapid road expansion were the main factors responsible for the 1990 threatened species listing of the northern spotted owl, 1992 threatened listing of the marbled murrelet (*Brachyramphus marmoratus*), multiple listings of Evolutionary Significant Units (ESUs) of salmonids (*Oncorhynchus* spp.), and pervasive and mounting water quality problems. Prior to the NWFP, ~9.6 million cubic meters of timber was being logged from old-growth forests (>150 years old) annually on federal lands alone—roughly 5 square kilometers per week (assuming stands averaged 300 cubic meters per hectare). USFWS [4] estimated that this rate of logging would have eliminated spotted owl habitat outside remote and protected areas within a few decades. Simultaneously, logging was on the brink of eliminating old-growth forests from surrounding nonfederal lands.

Older forests in the Pacific Northwest are a conservation priority because they harbor exceptional levels of forest biodiversity (e.g., >1000 species have been recognized) and numerous at-risk species [2]. Historically, such forests widely dominated much of the Pacific Northwest landscape, especially in wet areas (coastal) where the intervals between successive fires were centuries long [5].

Older forest communities vary considerably in dominant tree species composition among the southern Cascade Range (Oregon/California), central and northern Cascades (Oregon/Washington), Coast Range (California/Oregon/Washington) and Klamath Mountains (Oregon/California [6]). Forests are generally dominated by Douglas-fir (*Pseudotsuga menziesii*) on sites associated with western hemlock (*Tsuga heterophylla*, sometimes including Pacific and grand fir, *Abies amabalis*, *A. grandis*; western red cedar *Thuja plicata*, bigleaf maple *Acer macrophyllum*); mixed conifers (white fir *A. concolor* and sometimes incense cedar *Calocedrus decurrens*, ponderosa and sugar pine *Pinus ponderosa*, *P. lambertina*); and mixed-evergreens (Pacific madrone *Arbutus menziesii*, tan oak *Lithocarpus densiflorus*, and canyon live oak *Quercus chrysolepis*). Structurally, these forests are characterized by the presence of high densities of large (>100 cm in diameter) conifers (typically 16–23 trees/ha), varied tree sizes and multi-layered canopies, trees with broken and dead tops, high levels of snags and downed wood, and diverse understories [6].

Most forest types in this region generally begin acquiring older forest characteristics at 80 years, depending on site productivity and disturbance history, with full expression of structural diversity at 400+ years [7]. Upper elevation subalpine fir (*Abies lasiocarpa*) and Pacific silver fir are not considered old growth until they are 260–360 years old [8]. Notably, researchers have recently developed an old-growth structure index (OGSI) to represent a successional continuum from young to older forests. The OGSI is a continuous value of 0–100 used to delineate older forests based on four features: (1) large live tree density; (2) large snag density; (3) down wood cover; and (4) tree size diversity at the stand level [9]. Young forests <80 years old that originate from natural disturbance in older forests, known as complex early seral forest, also have high levels of structural complexity (e.g., snags and downed logs) and species richness (especially forbs, shrubs; [10,11]). These younger forests have only recently been recognized as a conservation priority and like old growth have been replaced by structurally simplistic tree plantations [10].

2. NWFP's Long-Term Objectives

FEMAT [2] aptly recognized that even with the plan's protective elements in place, it would take at least a century and possibly two to restore a functional, interconnected late-successional/old growth (LSOG) ecosystem because older forests were reduced to a fraction (<20%) of their historical extent, and 40% of the LSRs were regenerating from prior clearcut harvest that would require decades of restoration to eventually acquire older characteristics [12]. The NWFP also represented a tradeoff between conservation and timber interests with about 1.6 million ha (16%) of older forests placed into the "Matrix" (Figure 1) where the majority of logging would take place pursuant to the plan's management standards and guidelines. As the NWFP was implemented, the volume of timber anticipated for sale (known as the probable sale quantity) was projected at ~2.34 million cubic meters annually. Since then, the plan has achieved about 80% of the probable sale quantity (on average ~1.78 million m^3 annually [13]). The apparent shortfall has been variously attributed to protective measures implemented before timber volume can be offered for sale, ongoing public controversy (appeals and lawsuits) around logging of older forests in the Matrix, fluctuations in domestic housing starts and global timber markets. Congressional appropriations to federal agencies for administering timber sales also have contributed to a *de facto* limit on timber offered for sale. Consequently, the plan's timber goals remain controversial. Some contend that socioeconomic considerations tied to timber extraction have not been met [14]. Others contend that rural communities no longer depend on timber in a region where economic sectors are influenced mainly by external factors and local economies have largely diversified [15]. Nonetheless, while it is premature to judge the efficacy of a 100-year plan in just two decades, periodic monitoring has shown that it has put federal forestlands on a trajectory to meet many of its ecosystem management targets [1,9,16,17].

Restoring a functional, interconnected LSOG ecosystem requires protecting existing older forests and growing more of it over time from young-growth tree plantations within the reserves. Restoring LSOG from former tree plantations is an uncertain endeavor that will require many decades to centuries and has never been envisioned before on such a large scale, especially in the face of rapidly changing climate. Thus, periodic monitoring of several of the ecosystem-based components of the NWFP by federal agencies is being used to gauge restoration targets, assess implementation efficacy of the plan, and proactively respond to new stressors. For instance, an unprecedented level of old forest, aquatics, and at-risk species monitoring occurs at regular intervals, depending on factors assessed, in order to achieve compliance with the 1991 Dwyer court ruling and biodiversity requirements of the National Forest Management Act of 1976. Maintaining biodiversity is a fundamental goal of any large conservation effort and the NWFP is instructive for managers considering similar large-scale ecosystem management and conservation efforts.

2.1. Reserves as a Coarse Filter

Conservation scientists have long-recognized that effective conservation planning involves two complementary approaches: a coarse filter consisting of representative reserve networks, and fine filter that includes local protections for species outside reserves [18,19]. FEMAT [2] emphasized the need for a large, interconnected reserve network as fundamental to biodiversity conservation [1,20,21]

(IUCN protected areas categories: http://www.iucn.org/about/work/programmes/gpap_home/gpap_quality/gpap_pacategories/; accessed on 17 September 2015). Thus, the conservation foundation of the NWFP is rooted in a network of reserves (e.g., LSRs and Riparian Reserves) that are widely distributed (Figure 1) throughout the planning area. The reserve network was principally designed to support viability and dispersal of the northern spotted owl in what is otherwise a highly fragmented system (Figure 2).

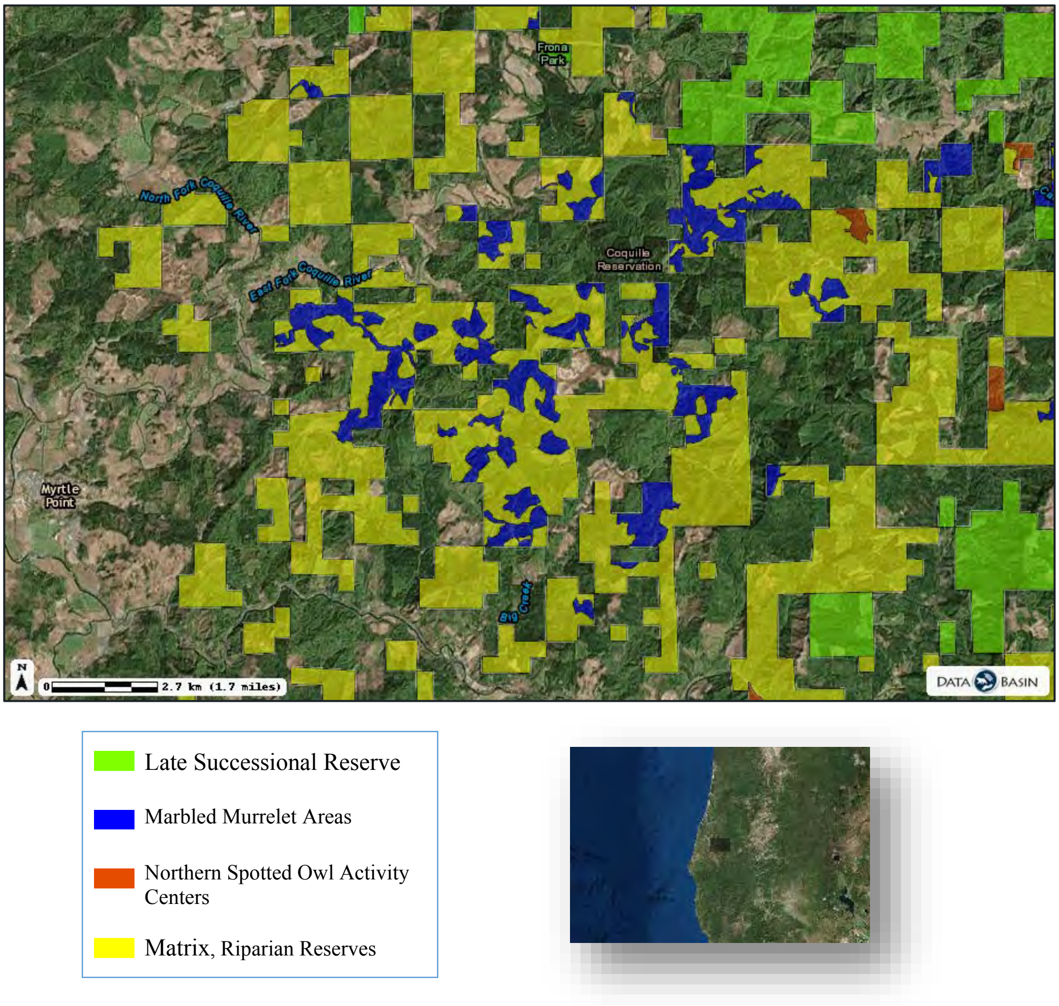

Figure 2. Satellite image of Southwest Oregon showing extensive fragmentation from a "checkerboard" pattern of clearcuts on private and public lands with NWFP land management allocations. Map created using Data Basin (www.databasin.org; accessed on 15 September 2015).

With reserves acting as a coarse filter, ecosystem-based approaches can be implemented to target geographic concentrations—or hotspots—of listed or rare species, thereby increasing conservation efficacy via multiple species benefits. Coarse filters are landscape characteristics of a natural environment that are easily measured, for instance, using satellite images, digital elevation models, and weather station data. Importantly, coarse filters are meant to capture the habitat needs of an entire species assemblage rather than habitat requirements for a particular focal species. For example, a land manager might use dominant vegetation identified through remotely sensed imagery to infer which species potentially occur across the landscape. Thus, the fundamental premise of coarse filters is that measuring the amounts and spatial distribution of biophysical features allows managers to assess the suitability of the landscape for multiple species and to represent key aggregate ecological attributes within a system of designated reserves. Effective coarse-filter reserves need to be defined at appropriate scales so that habitats and populations are sufficiently represented and reserves are distributed in redundant sequences to be robust to prevailing dynamics of natural biophysical disturbance (e.g., forest fires) and external land-management stressors in the surrounding landscape. These considerations were explicitly implemented by FEMAT when scientists designed alternatives that established the conservation architecture of the NWFP.

Three scales are important for estimating the amount and spatial arrangement of habitat needed to recover or conserve at-risk species, particularly those that are indicators of a broader community:

(1) **Species**: habitat needed to provide the resources and physical conditions required for a particular species to survive and reproduce.
(2) **Population**: habitat needed to support a local population of sufficient size to be resilient to background stochastic demographic and environmental events and short-term inbreeding depression.
(3) **Geographic range**: collective habitat required by multiple local populations of a species that are well distributed so that all populations do not respond synchronously to stochastic environmental events.

Central to its biodiversity focus, the NWFP was designed with explicit consideration of resilience, redundancy, and representation across multiple groups of taxa and communities. Resilient populations are those that are large enough, have sufficient genetic variation, and are sufficiently diverse with respect to the age and sex of individuals to persist in the face of periodic threats such as drought, wildfire, disease, and climate change. With respect to redundancy in populations or habitat areas, sufficient numbers of separate populations of a species and areas to support them are needed to provide a margin of safety in case disturbance eliminates some populations or important habitat types. In addition, sufficient genetic variation among populations of a species is necessary to conserve the breadth of the species' genetic makeup and its capacity to evolve and adapt to new environmental conditions. Representation refers to the plan's ability to capture a range of old growth conditions regionally within a reserve network.

2.2. Survey and Manage Program as Fine Filter

As a supplement to the Endangered Species Act, one of the fine-filters of the NWFP is the "survey and manage" program, an unprecedented precautionary approach designed to protect known locations and collect new information to address persistence probabilities and management uncertainties for rare and poorly surveyed species outside the reserve network [22]. Some 400 late-successional species of amphibians, bryophytes, fungi, lichens, mollusks, vascular plants, arthropod functional groups, and one mammal, including many endemics that otherwise may not persist outside the reserve network, were included in the program and given limited protections from logging if found (usually small site-specific buffers).

The survey and manage standards and guidelines for management might not be needed if the coarse filter reserves and older forests were fully functional and, therefore, resilient to short-term disturbance like fires and longer-term climate and land-use changes. However, that is not currently the case. In sum, the survey and manage program resulted in significant gains in knowledge, reduced uncertainty about conservation, and developed useful new inventory methods for rare species [22]. The program, however, remains one of the more controversial aspects of the NWFP, and federal agencies have repeatedly proposed its elimination given the restrictions it can place on the pace and cost of logging.

Thorough documentation of old forest species' distributions and diversity is still needed. In particular, some regions with diverse vegetation types (e.g., Klamath-Siskiyou of southwest Oregon/northern California [23]) have exceptional concentrations of endemic species that remain poorly studied and vulnerable to climate change [24]. Many rare species are inadequately known for development of effective management policies and practices, especially under a rapidly changing climate. The survey and manage program is also needed to ensure that rare species do not become at-risk species due to unforeseen population declines and conservation neglect.

2.3. Northern Spotted Owl Decline Slowed but Not Reversed

Spotted Owl Conservation Strategy—The northern spotted owl is the umbrella species for hundreds of late-successional species in the NWFP area [2]. When developing the conservation strategy for the owl, Thomas *et al.* [25] drew on fundamental principles from population viability analysis [26], island biogeography [27], and conservation biology [28–30] that applied both specifically to the owl and more generally to the community of late-successional associates. Thus, the NWFP is considered a model for conserving at-risk species [1]. Additional conservation biology principles guided the design of the NWFP [2]:

- Species that are widely distributed are less prone to extinction than those with more restricted ranges because local population dynamics are more independent [31].
- Large patches of habitat supporting many individuals are more likely to sustain those populations than small patches because larger populations are less subject to demographic and environmental stochasticity [32,33].
- Populations residing in habitat patches in close proximity are less extinction prone than those in widely separated patches because the processes of dispersal and recolonization are facilitated [34].
- The extent to which the landscape matrix among habitat patches (supporting local populations of the focal species) resembles suitable habitat, the greater the connectivity among local populations leading to lower extinction risks [35].
- Sustaining a species over the long-term requires that demographic processes be evaluated at three key spatial scales: territory, local population, and metapopulation [36].

Spotted Owl Population Trends and the NWFP—Even with the reserve network in place, spotted owl populations on federal lands have continued to show an alarming (3.8%) annual rate of decline [9] that has increased from the 2.8% annual decline reported previously [37]. Spotted owl populations are monitored across 11 large demographic study areas on federal (n = 8) and nonfederal (n = 3) lands where data on owl population dynamics are collected. Based on 2011 monitoring results for demography study areas, four study areas showed marked declines (both the point estimator and 95% confidence intervals) in mean annual rate of owl population change [38]. In 2015, the number of study areas with marked declines in owl populations increased to six (K.M. Dugger, pers. communication). Spotted owl declines were attributed to interference competition with barred owls (*Strix varia*; [39]), logging-related habitat losses (mostly nonfederal lands), and the lack of a fully functional reserve system [12,40].

Notably, total spotted owl detections and the number of previously banded owls was the lowest ever recorded for the demography study areas [41]. Spotted owl detections at historic territories remained unchanged from 2013–2014 at LSRs, whereas, a double-digit decrease in owl detections was noted in the Matrix that well exceeded the slight decrease in detections recorded for Wilderness areas. Anthony *et al.* [42] also reported that the decline in spotted owls was steepest on study areas not managed under the NWFP and therefore the downward trajectory of owl populations might have been much worse without the NWFP.

Spotted Owl Habitat Trends—Before the NWFP, the annual rate of LSOG losses on national forests was ~1% in California and 1.5% in Oregon and Washington [9,40]. Recent monitoring of older forests by federal agencies using multiple inventory methods shows, at the forest plan-scale, a slight reduction in the area of federal older forests (2.8%–2.9% in 2012 compared to 1993 levels Table 1).

Table 1. Total old forest area (hectares x million) for federal (USFS, BLM combined) *vs.* nonfederal lands using three old-forest estimates: an old-growth structure index at 80-years (OGSI-80); old-growth structure index at 200 years (OGSI-200); and Late-Successional/Old Growth (LSOG) [9]. Percent differences between time periods (parentheses) were repeated from Davis *et al.* [9] who used more significant figures in calculations not shown here and rounded to the nearest hundred thousand.

Time Period	Federal OGSI-80	Federal OGSI-200	Federal LSOG	NonFederal OGSI-80	NonFederal OGSI-200	NonFederal LSOG
1993	5.1	2.6	3.0	2.6	0.7	1.6
2012	4.9 (−2.9)	2.5 (−2.8)	2.6 (−2.0)	2.3 (−11.6)	0.6 (−18.1)	1.3 (−14.2)

Based on federal lands monitoring reports, wildfire accounted for 4.2%–5.4% of the gross older forest losses compared to logging, which accounted for 1.2%–1.3% old-forest reductions [9]. Such losses were within the 5% anticipated disturbance level for the NWFP area over this time frame; however, fire-related losses were >5% in some dry forest ecoprovinces (5.5%–7.1% Washington Eastern Cascades; 12.2%–15.3% Klamath Oregon; and 7.0%–13.1% California) [9]. Thus, one primary accomplishment of the plan was to drastically slow old forest losses from logging over the NWFP time period. Exceptions include BLM lands in western Oregon, where the rate of old forest loss was >2 times that of U.S. Forest Service lands over a 10-year period (Table 2).

Table 2. Estimated spotted owl habitat losses due to logging on U.S. Forest Service (USFS) *vs.* Bureau of Land Management (BLM) lands under different time periods. Estimates obtained from USFWS [43] data.

Federal Agency	Pre-Owl Listing (ha) (1981–1990)	Anticipated Rates (ha) (1991–2000)	Calculated Rates (1994–2003) (%)
USFS (WA, OR)	25,910	15,951	4,187 (0.21)
USFS (CA)	NA	1,903	669 (0.14)
BLM (OR)	8,907	9,474	1,988 (0.52)
Regional Total	NA	27,328	6,844 (0.24)

NA = not available.

Notably, extinction rates of spotted owls at the territory scale have been linked to the additive effects of decreased old-forest area and interference competition with barred owls [44]. Wiens *et al.* [39] also reported that the barred owl's competitive advantage over the spotted owl diminishes in spotted owl territories with a greater proportion of late-successional habitat. Thus, conservation of large tracts of contiguous, old-forest habitat is justified in any attempt to maintain northern spotted owls in the landscape.

Spotted Owls and Fires—USFWS [40] assumes that fire is a leading cause of habitat loss to owls on federal lands, However, few empirical studies have actually investigated northern spotted owl response to fire absent post-fire logging in or around owl territories [45,46]. Spotted owls may be resilient to forest fires provided low-moderate severity patches (refugia) are present within large fire complexes to provide nesting and roosting habitat. In the dry portions of the owls' range, where fire is common, owl fitness is associated with a mosaic of older forests (nesting and roosting habitat) and open vegetation patches (foraging areas; [47,48]). Such patch mosaics are produced by mixed-severity fires characteristic of the Klamath and eastern Cascade dry ecoprovinces [49,50] that may have contributed to maintenance of owl habitat historically [51]. However, if fire increases in severity or homogeneity of burn patterns due to climate change [52,53] and if LSOG losses outpace recruitment rates over time, the beneficial habitat effects of fire to owls would diminish. Currently, a deficit in high-severity fire exists in most of western North America compared to historical levels [49,54]. Recruitment of older forests in dry ecoprovinces of the region is projected to outpace fire losses for the next several decades [55].

Despite uncertainties about owl use of post-fire landscapes, federal managers in dry ecoprovinces have employed widespread forest thinning with the intent to reduce fire severity perceived as a threat to owl habitat. However, forest thinning may lead to cumulative losses in owl habitat that exceed those from severe fires. Using state transition models that accounted for recruitment of owl habitat over time *vs.* presumed habitat losses from severe fires, Odion *et al.* [55] concluded that thinning of suitable owl habitat at intensities (22% to 45% of dry forest provinces) recommended by USFWS [40] would reduce LSOG three to seven times more than loss attributed to high-severity fires. Projected thinning losses were consistent with empirically based studies of habitat loss from thinning that reduced overstory canopy below minimum thresholds for owl prey species [56]. The tradeoff between fire risk reduction and owl persistence in thinned forests has seldom if ever been systematically evaluated by the federal agencies.

2.4. Marbled Murrelet Continues to Decline but at a Slower Rate

Murrelet Population Trends—This federally threatened coastal seabird, nests in older-aged forests usually within 80-km of the coast from northern California to Alaska. The murrelet was listed as threatened in the Pacific Northwest due to habitat fragmentation from roads and clearcuts that expose murrelets to increased levels of nest predation [57–59]. Murrelet distribution and population trends are determined by the amount of suitable nesting habitat within five coastal "conservation zones" from Washington to California [60]. In general, as nesting habitat decreases murrelet abundance goes down, although abundance is also related to near-shore marine conditions (e.g., fish-prey abundance). Over the NWFP area, the trend estimate for the 2001–2013 period was slightly negative (~1.2%) (confidence intervals overlapped with zero [60]). At the scale of conservation zones, there was strong evidence of a linear decline in murrelet nesting populations in two of the five conservation zones both in Washington State. Declines in murrelets likely would have been worse without the NWFP [60,61].

Murrelet Habitat Trends—About 1 million ha of potential suitable nesting habitat for murrelets remained on all lands within the range of the murrelet at the start of the NWFP (estimate based on satellite imagery [60]). Of this, only ~186,000 ha was estimated as high quality nesting habitat based on murrelet nest site locations. Over the NWFP baseline (1993–2012), net loss of potential nesting habitat was 2% and 27% on federal and nonfederal lands, respectively [60]. Losses on federal lands were mostly due to fire (66%) and logging (16%); on nonfederal lands logging (98%) was the primary cause of habitat loss [60]. In sum, loss and degradation of murrelet habitat resulted from: (1) logging on nonfederal lands (*i.e.*, State and private); (2) logging and thinning in suitable habitat and in habitat buffers on federal lands, including within LSRs; and (3) a variety of natural and anthropogenic causes including fire, windthrow, disturbance, and development [62].

Given that the availability of higher-quality nesting habitat is related to the carrying capacity of murrelets, forest management should focus on conserving and restoring remaining nesting habitat. The conservation strategy for murrelets, therefore, should include protecting remaining large patches of older-aged forests with minimal edge, buffering nest sites from windthrow and predators, and maintaining habitat connectivity. Maintaining the system of LSRs continues to be critical to murrelet conservation as is balancing the short- and long-term management of forests within LSRs [60,61]. For example, thinning that accelerates creation of older forest conditions in forest plantations that eventually become suitable to murrelet nesting can have short-term negative impacts, including increasing access of predators (e.g., corvids) to murrelet nest sites, blowdown and unraveling of suitable habitat, and changing the microclimate critical to temperature regulation and habitat availability [61]. Increased edge resulting from forest fragmentation can lower moss abundance needed for murrelet nesting [63,64], and increase nest depredation rates by corvids, especially at the juxtaposition of large openings and forests and in areas with berry producing plants such as elderberry (*Sambucus* sp. [65–67]. These factors underscore the need to maintain suitable buffers (suggested minimum widths of 91–183 m [57]) to minimize fragmentation and edge effects, and reduce windthrow and predation risk within LSRs and adjacent to suitable murrelet habitat [60]. Landscape condition, juxtaposition of occupied murrelet habitat, and ownership should all be considered in thinning operations within LSRs or adjacent to older-aged forests.

Impacts to murrelets would increase if fire frequency and severity were to increase due to climate change. Greater storm intensity associated with climate change also may cause more windthrow, especially in fragmented landscapes. Because murrelet nesting and foraging habitat appear sensitive to climate variability [68], forest management for murrelets should consider the potential additive effects of climate change and habitat fragmentation. Maintaining the LSR network, protecting all occupied sites outside LSRs, and, in the long term, protecting all remaining habitat and minimizing fragmentation and edge effects are essential conservation measures [60–62].

2.5. The Aquatic Conservation Strategy Has Improved Watershed Conditions

The Aquatic Conservation Strategy of the NWFP established Riparian Reserves and Key Watersheds to restore and maintain ecological processes and the structural components of aquatic and riparian areas [69]. Protective stream buffers in Riparian Reserves preclude most logging and Key Watersheds are managed for water quality and habitat improvements for at-risk salmonids. Stream conditions across 214 watersheds are being evaluated on federal lands in two eight-year sampling periods (2002–2009 and 2010–2017, incomplete) [70].

At the regional scale, broad-scale improvements in pools (*i.e.*, deep water pockets that provide cover, food, thermal refuge for aquatic species), stream substrate, and aquatic macroinvertebrates were observed between sampling periods, but no trend was detected in physical habitat features in riparian area canopy cover condition or stream temperature (Table 3).

Table 3. Summary of aquatic trend analysis testing for linear relationship between sampling periods (2002–2009 and 2010–2013, incomplete) [69]. Macroinvertebrates were based on an observed to expected index (O/E) calculated by Miller *et al.* [69]. Pool scores were estimated by using the amount of fine (<2 mm) sediments that accumulate in the downstream portion of pools.

Aquatic Indicator	Trend Estimate	F-Test *	*p*-Value
Physical habitat	+0.1	0.33	0.59
Pools	−0.21	6.22	**0.03**
Wood	+0.09	3.14	0.11
Substrate	+0.10	9.90	**0.02**
Macro-invertebrates O/E	+0.01	10.84	**0.02**
Temperature	−0.09	1.19	0.31

* Includes Kenward-Roger approximation. $p < 0.05$ is significant as described in Miller *et al.* [69]

At the NWFP level, moderate gains in upslope/riparian conditions occurred due to forest ingrowth and road decommissioning; however, they were largely offset by declines in riparian forest cover following large fires, particularly in reserve areas [69]. Notably, the Aquatic Conservation Strategy anticipated that improvements in stream and habitat conditions would take place over many decades; repeated monitoring confirms short-term benefits as noted but long-term goals have yet to be realized [68,69,71]. With available data, watershed condition appeared best in Congressionally Reserved lands (primarily designated Wilderness Areas), followed by LSRs, and the Matrix, although statistical analysis could not be performed due to incomplete sampling [69]. Key Watersheds and roadless areas encompass many of the remaining areas of high-quality habitat and represent refugia for aquatic and riparian species [72]. Therefore, improved protection and restoration actions in those areas are critically important to conserving aquatic biodiversity. We note that in the smaller number of watersheds where riparian conditions have measurably declined in the past 25 years, largely due to wildfire, we can expect a pulsed, very rapid improvement of instream conditions in the coming decades. This is because of anticipated post-fire recruitment of large wood coupled with vigorous regrowth of vegetation in riparian areas and erosion-prone slopes—at least where these natural recovery processes have not been disrupted and delayed by post-fire logging.

In a recent review of the NWFP's Aquatic Conservation Strategy Frissell *et al* [73] documented a host of reasons to recommend expansion of Riparian Reserves, and reduction in logging compared to the original (baseline) NWFP. They recommended that Key Watersheds and LSRs receive more stringent protection to ensure their contribution to aquatic conservation and salmon recovery. They also called for more limits on or an end to post-fire logging, and more aggressive and strategically focused reduction of road density and storm proofing improvements in roads that remain. The BLM and the Forest Service, however, have increased logging in Riparian Reserves, are now proposing or suggesting reductions in the width and extent of Riparian Reserves, and have pressed for increasing road system density to provide access to more land for logging purposes. These agency recommendations do not explicitly consider ongoing stressors from land management in the surrounding nonfederal lands or increasing likelihood of climate-change-driven stress from drought, floods, and wildfire. Nor do they deal with the adverse watershed impacts from thinning projects relative to their putative but highly uncertain benefits for reducing the severity of future fire or insect outbreaks.

2.6. Climate Change and the NWFP

Climate change was not fully anticipated during development of the NWFP and thus represents a new broad-scale stressor that would exacerbate earlier projected and realized cumulative impacts to aquatic and terrestrial species and ecosystems throughout the region. Temperatures already have increased by 0.7 °C from 1895–2011 [53] and are anticipated to rise another 2 °C–6 °C by late century with warming most extreme during the summer [53,74]. Greater uncertainty exists in precipitation projections due to variability in emissions scenarios and climate models; however, summertime drying by the end of the century has higher certainty [53]. Summer drying coupled with increasing temperatures will likely impact timing of salmonid migrations in snow-fed streams [53,75] and increase future fire events [52,75].

Notably, a key characteristic of widely distributed species is that the dynamics of their multiple local populations experience environmental variation asynchronously. This decoupling of the dynamics of local populations within a metapopulation greatly increases overall persistence likelihood given inevitable large-scale disturbances [76]. Persistence is achieved because the spatial distribution of the species exceeds the spatial extent of most stochastic environmental events. Persistence may be compromised, however, when climate change operates as a top-down driver over very large spatial scales, increasing the synchrony of metapopulation dynamics and extinction probabilities for late-successional species. Persistence likelihood in the face of disturbances was addressed in the

NWFP via redundancy and distribution of the reserve network but it is unclear whether the reserves can accommodate unprecedented climate-related shifts. This does not mean that the reserves are ineffective, just that they may not be as effective as hoped, and increasing the number and size of LSRs would make the network more effective.

Environmental uncertainty caused by climate change also has implications for restoration objectives of the NWFP. The NWFP assumed that young plantations can be restored to an older forest condition, but this may be less certain as forest succession comes under the influence of novel climatic conditions and perhaps increasingly altered disturbance regimes [52]. Thus, as forest conditions are altered by climate change, this may impact the climate preferences of late-successional species (e.g., mesic species are expected to decline near coastal areas due to drying [24]). One important way to reduce this uncertainty is to conserve more LSOG along north-facing slopes as potential micro-refugia and a hedge against further losses [24].

2.7. Ecosystem Services and the NWFP

Older forests and intact watersheds generally provide a myriad of ecosystem services associated with high levels of biodiversity [77,78]. Some examples of ecosystem services that have benefited from the NWFP include net primary productivity, water quality, recreation such as camping and hunting, salmon productivity, and carbon storage and sequestration. Older forests with high biomass (>200 mg carbon/ha, live above ground biomass of trees) most abundantly provide these services in aggregate primarily on federal lands [79].

The storage of carbon on federal lands is especially noteworthy because the region's high-biomass forests are among the world's most carbon dense forest ecosystems [80,81]. When cut down, these forests quickly release about half their carbon stores as CO_2 [82]. Reduced logging levels and increased regrowth under the NWFP has resulted in the regional forests shifting from a net source of CO_2 prior to the NWFP to a net sink for carbon during the NWFP time period [83]. While most of the carbon losses on federal lands are the result of forest fires, logging (mostly on nonfederal lands) remains the leading cause of land-use related CO_2 emissions [84]. Forests regenerating from natural disturbances including fire also rapidly sequester carbon and can then store it for long periods via succession if undisturbed. By comparison, logging places forests on short-rotation harvests, thereby precluding long-periods of carbon accumulation [82,83].

3. Building on the NWFP

The NWFP was founded on the best available science of the time, and the plan's reserve network and ecosystem management approach remain fundamentally sound [1,16,40,61,85,86] (also see http://www.fws.gov/oregonfwo/species/data/northernspottedowl/recovery/Plan/; accessed on 29 July 2015). If federal agencies wish to retain the protective elements of the NWFP, then forest plan revisions need to be based first and foremost on an adaptive approach to long-term goals as informed by monitoring. Increases in conservation measures are warranted to accommodate new scientific knowledge and unprecedented challenges from climate change and land-use stressors.

More recent climate change policies have been enacted since the NWFP that should be incorporated into forest planning. Examples include President Barack Obama's November 2013 Climate Change

Executive Order directing federal agencies to include forest carbon sequestration in forest management, the Council on Environmental Quality's draft guidelines on reducing greenhouse gas emissions from land-used activities (Federal Register Vol. 80, No. 35/Monday, 23 February 2015), and emphasis on forest carbon and ecosystem integrity in forest planning on national forests [87]. Improvements to the NWFP's ecosystem and conservation focus are especially relevant today given: (1) the spotted owls' precarious status, including increased competition with barred owls; (2) continuing declines in murrelet populations; (3) other at-risk species recently proposed for listing (e.g., Pacific fisher *Martes pennanti*, North Oregon Coast Range distinct population segment of the red tree vole *Arborimus longicaudus*); (4) numerous forest associated invertebrates and lesser known species with restricted ranges that are vulnerable to extinction as a result of climate change [24]; and (5) additional ESU's of Pacific salmon that have been listed with none recovered to the point of delisting. Recent and ongoing land-use stressors acting alone or in concert, especially on nonfederal lands, also need to be reduced along with improved forest management practices and stepped up conservation efforts (Table 4).

Table 4. Land use stressors, the Northwest Forest Plan (current), and suggested additions based on adaptive management approaches.

Land Use Stressor	NWFP Current	Suggested NWFP Improvements
Climate-forced wildlife migrations	LSRs, landscape connectivity via riparian and other reserves	Enlarge LSR and riparian reserve network by protecting remaining older and high-biomass forests in the reserve system, increase connectivity for climate-forced wildlife displacement, reduce management stressors, shift older forests to the reserves and forest management to restoration of degraded areas, and identify and protect climate refugia [24], especially for rare and endemic species (continue the survey and manage program).
Livestock grazing	Aquatic Conservation Strategy standards and guidelines provide some protections for riparian and other sensitive areas	Remove cattle from riparian areas and reduce overall grazing pressure via large no-grazing zones given cumulative effects of grazing and climate change [88].
Wildfire	Thinning for fuels reduction and post-fire logging allowed in dry province reserves (trees <80 years) and Matrix	Prohibit post-fire logging in reserves, maintain all large snags in the Matrix (other than legitimate road side hazards), continue to protect older trees >80 years and maintain canopy closure at ≥60% in spotted owl habitat in thinning operations [55]. Plan for wildland fire to achieve ecosystem integrity objectives. Focus on flammable tree plantations and work cooperatively with private landowners on fire risk reduction.
Forest carbon loss	Not recognized other than if they overlap with reserves	Optimize carbon storage by protecting high-biomass forests from logging and by reducing logging frequency and intensity to sequester more carbon. Choose management alternatives with low emissions from forestry by making use of new assessment tools [89] (also see http://landcarb.forestry.oregonstate.edu/summary.aspx; accessed on 29 July 2015).
Aquatic ecosystem degradation	Riparian Reserves, Key Watersheds, LSRs, watershed restoration, watershed assessments/monitoring	Maintain or increase riparian buffer widths to ameliorate winter erosion, sedimentation, and flooding, restore floodplain connectivity and sinuosity, retain runoff and natural summer storage, increase efforts to improve and decommission failing roads, identify cold water refugia for increased protections [73,90], update watershed and LSR assessments to incorporate carbon and climate change. Where possible, support a closed forest canopy over perennial and intermittent streams and fully restore recruitment of large downed wood, including by prohibiting or severely limiting forest thinning in riparian reserves.

BLM Western Oregon Plan Revisions

A key contribution of the NWFP was its unprecedented emphasis on coordination among federal agencies via an overarching ecosystem management approach. In particular, the BLM manages ~1 million ha within the NWFP area (http://www.blm.gov/or/plans/wopr/oclands.php; accessed on 29 July 2015). BLM lands collectively provide irreplaceable ecosystem benefits to people and wildlife in western Oregon where there are relatively fewer national forest lands near the coast. Benefits include some 480,000 ha of watersheds that overlap with Surface Water Source Areas that produce clean drinking water for >1.5 million people from Medford to Portland, Oregon (State of Oregon water quality datasets; http://www.deq.state.or.us/wq/dwp/results.htm; accessed on 29 July 2015), connectivity and dispersal functions for wildlife linking the Coast and Cascade ranges (east-west, north-south linkages) [91], and habitat for at-risk species (Table 5). Unfortunately, the BLM has signaled its intent to move away from the Aquatic Conservation Strategy stream buffers and the survey and manage protections (http://www.blm.gov/or/plans/wopr/oclands.php; accessed on 29 July 2015).

Table 5. Summary of important ecological attributes of a subset of BLM lands in western Oregon essential to the coordinated management of the Northwest Forest Plan (summarized from Staus *et al.* [91]).

Attribute	**BLM Lands**
Late-successional forests	360,000 ha of old growth (>150 years, 22% of BLM Land), 236,000 ha mature (80–150 years, 15% of totals for western OR)
Northern spotted owl critical habitat	400,000 ha (27% of BLM land); LSRs: 240,000 ha
Marbled murrelet critical habitat	~192,000 ha, 32% of total critical habitat in western OR, 83% of which is within BLM LSRs
Evolutionary Significant Units of coho (*Oncorhynchus kisutch*)	~720,000 ha of coho ESU area, 260,000 ha of coho ESU's in BLM LSRs—35% of ESU area on BLM land. Of the 10,075 km of spawning and rearing habitat within western Oregon, 12% is located on BLM lands, 100% in Riparian Reserves, and 44% of which is within LSRs.
Evolutionary Significant Units of chinook (*O. tshawytscha*)	~148,000 ha of ESU habitat, 16% of BLM land in western Oregon; 25,200 ha of chinook ESU habitat in BLM LSRs—17% of the total ESU area on BLM land.
Evolutionary Significant Units of steelhead (*O. mykiss*)	87,200 ha of steelhead ESU habitat, all of which is found in the Salem and Eugene districts. Nine percent of BLM land in western Oregon contains steelhead ESU habitat with 14,000 ha of steelhead ESU habitat in BLM LSRs—16% of the total ESU area across BLM land.
Key Watersheds	Western Oregon contains ~1.6 million ha of Key Watersheds, 61,600 ha (4%) of which are located within BLM LSRs. In the Coast Range, LSRs protect 9% of Key Watersheds overall, over 25% of 10 of the 38 key watersheds in this area.
Survey and Manage Species	Of the 404 survey and manage species (primarily rare species at risk of local extirpation) recognized in the NWFP, 149 species are found on BLM land and 93 are found within BLM LSRs. LSRs in the Salem BLM District contain the highest concentration of these species (54), followed by Roseburg (39), and Coos Bay (35). Species include red tree vole (*Arborimus longicaudus*, an important food source for spotted owls), and many species of vascular plant, aquatic mollusk, lichen, fungi, and bryophyte.

4. Robust Conservation Additions to the NWFP

The NWFP provided a much-needed starting-place for a robust conservation strategy on federal forests in the face of climate change. For clarity, we organize our recommendations to improve the plan based on widely recognized principles of conservation biology and ecosystem management that also apply more broadly to large-landscape conservation planning.

4.1. Reserves

The large, well distributed, and redundant system of reserves was chosen based on specific requirements for the northern spotted owl that are still supported by the best available science [1,16,17,40–42,85]. At a minimum, we recommend continuation of the reserve network as a foundation for at-risk species in a changing climate and with increased stressors in the surrounding nonfederal lands. The NWFP reserves along with the survey and manage program function together as precautionary measures for species that are less mobile (e.g., many endemics) due to increasing stressors in the surroundings and climate change [19,24]. Given the redundancy and spacing requirements of the reserve system to address owl viability requirements, the network is likely to maintain older forest conditions over time by accommodating temporary losses from fire and other natural disturbances without compromising the integrity of the network [2,9], unless disturbances increase dramatically due to climate change [53]. The reserve system also is arranged along north-south gradients, including the Coast and Cascade ranges, elevation gradients, and topographically diverse areas, presumably allowing for climate-forced wildlife dispersal and climate refugia [24]. Large, contiguous federal ownerships and coordinated management of federal agencies under the standards and guidelines of the NWFP should continue to allow for adaptive responses to climatic change. Blocks of federal ownership also provide opportunities for wildland fire needed to restore and maintain ecosystem processes across a successional gradient [10,92,93].

The NWFPs' combination of coarse- and fine-filter approaches should continue to provide time for many wildlife to adjust and adapt to changing climatic conditions. Any effort to scale-back the reserves (as is currently being considered by federal agencies) must acknowledge that the NWFP architects aptly recognized that LSRs, Riparian Reserves, and Key Watersheds fit together in a cohesive manner to maintain long-term benefits to terrestrial and aquatic ecosystems. Reducing protections to reserves would create cumulative impacts across ecosystems. With new stressors like climate change and ongoing land-uses, reserve synergies and integrated strategies are even more important.

4.2. Forest Carbon

Regional carbon storage capacity can be increased if managers both protect carbon stores in older high biomass forests and allow young forests to re-grow for longer periods [83,84]. Managing for high-biomass forests is also associated with the multifunctionality of ecosystems because carbon dense forests are associated with high levels of biodiversity and numerous other ecosystem services [79]. Prudent management should integrate forest carbon policies with multiple use management objectives of federal agencies by optimizing carbon stored in older forests and extending timber harvest rotations to allow for longer periods of carbon sequestration and storage. Thus, forest managers can select management alternatives to minimize carbon flux from logging and land-uses by evaluating alternatives based on new carbon assessment tools (Table 4).

4.3. Aquatic Conservation

The variety of requirements for watershed analysis, reserve assessments, and monitoring under the NWFP has provided a foundation for tracking the plan's implementation objectives for aquatic ecosystems, at least at a regional scale. With improvements, aquatic ecosystem monitoring could provide integrated and sensitive indicators of ecosystem changes associated with climate shifts. Current Aquatic Conservation Strategy provisions, therefore, could be strengthened to help make aquatic ecosystems more resilient to climate change by (1) lessening cumulative watershed impacts particularly from the extensive road network on federal lands; (2) reducing the imprint of management disturbance on relatively high-integrity watersheds and roadless areas; (3) emphasizing maintenance of riparian areas, shade, floodplain processes, and recruitment of large wood from both near stream areas and unstable slopes; and (4) restoring migratory connectivity and fish passage to allow cold-water fisheries a better chance to occupy refugia less stressed by climate change.

4.4. At-Risk Species Recovery

Our understanding of threats to at-risk species has greatly advanced since passage of the Endangered Species Act (ESA) in 1973 and the NWFP in 1994. Specifically, the recognition that avoiding extinction is different than achieving recovery when it addresses the original ESA goal of "… preserving the ecosystems upon which threatened and endangered species depend." Hence, implementation of the NWFP and enforcement of the ESA are linked objectives that together provide for the ecosystem and population needs of at-risk species among a host of other benefits.

To build on the complementarity of the NWFP and ESA, we recommend that at-risk species recovery (e.g., spotted owl, marbled murrelet, Pacific salmon) on federal lands include more habitat protections to reduce interactions with their competitors (e.g., spotted owls *vs.* barred owls), maintain genetic diversity [94], provide for resilient populations, and enable multiple local populations to be well-distributed throughout the NWFP area. Additionally, at least until land-use stressors are reduced, the survey and manage program should be continued to avoid the need for listing future at-risk species and expanded to include species that require complex early seral forests [10]. Managers can then select a broad suite of focal species that depend on all segments of successional gradient.

4.5. Adopting New Policies and Approaches

The foundation of the NWFP can be easily amended to accommodate new scientific information and elevated and novel stressors by building on its foundational elements (e.g., reserves, stream buffers, survey and manage). This can best be accomplished by incorporating recent national forest policies that emphasize ecosystem integrity [87] and climate change planning on federal lands (President Barack Obama's 2013 Climate Change Executive Order), reducing land-use stressors, and maintaining or restoring landscape connectivity to enable climate-forced wildlife migrations (Figure 3).

Additionally, recent mapping of high-biomass forests [84] and carbon accounting in forestry practices (http://landcarb.forestry.oregonstate.edu/summary.aspx; accessed on 29 July 2015) provide new opportunities for retaining carbon in older forests while reducing forestry related CO_2 emissions.

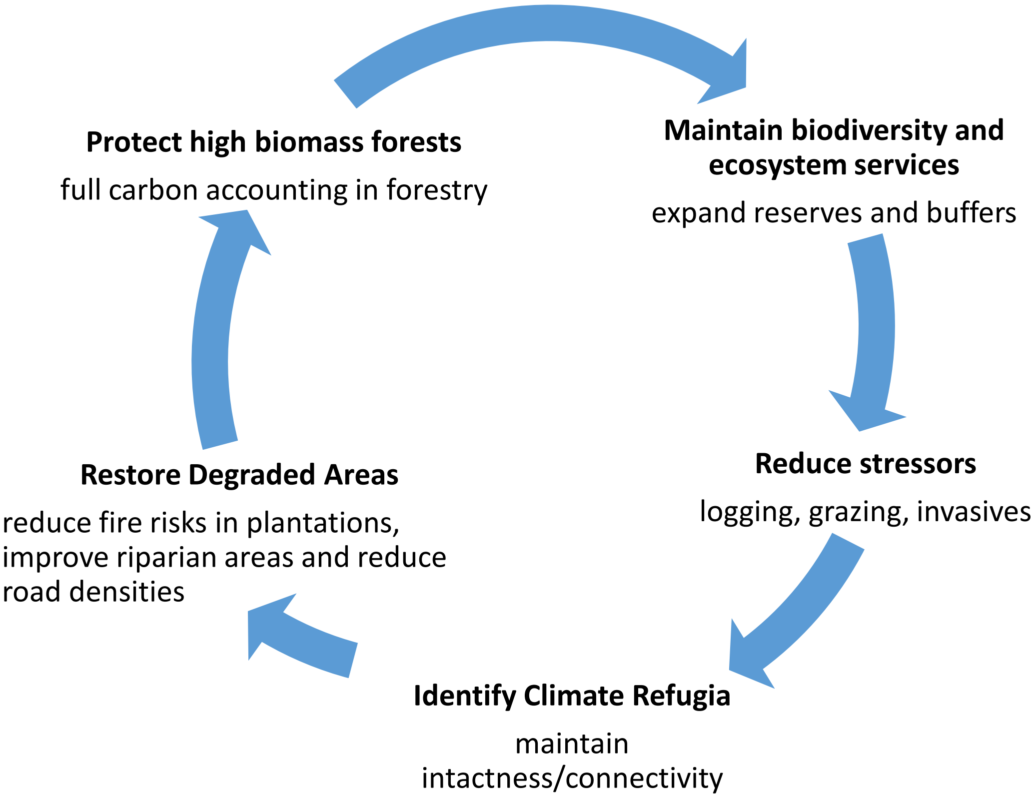

Figure 3. Integrating ecosystem management and conservation biology with recent forest policies related to climate change (e.g., President Barack Obama's 2013 Climate Change Executive Order), forest carbon, and ecosystem integrity in forest planning [87].

5. Conclusions

The foundation of the NWFP is its reliance on best available science for conserving, restoring, and responsibly managing federal lands within the range of the northern spotted owl and, for the first time ever, an entire ecosystem, which is why it is considered a global model [1]. Although the plan is only two decades into its century-long implementation, its key conservation goals and species recovery mandates are far more likely to be met with the plan's management and conservation measures intact.

As forest plan revisions go forward in the region, the reserve network needs to be expanded in response to increasing land-use stressors to ecosystems and at-risk species, and to provide for a more robust conservation framework in response to climate change. Climate change may trigger more forest fires in places and, correspondingly, more logging and livestock grazing as these practices almost always follow forest fires on federal lands. Notably, burned forests successionally link complex early seral forests [10,11] to future old-forest development [92] and are not ecological disasters as often claimed. Depending on fire severity, burned forests provide nesting and roosting (low-moderate severity) or foraging (high severity) habitat for spotted owls [45,46,51]. Federal managers, however, have increasingly proposed massive post-fire logging projects that degrade complex early seral forests [95] and spotted owl habitat [45,46], and that can elevate fuel hazards and re-burn potential [96,97]. Post-fire logging over large landscapes may cause type conversions whereby fires burn intensely in logged areas only to be replanted in densely stocked and flammable tree plantations to burn intensely again in the next fire and so on [98]. Livestock grazing in combination with climate change is also now the biggest impact to biodiversity on federal lands that needs to be offset by new protections such as large blocks of ungrazed areas [88].

In sum, changes in ecosystem management practices on federal lands, triggered by the NWFP, have for the most part arrested an approaching ecosystem-wide collapse set in motion by decades of large-scale logging and mounting land-use stressors. Implementation of the plan has been challenging due, in large part, to socio-economic pressures to increase logging without full consideration of the environmental consequences and understanding of the science and conservation principles underpinning the NWFP. Moreover, despite substantive improvements in federal land management practices compared to those previous to the NWFP, amendments that respond to emerging contemporary threats are clearly needed. Scientific information and robust conservation principles can provide federal managers with the knowledge needed to adapt the next generation of forest plans. Improvements should be grounded in careful evaluation of the effects of past actions along with ongoing and future stressors as they pertain to the region's underlying ecological fabric and its link to sustainable economies. Science-based revisions of the plan should seek to improve its implementation in an adaptive context by addition rather than subtraction. Unfortunately, attempts to revise the plan have been bogged down by ongoing controversy over timber *vs.* biodiversity values that has led to a perpetual tug-of-war between decision makers that either support or seek to dismantle the NWFP. If this trend continues, federal land management may regress and recreate many of the problems the NWFP was implemented to correct, including re-inflamed social conflict, a cascade of endangered species listings, permanently increased conservation burdens on private landowners due to additional endangered species listings, and loss of ecological integrity that underpins the region's ecosystem services and their adaptive capacity to climate change.

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Conflicts of Interest

The authors declare no conflict of interest.

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Have western USA fire suppression and megafire active management approaches become a contemporary Sisyphus?

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ABSTRACT

Fire suppression policies and “active management” in response to wildfires are being carried out by land managers globally, including millions of hectares of mixed conifer and dry ponderosa pine (*Pinus ponderosa*) forests of the western USA that periodically burn in mixed severity fires. Federal managers pour billions of dollars into command-and-control fire suppression and the MegaFire (landscape scale) Active Management Approach (MFAMA) in an attempt to contain wildfires increasingly influenced by top down climate forcings. Wildfire suppression activities aimed at stopping or slowing fires include expansive dozerlines, chemical retardants and igniters, backburns, and cutting trees (live and dead), including within roadless and wilderness areas. MFAMA involves logging of large, fire-resistant live trees and snags; mastication of beneficial shrubs; degradation of wildlife habitat, including endangered species habitat; aquatic impacts from an expansive road system; and logging-related carbon emissions. Such impacts are routinely dismissed with minimal environmental review and defiance of the precautionary principle in environmental planning. Placing restrictive bounds on these activities, deemed increasingly ineffective in a change climate, is urgently needed to overcome their contributions to the global biodiversity and climate crises. We urge land managers and decision makers to address the root cause of recent fire increases by reducing greenhouse gas emissions across all sectors, reforming industrial forestry and fire suppression practices, protecting carbon stores in large trees and recently burned forests, working with wildfire for ecosystem benefits using minimum suppression tactics when fire is not threatening towns, and surgical application of thinning and prescribed fire nearest homes.

> *“One obvious way to weaken the cause is to discredit the person who champions it. And so the masters of invective have been busy; I am a bird lover, a cat lover, a fish lover, I am a priestess of nature and I am a devotee of some …cult that has to do with the laws of the universe, which my critics somehow consider themselves immune to. Another well known and much used device is to misinterpret my position and then to attack things I've never said…*
> *Is industry becoming a screen through which facts must be filtered? So that the hard uncomfortable truths are kept back and only the powerless morsels are allowed to filter through? I know many thoughtful scientists are deeply disturbed that their organizations are becoming fronts for industry…”.*
> Rachel Carson, Address to the Women's National Press Club, December 5, 1962 (https://awpc.cattcenter.iastate.edu/2018/01/08/address-to-the-womens-national-press-club-dec-4-1962/).

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1. Command-and-control and the lesson of Sisyphus

Post-Homeric legend teaches us that when Hades (the harbinger of death) came for Sisyphus, Sisyphus cheated death by putting Hades in chains so no human would ever suffer. But Hades outwits Sisyphus and, for his punishment, Sisyphus is forced to roll an enormous boulder up a steep hill for eternity. Modern fire suppression tactics began in earnest after World War II and since then all fire management agencies, particularly the U.S. Forest Service (USFS), have increasingly conducted militarized operations using command-and-control suppression tactics that now amount to billions of dollars annually in wildfire fighting costs. In addition, both the USFS and the US Department of Interior Bureau of Land Management (BLM) log millions of hectares annually, much of which is with minimal environmental safeguards under the rubric of “hazardous fuel reduction.”

The resultant attempted subjugation of nature to control wildfire via suppression and “active management” is analogous to 20th century control of apex predators (e.g., *Ursus arctos horribilis*, *Canis lupus*), which led to cascading ecological effects (Ripple et al., 2014). Wildfires are now summarily treated as a predatory process to be constrained at all costs. Consider recent calls by decision makers demanding land management agencies start immediately to put out all fires (https://goodday sacramento.cbslocal.com/2021/08/02/doug-lamalfa-forest-service-fighting-fires/, accessed August 9, 2021), even though they can only feasibly steer, not “control” wildfires under extreme fire weather. Citing a “wildfire crisis,” USFS Chief Randy Moore “temporarily” suspended the agency's policy to manage wildfires for resource benefits, including prescribed fire (https://wildfiretoday.com/2021/08/03/forest-service-chief-says-wildfires-will-be-suppressed-rather-than-managed-for-now/, accessed August 12, 2021). In this fashion, the Sisyphean response has been to do more of the same even as the area burned by wildfire goes up (Fig. 1).

It is widely recognized that, despite recent increases in area burned by wildfire in the western USA, there remains a wildfire deficit in fire-dependent dry ponderosa pine (*Pinus ponderosa)* and mixed conifer forests compared to historical times (Marion, 2012, Baker, 2015, 2017, Parks et al., 2015). In fact, the majority of burned area in regions such as California over the last two decades has been in non-conifer ecosystems (e.g., chaparral; Calhoun et al., 2021). However, due to the recent uptick in so called “megafires” (i.e., fires affecting large landscapes), there have been increasing calls to curb fire activity. Some believe that contemporary fires are undermining forest regeneration due to excessive high severity fire effects, hotter drier conditions in postfire environment due to climate change, and the landscape is too permeable to megafires via “fuel continuity” from a lack of management and fire suppression (Hessburg et al., 2021). Evidence-based reviews that conflict with this viewpoint (e.g., Odion et al., 2014a; Baker, 2015; Law and Waring, 2015; DellaSala and Hanson, 2019; Hanson, 2021) are routinely dismissed (Hagmann et al., 2021) and independent conservation scientists, who are not funded by federal agencies, are personally attacked and accused of “agenda-driven bias” (Hessburg et al., 2021). Terms like “active management,” “healthy forests,” “climate-smart forestry,” and “disturbance resilience” are routinely introduced, poorly defined, and impactfully implemented with little analysis of consequences to fire-mediated biodiversity, natural carbon storage, and the climate. MFAMA advocates go as far as claiming that the science supporting proposed treatments is all but settled (https://www.mailtribune.com/top-stories/2021/11/06/the-work-doesnt-stop/; accessed November 8, 2021) and those that question it have an agenda (Hessburg et al., 2021 also see Prichard, https://www.huffpost.com/entry/biden-deforestation-old-growth-forests-cop26_n_61841ea9e4b06de3eb726e8a, accessed November 6, 2021). Given the planetary climate and biodiversity crises, we argue that scientists can and should be advocates as concerned citizens for nature while remaining true to the science and responsive to root causes of the crises at hand (DellaSala, 2021).

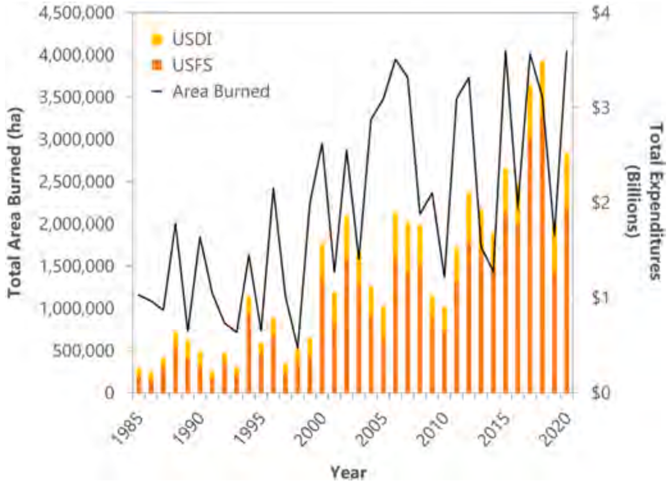

Fig. 1. Total area burned and wildfire suppression expenditures by federal land management agencies from 1985 to 2020. Data compiled from the National Interagency Fire Center suppression reports and from fiscal year agency budgets, with USDI mainly being National Park Service that since 1972 has been managing wildfires as a natural part of the park systems ecology (https://www.nifc.gov/fire-information/statistics/suppression-costs; accessed August 9, 2021).

Our objectives are to: (1) document impacts of widespread fire suppression and MFAMA that are contributing to the growing subjugation of nature and the planetary crises; and (2) respond to highly subjective labeling of “agenda-driven science” increasingly being used by developers and certain land managers and researchers (Hessburg et al., 2021) to discredit and reject the burden of proof standard in the precautionary principle underlining many of our core environmental policies and laws (Whittaker and Goldman, 2021). We focus mainly on dry forests of the western USA that include periodic mixed-severity fires in montane ponderosa pine and mixed conifer forests dominated by firs (*Abies* spp.) and Douglas-fir (*Pseudotsuga menzeisii*). Our findings also may have broader application regarding ongoing human domination of natural systems in response to wildfire increases affecting the built and natural environments globally.

1.1. *Wildfire suppression*

Contemporary fire suppression, when used singularly or in combination with active management approaches, can create long-lasting impacts that reduce the integrity and rejuvenation properties of ecosystems, both spatially and temporally. During active wildfires, expansive firelines are cut across both roaded and unroaded areas (e.g., Wilderness and Inventoried Roadless Areas) (Fig. 2), typically using bulldozers. In some cases, up to 74% of the lines may only serve as contingency lines that never intersect a fire or get utilized by firefighters (Baker and Halsey, 2020). Not only can these firelines spread invasive plants into remote areas (Backer et al., 2004), but they can also act as unplanned roads for off-highway vehicles that may delay forest succession and contribute to human caused fires. During periods of high fire activity, thousands of firefighters may be employed on a single large fire or fire complex, cutting down trees, building tens of kilometers of dozerlines and handlines to act as fire breaks, creating helicopter landing pads, hoist sites, large staging areas and safety zones, setting backburns over vast areas using ignitable chemicals– at times under unfavorable conditions– or on lower slope positions, dropping chemical retardants (e.g., PHOS CHEK) from helicopters and tankers, and extracting water from lakes, rivers, streams, and even the Pacific Ocean. Such suppression activities can result in greater fire extent, exaggerated fire severity, lack of burn refugia (i.e., due to backburns and burning out “green islands” within the fire perimeter), and damage to both soil and aquatic systems (Backer et al., 2004) that are seldom factored into fire

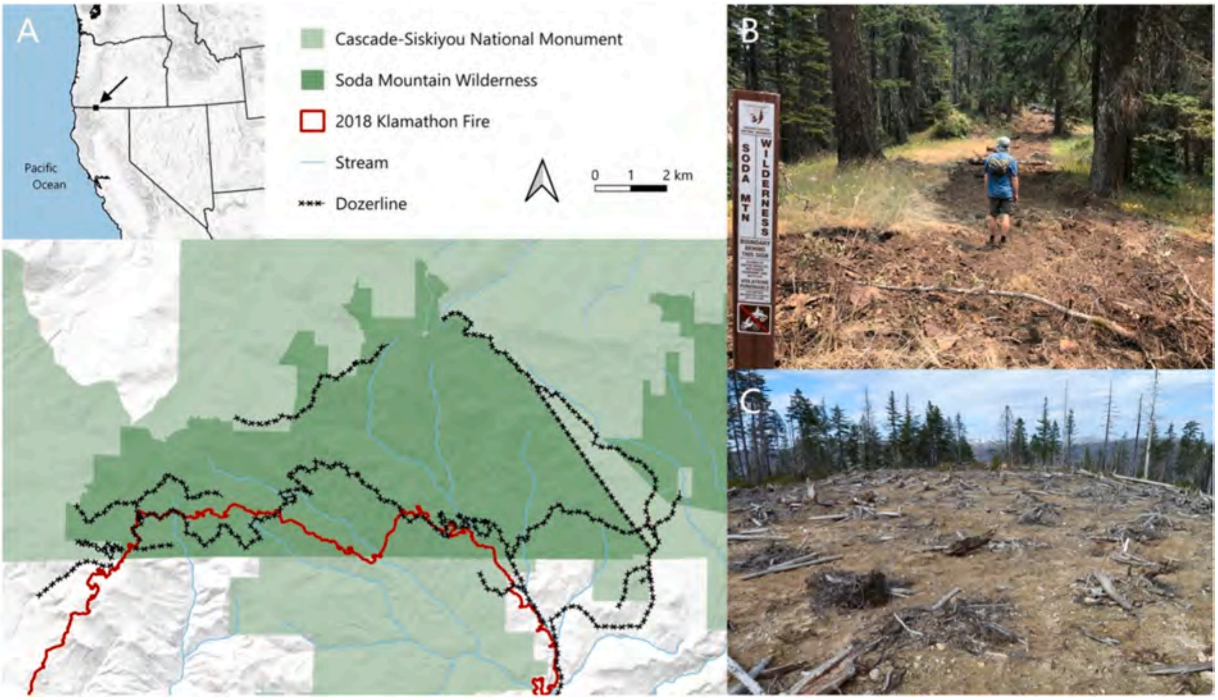

Fig. 2. (A). Extent of dozerlines built during the 2018 Klamathon fire in the Soda Mountain Wilderness within the Cascade-Siskiyou National Monument, southwest Oregon. (B) Close up of dozerline within the Soda Mountain Wilderness. The fire never reached this fireline because handlines built below were used for containment. (C) Helicopter landing in an inventoried roadless area within the Buckskin 2013 burn area, southwest Oregon. Photos: L. Ruediger.

perimeter and severity reporting. Thus, attempting to suppress the intensity and extent of megafires comes with substantial consequences to ecosystems that accumulate spatially and temporally and that may act in concert with MFAMA.

1.2. *Megafire active management approach*

Active management has been communicated as some form of benign action with short-term impacts involving mainly thinning of small trees and the use of prescribed fire (Hessburg et al., 2021). While we agree with the need to protect "large trees" (undefined), in practice the MFAMA, which proponents are calling for massive increases (Hessburg et al., 2021; Prichard et al., 2021; Hagmann et al., 2021), has been implemented by federal agencies using selective logging of large-fire resistant trees to pay for treatment costs (DellaSala et al., 2013); burning slash piles (often mistakenly referred to as "prescribed fire") that can cause localized soil impacts and extended periods of smoke; damage to soils from yarding operations, new road and landing construction; operation of an expansive road system and associated impacts to wildlife and aquatics (e.g., Ibisch et al., 2016); spread of invasive weeds from soil disturbance, roads, and concomitant livestock grazing (Keeley 2006, Beschta et al., 2013); landscape-scale pre- (Odion et al., 2014b) and post-fire logging that may destroy natural forest regeneration and increase fire hazards (Donato et al., 2006); removal of overstory canopy trees in critical habitat for threatened species such as the Northern Spotted Owl (*Strix occidentalis caurina*, Odion et al., 2014b); biomass burning and associated carbon emissions (Sterman et al., 2018); mastication of ecologically beneficial shrubs important to many shrub-nesting birds, raptors, small mammals, conifer-shrub symbioses, nutrient cycling, and mycorrhizae development (Johnson and Curtis, 2001). Importantly, protections of large trees (>50 cm dbh) in dry pine and mixed conifer forests of eastern Oregon and Washington were recently lifted by federal land managers with the support of MFAMA proponents (Johnston et al., 2021) seeking greater management "flexibility" to reduce densities of large firs even though large trees of all conifer species store up to 46% of the above ground carbon and remain at historical deficits (Mildrexler et al., 2020).

A consequence of the MFAMA is that it contributes to ongoing commodification of nature, where vegetation is "treated" as "fuel," 2 × 4 s the "byproduct" of "restoration," "feedstock" for biomass burning, and logs to keep sawmills open (e.g., https://www.nytimes.com/2021/04/10/opinion/sunday/loggers-environmentalists-oregon.html, accessed August 10, 2021; Prichard et al., 2021). Concerns over wildfire activity have led some to subjectively argue for "good" (low-moderate severity) fire at the expense of "bad" (high severity) fire (https://blog.nature.org/science/2013/05/15/good-fire-bad-fire-an-ecologists-perspective//, accessed August 9, 2021; https://www.nationalgeographic.com/history/article/good-fire-bad-fire-indigenous-practice-may-key-preventing-wildfires; accessed August 9, 2021) with little attention to the ecological importance or impacts to biodiverse, high severity fire patches (DellaSala and Hanson, 2015). Such patches were historically and still are intrinsically important elements of large fire complexes (Baker, 2015) especially during periods of prolonged droughts (Keeley and Syphard, 2021).

We do not disagree with ecologically justified active intervention (see Section 8) and passive (protection from logging and cessation of destructive actions) management when properly defined based on examination of all available historical and/or reference evidence and reduction of anthropogenic stressors. However, industrial logging and thinning may reduce resilience, compared to actual prescribed (i.e., planned application of fire over a defined area of interest under specified conditions) and natural fire that have biodiversity benefits in mixed severity systems. Moreover, active management through logging cannot restore the extensive deficiency of large, old trees from past agency management. Passive management may be able to do this restoration at low cost over very large areas (Baker, 2021). While MFAMA advocates (e.g., Hessburg et al., 2021; Prichard et al., 2021; Hagmann et al., 2021) recognize the importance of putting more fire on the landscape, they call for extensive active management (thinning) as a pre-requisite and have an inherent bias for low-moderate fire severity (i.e., "good fire") in what is otherwise mixed-severity fire regimes that include small and large patches of high severity (DellaSala and Hanson, 2015). Thus, the

MFAMA represents a growing divide between biodiversity conservation and climate science vs a singular focus on "fuel reduction" that overemphasizes vegetation treatment. We suggest that managers and decision makers become keenly aware of such conflicting perspectives and ascribe greater attention to limiting the grossly under-reported consequences of MFAMA.

Notably, empirical evidence shows that very few treatments (<1% annually) actually encounter a wildfire in the period when flammable vegetation is lowest (Schoennagel et al., 2017). MFAMA advocates (e.g., Hessburg et al., 2021; Prichard et al., 2021) claim that this is because not enough of the landscape is treated. However, some 7 million ha already have been treated by 2015, yet wildfires continue to increase (Schoennagel et al., 2017). As a proxy for the extent of "hazardous fuel treatments" on federal lands, the US Forest Service fiscal year budget for the past five years has been ~\$354 million (FY 2018), \$435 million (FY 2019), \$445 million (FY 2020), \$180 million (FY 2021), and \$321 million (FY 2022), totaling some \$1.7 billion dollars (prior to FY 2018 this category is not easily trackable). Unprecedented increases in government subsidies will expand the ecological and climate impacts of MFAMA. For instance, H.R. 3684, the Infrastructure Bill, was recently signed into law and includes 12 million hectares of logging over 15 years with the intent to modify wildland fire behavior on federal lands, supported with > \$2 billion in logging subsidies, and new categorical exclusion (CE) authorities that bypass comprehensive environmental analysis otherwise mandated under the National Environmental Policy Act (NEPA). The Reconciliation Bill (HR 5376), which passed in the House but stalled in the Senate, contained an additional \$14 billion in logging subsidies on federal lands—more than double existing levels—as well as billions for private forestlands logging plus another ~ \$1 billion for forest biomass energy, wood pellet facilities, and mass timber (cross-laminated timber) under the heading of "wood innovation." Clearly, the MFAMA approach has been deeply inculcated in wildfire policies and massive federal subsidizes without regard to ecosystem and climate costs.

It is urgent that collateral impacts of greatly scaled up MFAMA activities be fully realized to address the growing climate and biodiversity emergencies, lest cumulative maladaptive responses are anticipated that would further the Sisyphean response to wildfires.

2. Are high severity burn patches increasing, requiring more active management?

2.1. High severity burn patches are biologically rich and undervalued

Reoccurring wildfires are a keystone ecosystem change agent that has shaped the ecology of fire-adapted dry pine and mixed conifer forests in the western USA for millennia. In these forested ecosystems, fires of varied intensity (a measure of heat energy from fire) produce mixed-severity effects on vegetation at landscape scales that result in heterogenous patches of tree mortality (patch severities), burn patch sizes, configurations, and arrangements – the "pyrodiversity begets biodiversity" hypothesis (see DellaSala and Hanson, 2015). Pre-contact Indigenous peoples managed ignitions in places for culturally important plants and wildlife which, in combination with lightning strikes, maintained diverse landscapes, including small and large very high-severity patches (e.g., most trees are killed; Odion et al., 2014a) that by some accounts have not increased in recent decades (DellaSala and Hanson, 2019).

Many plants have specialized adaptations to intense fire such as the thick bark of large diameter fire-resistant ponderosa pine, fire-resistant crowns of old growth giant sequoia (*Sequoiadendron giganteum*), "seed rain" of serotinous cones of lodgepole pine (*Pinus contorta*) and knobcone pine (*Pinus attenuata*), post-fire resprouting of coast redwood (*Sequoia sempervirens*) and many hardwood species, epicormic branching of Douglas-fir, and post-fire needle flushing of pines and firs thought to have been initially killed by fire (Kauffman, 1990; Hanson and North, 2009). Native shrubs and forbs also contain fire adaptations such as sprouting (*Sambucus* spp., *Spiraea betulifolia*) and vigorous fire-mediated germination (*Arctostaphylos* spp., *Ceanothus* spp.), with some species even displaying post-high severity fire endemism (*Eriodictyon parryi*). Numerous birds (e.g., songbirds, cavity nesters), bats, small mammals, and invertebrates have specialized adaptations for nesting and foraging in post-fire landscapes especially within the most severe burn patches (DellaSala and Hanson, 2015). High severity fire can also trigger extensive native wildflower blooms that benefit pollinator species (Galbraith et al., 2019).

2.2. Good vs. bad fire terminology is subjectively misleading

Labeling high severity fire using subjective good vs bad terminology (Parks and Abatzoglou, 2020) (also referred to as euphemisms see Johns and DellaSala, 2017), when high-severity fires are a natural process in dry forests (Baker, 2015; Odion et al., 2014a; DellaSala and Hanson, 2015), contributes to the perspective that such important burn areas can be logged with minimal environmental review since they produce "bad" fire effects (e.g., large-scale post-fire logging of the Rim fire in the Sierra (USDA Forest Service, 2014) and Biscuit burn area in southwest Oregon (USDA Forest Service, 2003)). Federal agencies target high severity patches for logging believing that the trees are dead anyway and can be expeditiously logged with a substantial amount of timber revenue generated under minimal environmental standards (Hanson, 2021). Such logging is known to reduce carbon sequestration (Serrano-Ortiz et al., 2011, Kauffman et al., 2019) and emit carbon stored in dead wood (Bradford et al., 2012), can increase surface fuels that contribute to fire spread while killing natural conifer establishment (Donato et al., 2006; Mattson et al., 2019), can impact streams from chronic sedimentation due to logging on steep slopes and from roads (Karr et al., 2004), can contribute to reburn severity (Thompson et al., 2007), can cause nest site abandonment in spotted owls (Lee, 2018), and reduce the abundance of numerous bird species among many other impacts (Lindenmayer et al., 2008; Thorn et al., 2018).

Good-bad fire terminology used by the wildland fire community and the news media also has implicit anti-fire bias (i.e., "pyroganda," Ingalsbee, 2014) that perpetuates command-and-control attitudes about wildfire in particular and nature in general. Perspectives matter when it comes to describing wildfire effects as MFAMA advocates see landscapes as "fuels" that need to be removed to limit "bad fire" (Hessburg et al., 2021; Prichard et al., 2021; Hagmann et al., 2021) while others see the intrinsic connection between pyrodiversity and biodiversity in large fire complexes as part of natural ecosystem and evolutionary processes that so far remain within historic bounds (DellaSala and Hanson, 2015; DellaSala and Hanson, 2019). Unfortunately, the dominant fuels-centric language, and related economic pressures, are inculcated in agency research funding priorities with little examination of potential impacts, forest and fire management policies that seek to bypass environmental laws and safeguards, and in the training of foresters in general. We suggest more ecologically inclusive terminology replace phrases like "fuels" with flammable vegetation or habitat, "consumed" or "destroyed" with "affected" by wildfire, "fire scar" with "burn perimeter" or "fire footprint," "catastrophic" with "forest renewal," and "salvage logging" and "thinning" with "post-fire logging" and "live tree logging." Further, land managers could report on area restored by natural wildfire ignitions managed for ecosystem benefits instead of counting only fuel-reduction from mechanical thinning and prescribed fire.

2.3. High severity burn patches are not larger or more prevalent in protected areas

Often it is claimed that protected areas like Late-Successional Reserves (i.e., Northwest Forest Plan - NWFP), wilderness, national parks, and roadless areas are contributing to greater risks of high severity fires and should be actively managed with some forms of logging (e.g., see

Bradley et al., 2016 vs. Spies et al., 2018). Research that has accounted for forest type concludes that protected forests have far lower fire severity levels than logged lands showing the highest proportions of high severity fire effects (Bradley et al., 2016). Absent forestry reforms, and in a rapidly changing climate, we expect this trend toward more intense fire in heavily logged areas to continue (e.g., see Zald and Dunn, 2018).

2.4. *High severity burn patches link successional processes*

A complete or near-complete lack of conifer recruitment, and type conversion to hardwood forest or shrubland, is often assumed by MFAMA proponents when justifying post-fire logging and reforestation projects (e.g., both the Biscuit (USDA Forest Service, 2003) and Rim fire (USDA Forest Service, 2014) projects included massive postfire logging and tree planting). However, several studies have found relatively abundant levels of natural conifer regeneration in large, severe burn patches (Donato et al., 2009a; Haire and McGarigal, 2010; Owen et al., 2017; DellaSala and Hanson, 2019), with many severe patches regenerating hundreds of meters away from nearest seed sources (Hanson, 2018; DellaSala and Hanson, 2019; Kauffman et al., 2019). Research has also shown that natural conifer regeneration in high severity burn patches may be underreported and conifer failures grossly overstated due to methodological problems with sample plot size and placement (Hanson and Chi, 2021). Importantly, recently burned forests (complex early seral) provide the structure for development of old-growth characteristics over time (Swanson et al., 2011; Donato et al., 2012). Thus, what land managers do to the forest following a natural disturbance has legacy implications throughout forest succession.

While conifer regeneration is expected in the years following high severity fire due to naturally high perimeter to area ratios and abundant low/moderate-severity inclusions within large high-severity patches (DellaSala and Hanson, 2019), localized areas of prolonged native shrub and forb cover should also be expected in some cases (Odion et al., 2010). Multi-decadal delays in tree regeneration after fire and type conversion to shrublands or grasslands characterized historical dry forest landscapes (Baker, 2018). Thus, areas with relatively low densities of conifers and/or increased non-conifer cover should be maintained for their contribution to both spatial and temporal heterogeneity at multiple spatio-temporal scales (Swanson et al., 2011; Hanson, 2018), nutrient cycling by typically abundant native N-fixing shrubs (Johnson and Curtis, 2001), and resilience to future climatic changes and disturbances (Baker, 2018; Busby et al., 2020). Despite concern over short intervals between high severity fires, few studies have analyzed whether type conversion is occurring at ecologically, spatially, and temporally meaningful scales or outside historical rates under these circumstances; although, it is anticipated in places due to climate change. Moreover, natural abundant conifer regeneration was even documented in areas that experienced only a 15-year high severity fire interval (Donato et al., 2009b).

2.5. *Long-unburned forests do not necessarily burn more severely*

Hessburg et al. (2021), Prichard et al. (2021), and Hagmann et al. (2021) all assume that long-unburned forests will burn much more severely due to higher forest density and forest biomass, and therefore recommend widespread thinning to address forest density in many forests before prescribed fire or managed wildfire. However, long-unburned forests may in fact experience lower fire severity effects such as in the Klamath (e.g., Odion et al., 2010) and Sierra (van Wagtendonk et al., 2012) regions. Some studies indicate that prescribed fire alone can lower fire intensity in Australia and USA forests (Fernandes, 2015), the southwest (e.g., van Mantgem et al., 2013), and central Sierra Nevada regions (Knapp et al., 2017).

3. Do dead trees contribute to wildfire risks and carbon emissions?

Simply put, trees die, forests burn, and these are natural processes that are increasing in places due to climate change (Keyser and Westerling, 2017). For some, this raises concerns about reburn potential (Hessburg et al., 2021). Importantly, dead trees either singularly or in patches act as critically important "biological legacies," transferring their ecological functions (structure, habitat) and carbon from the pre- to post-disturbed forest (DellaSala, 2020) and providing microclimate conditions (shading) to reduce climate impacts (Kauffman et al., 2019). In contrast, most commercial forestry practices remove legacies, increase heat exposure of regenerating forests, and transfer much of the stored carbon to the atmosphere, declaring instead that burned forests are "unhealthy," such as the "healthy forest" initiatives of the USFS.

3.1. *Tree mortality is varied but typically highest in young forests*

While background tree mortality rates in old forests have been climbing in places (van Mantgem et al., 2009), young trees often have higher mortality particularly in the early stages of forest succession due to dense packing of small trees and competition for limited resources (Larson and Franklin, 2010). For instance, in mature Douglas-fir forests of the Pacific Northwest annual mortality rates averaged ≤1% compared to more than twice that in 45 to 80-year-old stands, with some young stands exceeding 5% (Lutz and Halpern, 2006). Stanke et al. (2021) reported rates of tree species declines were highest in subalpine conifers and much higher in the smallest size classes compared to large Douglas-fir and ponderosa pine during the last two decades in western forests. Additionally, giant sequoia had annual mortality rates of 0.3% in 1100-year-old stands (Lutz and Halpern, 2006). In general, tree mortality mostly has been concentrated in forests subject to unprecedented droughts, climate-related increases in overwintering beetles (Harvey et al., 2016), and in forests subject to temperature stress (Stanke et al., 2021). Although thinning can reduce tree competition for limited resources in drought conditions, it can also increase overall tree mortality (Six et al., 2014; Hanson, in press), and it comes at the expense of carbon emissions with limited efficacy in containing insect outbreaks that are increasingly influenced by an overheating climate reducing overwintering insect mortality (Black et al., 2013). Depending on logging intensity, pre- and post-disturbance logging can compound natural disturbances that then limit the capacity of forests to regenerate (Paine et al., 1998; Donato et al., 2006; Black et al., 2013).

3.2. *Snags are more than fuels*

One way to examine potential fire hazards from large dead tree recruitment pulses is in snag forests where fire concerns have been especially prevalent but biodiversity is exceptional (Swanson et al., 2011; DellaSala and Hanson, 2015). In the San Bernardino Mountains of California, for instance, researchers found pre-fire beetle kill forests were unrelated to subsequent fire severity and that the locations dominated by the largest trees (>60 cm dbh) burned in lower fire severities compared to smaller (28–60 cm dbh) trees that burned more severely (Bond et al., 2009). In the Greater Yellowstone Ecosystem, beetle-killed snag forests had lower canopy and surface fuels, representing reduced fire potential in outbreak stands (Donato et al., 2013). The net effect was to shift stand structures from closed canopy mesic forests toward more open conditions with lower canopy fuels. In other words, the insects did the work for free that foresters would like to see happen and with far less-damaging consequences to ecosystem integrity. Additionally, researchers found no increase in fire severity during the red (1–3 years post outbreak) or subsequent gray-needle stage (4–14 years post outbreak) in peak wildfire activity years (Hart et al., 2015) while others have further demonstrated that fire severity in post-outbreak forests is driven primarily by weather and topography

(Harvey et al., 2016). In a comprehensive review of western forests, insect outbreaks actually decreased live vegetation susceptible to wildfire by reducing subsequent burn severity (Meigs et al., 2016). Consequently, Black et al. (2013) and Meigs et al. (2016) recommended a precautionary approach in forest management intended to reduce wildfire hazard and increase adaptation to climate change. Importantly, surviving young trees in dry pine, mixed conifer forests of western USA may possess genetic adaptations that confer unique adaptations and resilience (Baker and Williams, 2015). However, silviculturists have no way of identifying these trees in the field or in their marking guidelines (Six et al., 2018). Notably, Six et al. (2014) concluded that weakening environmental laws to allow more logging for beetle control is a maladaptive strategy because of uncertainties in efficacy of the treatments, high financial costs, impacts to other values, and the possibility that in the long-run logging may interfere with adaptive resilience to climate change.

3.3. Large dead trees are not a major source of fire emissions

Most fires, even the largest and most severe ones, consume only the needles, leaves, twigs, duff, outer bark surface, and ground foliage, which is a small portion of the overall combustible materials in a forest (Mitchell, 2015). Highest combustion factors measured post-fire are mostly in small trees due to their relative fire susceptibility (Mitchell, 2015; Harmon et al., in press).

Regarding climate concerns, logging over vast areas to potentially mitigate wildfire effects comes with a substantial emissions costs often grossly underestimated by land managers and some researchers (e.g., Johnston et al., 2021). For instance, Campbell et al. (2012) documented in western USA forests high C losses associated with vegetation treatments to lower fire intensity, only modest differences in the combustive losses associated with high- and low-severity fire that treatments were meant to encourage, and a low likelihood that treated forests would even encounter fire. In general, in order to improve the odds of fire encountering a treated area, ten times more area than the specific site would be needed, which means even more treatment related emissions and co-lateral damages can be expected. Likewise, in a synthesis of emissions estimated from natural disturbances vs. logging, Harris et al. (2016) concluded that logging during 2006–2010 nationwide released up to 10 x more emissions than wildfire and insects combined. Thus, putting more carbon dioxide into the atmosphere in attempts to limit fire effects may create a dangerous feedback loop (or "landscape trap," Lindenmayer et al., 2011) such that logging produces emissions (Harris et al., 2016) that then contribute to climate-related increases in extreme-fire weather and the Sisphean response.

4. Is thinning needed to protect large trees from wildfire?

4.1. Large trees are often removed in logging operations

MFAMA advocates claim that "fuel reduction" is mainly about the removal of small trees and shrubs (Hessburg et al., 2021) but most often in practice such logging typically removes large live and dead trees (e.g., calls to lift the large-tree protection standards in Oregon and Washington, Johnston et al., 2021) along with substantial shrub mastication that is functionally equivalent to clearcutting the forest understory. Reasons given by land managers vary including the safety of fire fighters and others working in forests to even the "protection" and regeneration of large trees (diameters seldom specified). In practice, these activities have substantial negative consequences to fire-adapted forests, including remote areas and reserves (Fig. 3). For instance, tree marking guidelines often include large fire-resistant trees to pay for timber sales designed as "fuels reduction" (Fig. 3). Additionally, the USFS claimed that a massive post-fire logging project in the Biscuit burn area (USDA Forest Service, 2003), including within Inventoried Roadless Areas and Late-Successional Reserves, was needed to "restore" old forest characteristics and reduce "fuels" despite evidence to the contrary (Donato et al., 2006).

In many cases, forests are so heavily thinned that they are type converted to weed-infested woodlands or savannahs that look nothing like the original forest (Fig. 4). Often these approaches are justified by land managers operating through multi-stakeholder "collaboratives" supported by even some conservation groups (e.g., The Nature Conservancy) that emphasize aggressive "fuel reduction" and "landscape restoration" despite scientific and public controversy over minimal review or safeguards.

5. Do actively managed areas burn at lower severity?

5.1. Common fire severity classification methods underestimate high severity extent in thinned areas

One of the primary justifications for thinning projects on federal lands is the assumption that such activities will reduce subsequent fire severity and the prevalence of active crown fire. Studies that have reported a reduction in fire severity in areas that were thinned prior to wildfire (e.g., Shive et al., 2013, Kennedy and Johnson, 2014) have typically used the delta normalized burn ratio (dNBR) and relativized dNBR (RdNBR), which are based on discriminating among certain spectral bands of pre- and post-fire 30-m resolution Landsat images (Key and Benson, 2005). While RdNBR has been shown to more accurately classify fire severity in sparsely vegetated areas compared to dNBR

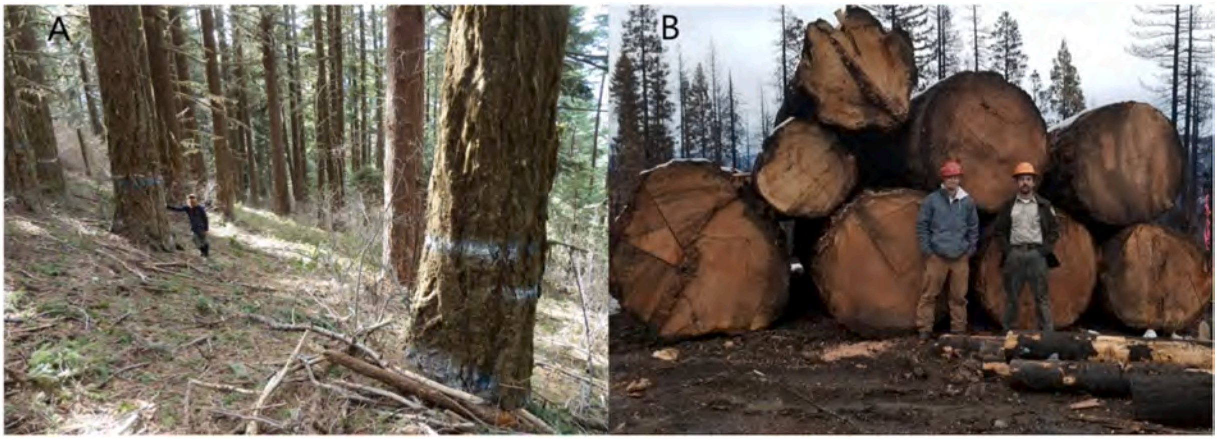

Fig. 3. (A) Nedsbar Timber Sale Medford District BLM Applegate Watershed (for "fuel reduction") showing "take tree" markings. (B) Postfire logging on Takilma Happy Camp Road in response to the Slater fire, Rogue River-Siskiyou National Forest. These trees were regarded as fire hazards. Photos: L. Ruediger.

Fig. 4. (A) Older mixed conifer forest in the Santa Fe watershed, New Mexico. (B) Heavy thinning just upslope of (A) ostensibly to reduce flame heights. (C) Southwest Jemez Mountains "Landscape Restoration Project" approved by collaboratives on the Santa Fe National Forest. Photos: D. DellaSala.

(Miller and Thode, 2007), many studies over the last decade have continued to use dNBR to assess fire severity in thinned areas to determine efficacy in altering crown fire occurrence. Moreover, the question of whether dNBR or RdNBR accurately estimates fire severity—particularly high severity—in thinned compared to unthinned areas has not been sufficiently addressed. Thus, there is reason for concern that high-severity fire is substantially underestimated in thinned areas (Online supplemental materials, Fig. S1, Table S1). Moreover, we note that articles reporting localized fire-severity reductions from thinning (e.g., Hessburg et al., 2021) do not account for tree mortality from thinning itself, before wildfire occurs, which is substantial oversight in assessing treatment effect (Hanson in press).

5.2. *Uncertainties in "fuels reduction" efficacy are often ignored in practice*

Prichard et al. (2021) state that "[t]here is little doubt that fuel reduction treatments can be effective at reducing fire severity…" Yet these authors repeatedly express cautions regarding their own proposition. For example, they acknowledge that thinning can cause "higher surface fuel loads," which "can contribute to high-intensity surface fires and elevated levels of associated tree mortality," and mastication of such surface fuels "can cause deep soil heating" and "elevated fire intensities." Prichard et al. (2021) also acknowledge that thinning "can lead to increased surface wind speed and fuel heating, which allows for increased rates of fire spread in thinned forests," and even the combination of thinning and prescribed fire "may increase the risk of fire by increasing sunlight exposure to the forest floor, drying vegetation, promoting understory growth, and increasing wind speeds." We have repeatedly reported on these same limitations yet claims are made that the science is all but settled and those questioning it have an agenda (Hessburg et al., 2021).

Further, the studies relied upon by Prichard et al. (2021) do little to dispel doubt regarding the effectiveness of MFAMA in moderating fire effects. For instance, pre-fire logged sites in the Rim fire of 2013 in the Sierra Nevada under a "fuel reduction" approach actually experienced predominantly high-severity fire effects during the fire (Povak et al., 2020: Figs. 1 and 2d). The most the authors could assert was that "some" of the fuel-reduction units experienced low-severity fire. In an analysis of the 2014 Carlton Complex fire in ponderosa pine forests of the eastern Cascades of Washington, Prichard et al. (2020) reported that thinning plus pile burning had the highest fire severity of any category, and fire severity was approximately the same for thinning plus prescribed burning as for re-burning of previous wildfire areas (Prichard et al., 2020: Fig. 3). In light of this, would it not be more prudent to conclude that managing natural wildfire ignition is the most effective approach, especially given that a substantial (but undisclosed) portion of the trees in the thinned units were killed by loggers, and the carbon removed from the ecosystem by thinning prior to the Carlton Complex fire? A similar question is raised by the results of Yocum Kent et al. (2015) regarding the 2002 Rodeo-Chediski fire in Arizona. In addition to an apparent discrepancy between the fire severity map (showing much higher fire severity) and the plot data used for the analysis of thinning plus prescribed fire (Yocum Kent et al., 2015: Figs. 1 and 2), the authors reported that unmanaged forests with wildfire alone had 22% more live tree carbon and 40% more total aboveground carbon than forests with thinning plus prescribed fire that later burned in the Rodeo-Chediski fire (Yocum Kent et al., 2015: Table 2). In the example of the Wallow fire of 2011 in Arizona, which was referenced by Prichard et al. (2021), the amount of high-severity fire reported in thinning units (Kennedy and Johnson, 2014; Johnson and Kennedy, 2019) was dramatically underestimated (Online supplemental). Thus, there is indeed evidence that thinning is not full proof (also see Dixie Fire example, Figs. S2-S3), can be unnecessary, and counter-productive as a landscape fire management tool especially when fires are driven largely by extreme-fire weather that is increasing across the West due to climate change (Abatzoglou and Williams, 2016).

6. Is the precautionary principle constraining active management?

6.1. The precautionary principle is needed as a check on damages from MFAMA

Hessburg et al. (2021) claim that the precautionary principle has become "the paralyzing principle" and a ploy of "agenda-driven science," despite millions of hectares logged and burned on federal lands at a cost of billions of dollars and often with minimal environmental review (e.g., under Categorical Exclusions, see below). Notably, the precautionary principle arose out of concerns to address risky regulatory decisions affecting ecological and human health (Whittaker and Goldman, 2021). It has its origins in the Stockholm Declaration of the 1970s that laid the groundwork for its establishment in international law, gained traction at the 1992 Earth Summit, has been used by governments in environmental and human health for decades (e.g., Canada, Denmark, Sweden, Germany, USA Endangered Species Act), is inculcated in United Nations sustainable development policies (e.g., Principle 7 UN Global Compact; https://www.unglobalcompact.org/what-is-gc/mission/principles/principle-7, accessed November 22, 2021), and is supported by thousands of scientists concerned about the ethics of the planetary biodiversity and climate crises (Ripple et al., 2021). By contrast, opposition to the precautionary principle has a long history of pro-development interests (Whittaker and Goldman, 2021) so it is no surprise that MFAMA advocates (Hessburg, Prichard, Hagmann) are joining these ranks by adding the highly subjective and indefensible tag of "agenda science" to those that raise science-based concerns about nature subjugation inherent in MFAMA and widespread command-and-control tactics.

Kriebel et al. (2001) cite four fundamental components of the precautionary principle: (1) take preventive action in the face of uncertainty; (2) shift the burden of proof to the proponents; (3) explore a range of alternatives instead of harmful actions; and (4) increase public participation in decision making (also see Whittaker and Goldman, 2021). However, the USFS and the BLM routinely bypass the burden of proof standard in NEPA via widespread use of CEs and emergency timber sale authorities that are designed to expedite large-scale logging with minimal review; limit legitimate appeals from citizen scientists and the public concerned about overreach; constrain the range of alternatives otherwise required under NEPA to just the no-action vs a single proposed action; and shift analysis from comprehensive impact statements to general environmental assessments (a lower analysis and burden of proof standard). In doing so, the burden of proof is inappropriately shifted by proponents of impactful actions to those that raise legitimate concerns.

As an example, the BLM routinely excludes from extensive review "salvaging dead and dying trees resulting from fire, insects, disease, drought, or other disturbances" in logging units not to exceed 400 ha or ≤1200 ha for a total project area (https://www.doi.gov/sites/doi.gov/files/uploads/doi_and_bureau_categorical_exclusions.pdf, accessed August 24, 2021). Likewise, the USFS has been using roadside "hazard" tree sales as a proxy for large-scale unit-based, post-fire "salvage" logging without the required NEPA process. For example, during the 2021 Slater Fire on the Rogue River-Siskiyou and Klamath National Forests in southwest Oregon and northwest California both national forests approved "emergency" logging authorizations to conduct "roadside hazard tree removal" over vast areas with minimal review. Additionally, supported in court by the timber industry, the USFS on the Willamette National Forest, Oregon, proposed cutting "a large number of trees" with a "low likelihood of failure within five years" along 640 km of roads, claiming it was needed for "post-fire road repair" and did not require environmental review. The project was so egregious it was deemed illegal by a federal judge (https://www.opb.org/article/2021/11/05/roadside-logging-willamette-national-forest/; accessed November 22, 2021).

The Rogue River-Siskiyou National Forest authorized removal of ~11,800 cubic meters of timber volume utilizing wet weather, ground based logging on ~5 km of roads at a popular snow park formerly supporting old-growth forest. Nearly a year later, the Klamath National Forest refused to declare containment of the fully extinguished Slater Fire and instead utilized emergency fire authorizations to approve 240 km of roadside hazard logging. Implemented with services performed by contractors, rather than officially authorized timber sales, trees were sold as "deck sales" with no public oversight, no NEPA review, and few if any available legal remedies. Utilizing a CE normally intended specifically for minimal road maintenance and repair actions, the Rogue River-Siskiyou National Forest also approved 232 km of "roadside hazard logging" authorizing removal of trees "likely to fall" up to 60-m on either side of the road. Tree removal criteria identified no diameter limit and allowed both live or "green" tree logging and removal of all snags. The CEs also included 136 km of roadside timber removal on ~1643 ha within Late-Successional Reserves, Riparian Reserves, Special Wildlife Sites and Northern Spotted Owl nesting cores.

Calls to do away with the precautionary principle have included proposed elimination of Late-Successional Reserves in dry pine, mixed conifer forests where fire is frequent under the NWFP (Spies et al., 2018), weakening of the Endangered Species Act and other laws (Mealey et al., 2005), and logging in Northern Spotted Owl critical habitat on the Rogue Siskiyou National Forest out of misplaced fire concerns and with the support of organizations like The Nature Conservancy (see Odion et al., 2014b). All the time, the ad hominem attacks about "agenda-driven" science that we believe do not pass the bar for scientific discourse have escalated (Hessburg et al., 2021, statements made in the media by Prichard https://www.google.com/search?q=huffington+post+dellasala&oq=huffing&aqs=chrome.2.69i57j0i131i433i512j69i59j0i512j0i131i433i512l2j0i512j69i61.4542j0j4&sourceid=chrome&ie=UTF-8; accessed November 22, 2021). Such red-herring arguments about presumed agendas deflect from acceptance of comprehensive evidence reviews needed to minimize harmful actions, particularly when those criticizing conservation scientists have called for stepped-up "fuel" reduction (Hessburg et al., 2021; Prichard et al., 2021; Hagmann et al., 2021; Johnston et al., 2021) that most often requires massive commercial logging and federal subsidizes that benefit timber companies. Given that the planetary climate and biodiversity crises have been contributed to, in part, a complete lack of adherence to the precautionary principle, scientists can and should ask for comprehensive evidence reviews that legitimately (following the scientific method) question MFAMA and seek to limit its damages. To do otherwise is to be complicit (DellaSala, 2021).

7. Did Native American burning and mixed-severity wildfire coexist?

7.1. Native American cultural burning and mixed-severity wildfires both occurred historically

With increased attention regarding the potential use of prescribed fire in many areas across the western USA, cultural burning conducted by Native Americans, particularly pre-Euro-American colonization, has been cited as a reason for a lack of megafires and significant amounts of high severity fire during that period (Prichard et al., 2021). Reconstructions of fire history that promote this view have generally relied on tree ring and fire-scar analysis that can underestimate past high severity fire, fire rotation, and occurrence of large fires (Baker, 2017). Using charcoal deposits in lake sediments in Yosemite National Park, California, researchers were able to estimate local and regional fire extent over the last 1400 years. Their results indicated that burning by

Native Americans decoupled the fire-climate relationship at small, localized scales (e.g., nearest villages, game, and travel routes) while regional burning patterns were more subject to the top-down control of climatic factors (Vachula et al., 2019). It is likely that cultural burning co-existed with mixed-severity fire—one did not preclude the other—and both have been subject to suppression over the last several decades and barriers to both should be reduced.

8. Redefining active management approaches

By some accounts, we have entered the Anthropocene, a time of human-dominated command-and-control subjugation of nature from apex predators to keystone ecosystem processes and the dangerous transfer of carbon long buried in the Earth and stored in forests to the atmosphere. This comes with substantial and often underestimated costs along with devaluation of nature as commodities to be extracted and turned into 2x4s, “feed-stock,” and “fuels” to be removed at all costs. Past single-minded extensive active management aimed at putting out all fires and logging the large, fire-resistant and carbon-dense trees to make fast-growing timber plantations have proven highly consequential to biodiversity and the climate. These impacts took decades to realize, were long resisted by land managers and researchers funded by them, and were only partially mitigated by our nation's environmental laws and policies that adhere to the foundational elements of the precautionary principle. Many of those laws are still being questioned and weakened such as through sweeping use of CEs at the same time MFAMA advocates falsely claim paralysis from too much precaution. We believe the risks of contemporary MFAMA are likewise being grossly underestimated, the benefits greatly exaggerated, and calls to do away with precautionary science-based principles to usher in massive increases in MFAMA activities (Hessburg et al., 2021; Prichard et al., 2021; Hagmann et al., 2021) are troubling signs that will only intensify both the biodiversity and climate crises. Simply put, we no longer have the luxury of decades to fully understand such leap-before-you look, highly-consequential approaches. Treating wildfires using bottom-up fuels reduction approaches when top-down extreme climate factors are increasingly overriding such efforts (Abatzoglou and Williams, 2016) could push ecosystems beyond resilience thresholds (Paine et al., 1998, Lindenmayer et al., 2011) at the further expense of biodiversity and the climate.

We believe there is a more holistic way that strives for coexistence among humans, nature, and wildfires (Moritz et al., 2014; DellaSala and Hanson, 2015; Schoennagel et al., 2017). This means first and foremost addressing root causes of the wildfire problem by getting off of fossil fuels and cutting emissions from the land-use sector. Our view on the climate and biodiversity crises is supported by thousands of scientists having an evidence-based, noble “agenda” of saving humanity and nature from imminent collapse (Ripple et al., 2021). Doing so, means placing much needed restrictive bounds on MFAMA to properly mitigate impacts rather than down playing them as a paralysis of management and attacking those that raise the alarm of precaution. It means judiciously choosing management alternatives that limit emissions from logging, allowing careful examination of impacts by the public and citizen scientists rather than sweeping use of CEs, and reforming industrial forestry practices that contribute to uncharacteristically severe fires in the first place (Zald and Dunn, 2018). And we note that while we focused on the western USA, similar concerns are mounting in forests globally, exemplified in British Columbia (Wood, 2021) and Australia (Lindenmayer et al., 2020) where large-scale clearcutting and timber plantations are contributing to unprecedented fires and misdirected calls for more of the same management (https://www.focusonvictoria.ca/forests/90/; accessed August 12, 2021). At the same time massive fire suppression has produced questionable benefits at considerable costs (see https://thehill.com/policy/equilibrium-sustainability/569797-attacking-fires-by-air-often-does-no-good-expert-says, accessed September 1, 2021).

Additionally, we must address the reoccurring urban fire disasters by redirecting MFAMA money to wildfire community adaptation around homes. This will require focusing from the home-outward rather than the wildlands-inward by hardening homes and defensible space, along with safe evacuation routes and assistance, and addressing ingress/egress concerns (Schoennagel et al., 2017). Despite assumptions that actively managing vast areas of wildlands will lower home losses (Hessburg et al., 2021), empirical evidence indicates a narrow zone around the structures themselves is the best way to prevent urban catastrophes (Cohen, 2000; Syphard et al., 2014); vegetation management beyond 30 m from homes provides no additional benefit (Syphard et al., 2014). Examples across the West show where unprepared homes burned to the ground, while surrounding trees did not (see https://www.latimes.com/local/california/la-me-camp-fire-lessons-20181120-story.html, accessed September 1, 2021, and https://www.oregonlive.com/wildfires/2020/10/opal-creek-burned-badly-by-wildfires-jawbone-flats-almost-completely-destroyed.html; accessed November 22, 2021). We must also improve land use zoning by avoiding additional ex-urban sprawl into dangerous areas where millions of homes have been built and more building is underway.

Given the extensive and expansive damage already inflicted by widespread wildfire suppression often acting in concert with MFAMA, and the certain climatic changes ahead from dumping even more emissions into the atmosphere from trying to contain fires, it is prudent to scale up ecologically based restoration that includes both active and passive methods that specifically address the root causes of the biodiversity and climate crises rather than purely the effects (e.g., more fires). We suggest focusing primarily on process-oriented restoration (Baker et al. in review) and the reduction of land-use stressors that make ecosystems less resilient, including prohibitions on logging and road building with clear and enforceable standards around “large tree protections;” managing for ecosystem integrity including landscape connectivity (up-down elevation and latitudinal corridors), protection of climate and wildfire refugia and structurally complex early seral forests (DellaSala and Hanson, 2015); recovering endangered species, particularly apex predators; and preventing invasive species invasions and ecosystem type conversions from overzealous thinning projects (DellaSala et al., 2017). It also means upgrading culverts to handle increasing storm intensity, obliterating sediment producing roads for aquatic integrity and connectivity, and the appropriate use of prescribed fire (human and natural ignition), including in collaboration with Indigenous people and proper smoke management. It also means limiting unintended human-caused fire ignitions (i.e., seasonally closing and decommissioning some roads) that have contributed substantially to national increases in wildfires (Balch et al., 2017) that are almost never considered in “fuels centric” approaches. Above all, it means shifting management and consumption patterns to keep much more carbon in our forests and to mitigate the climate crisis (Griscom, 2017, Moomaw et al., 2019).

Under this improved approach, land managers would work with individual wildfires (or fire complexes) for ecosystem benefits whenever safely possible, and when necessary for public safety, utilizing a full suppression approach. By focusing immediately on aggressively protecting, preparing and defending communities both before and during fire season, fire managers can more effectively protect the built environment and public safety by redirecting fire into places that would benefit ecologically and away from those that will not. This means monitoring fires in remote areas, loose herding, confinement, and full suppression strategies where necessary (to save lives and towns), and the utilization of Minimum Impact Suppression Tactics (MIST) (Ingalsbee, 2014), the minimization of fireline and other related impacts, and the appropriate use and monitoring of backburning strategies (DellaSala et al., 2017). Doing away with precautionary measures in a climate and biodiversity planetary crisis is irresponsible and we suggest that managers adhere to the principles by upholding the burden of proof standard. To do otherwise, perpetuates the Sisyphean myth of doing more of the same regardless of efficacy problems and substantial consequences.

That view only move us further away from safely and responsibly getting to coexistence with natural forces like wildfires that are instead subjected to command-and-control hubris.

CRediT authorship contribution statement

Dominick DellaSala (conceptualization, funding acquisition, lead writing), Bryant Baker (writing, graphics, tables, data, online supplemental, GIS), Chad Hanson (data, writing, online supplemental), Luke Ruediger (field work, photos, writing), and William Baker (writing and supporting research).

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109499.

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Mature and old-growth forests contribute to large-scale conservation targets in the conterminous United States

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Mature and old-growth forests (MOG) of the conterminous United States collectively support exceptional levels of biodiversity but have declined substantially from logging and development. National-scale proposals to protect 30 and 50% of all lands and waters are useful in assessing MOG conservation targets given the precarious status of these forests. We present the first coast to coast spatially explicit MOG assessment based on three structural development measures—canopy height, canopy cover, and above-ground living biomass to assess relative maturity. MOG were displayed by major forest types (n = 22), landownerships (federal, state, private, and tribal), and Gap Analysis Project (GAP) management status overlaid on the NatureServe's Red-listed Ecosystems and species, above-ground living biomass, and drinking water source areas. MOG total ∼67.2 M ha (35.9%) of all forest structural classes and were scattered across 8 regions with most in western regions. All federal lands combined represented the greatest (35%) concentrations of MOG, ∼92% of which is on national forest lands with ∼9% on Bureau of Land Management (BLM) and ∼3% on national park lands (totals do not sum to 100% due to minor mapping errors in the datasets). MOG on national forest lands supported the highest concentration of conservation values. However, national forests and BLM lands did not meet lower bound (30%) targets with only ∼24% of MOG in GAP1,2 (5.9 M ha) protection status. The vast majority (76%, 20.8 M ha) of MOG on federal lands that store 10.64 Gt CO_2 (e) are vulnerable to logging (GAP3). If federal MOG are logged over a decade, and half their carbon stock emitted, there would be an estimated 0.5 ppm increase in atmospheric CO_2 by 2030, which is equivalent to ∼9% of United States total annual emissions. We recommend upper bound (100%) protection of federal MOG, including elevating the conservation status of Inventoried Roadless Areas. This would avoid substantial CO_2 emissions while allowing ongoing carbon sequestration to act as natural climate solutions to aid compliance with the Paris Climate Agreement and presidential executive orders on MOG and 30% of all lands and waters in protection by 2030. On non-federal lands, which have fewer MOG, regulatory improvements and conservation incentives are needed.

KEYWORDS

United States, mature forests, biodiversity, carbon, drinking water

Introduction

Forest conservation in the United States has for decades centered on protection and ecological restoration of forests in the later stages of stand structural development because of their irreplaceable biodiversity and ecosystem services (e.g., Davis, 1996; Strittholt et al., 2006). Terms like primary forest, late-successional forest, mature forest, old-growth forest, and ancient forest are routinely used, sometimes interchangeably (Mackey et al., 2014). However, verifiable metrics for national-scale inventory and conservation target setting for these forests are lacking.

Precisely when a forest is considered to be in the later structural development is typically based on several diagnostic features such as the age, height, and diameter-at-breast height (dbh) of the dominant-codominant trees; canopy and understory complexity (vertical and horizontal layering); large standing dead (snags) and down trees (logs); and large trees with broken and highly branched tops. These structural characteristics vary among regions, major forest types, and site conditions (e.g., productive vs. slow growing sites). In particular, gap-phase dynamics, the result of tree death (singular or in cohorts), and blow-down along edges and exposed ridgelines, are important drivers of structural development in later forest development stages. When gaps are formed, the resultant increased light and nutrient levels release suppressed trees to fill the gaps over time (e.g., in the eastern forests, Davis, 1996; Pacific Northwest, Franklin and Van Pelt, 2004; Spies, 2004). The lack of severe stand-level disturbances over extended periods allows trees to acquire impressive stature and old ages associated with increasing biological complexity.

Old-growth forests (the most structurally advanced stage) generally have exceptional levels of biodiversity compared to logged forests (the least structurally advanced) (Luyssaert et al., 2008; Keith et al., 2009; Lindenmayer et al., 2012, 2014; Cannon et al., 2022). However, because of the timber value of older trees they are declining globally (Lindenmayer et al., 2012, 2014; Mackey et al., 2014). The loss of old-growth forests is coupled with changes to the global climate (Lawrence et al., 2022), reducing opportunities for natural climate solutions (Griscom et al., 2017; Moomaw et al., 2019). In the United States, conservation importance of old-growth forests has been recognized in every forested region, including Alaska (DellaSala, 2011; Orians and Schoen, 2012; Vynne et al., 2021; DellaSala et al., 2022), Pacific Northwest (Strittholt et al., 2006; Krankina et al., 2014), West (Rockies, Pacific Southwest, Southwest collectively: Kauffman et al., 1992, 2007), Central (Shifley et al., 1995), Great Lakes (Alverson et al., 1994; Carleton, 2003), Southeast (Hanberry et al., 2018), and Northeast (Davis, 1996; Leak and Yamasaki, 2012; Ducey et al., 2013).

Old-growth forest importance can also be described along a spatial gradient from individual trees within a stand to their context within watersheds and landscapes. At the tree level, the largest trees in old-growth forests may represent just 1% of all stems yet store at least 40% of the above-ground carbon as carbon stock increases with tree size as trees age (Stephenson et al., 2014; Lutz et al., 2018; Mildrexler et al., 2020). At the stand level, old-growth forests store 35 to 70% more carbon, including in the soils, compared to logged stands (Keith et al., 2009; Mackey et al., 2014; Mayer et al., 2020). Old-growth forest stands may also act as a natural buffer against extreme climate conditions (De Frenne et al., 2013; DellaSala et al., 2015; Frey et al., 2016; Betts et al., 2017). At the watershed level, old-growth forests maintain hydrological cycles (Perry and Jones, 2016; Crampe et al., 2021). In the Pacific Northwest, old-growth forests may function as fire refugia in large wildfire complexes (Lesmeister et al., 2021).

Aside from select portions of the West, most old-growth forests in the conterminous United States were eliminated decades-centuries ago as logging and development proceeded from east to west coast. What remains is largely on federal lands where the government has untapped policy options for stepped-up conservation. Some of the remaining old-growth forests on national forest land are within Inventoried Roadless Areas (IRAs) that are at least 2,000 ha. Road building and most forms of logging are prohibited within IRAs but only administratively and not by an act of Congress, meaning protections are not inviolate or permanent (i.e., classified as GAP3 multiple use management). Importantly, significant portions of eastern forests are approaching maturity (100 + years, Gunn et al., 2013). As mature forests with advanced structure recover from historical logging, they could develop old-growth characteristics within just a few decades.

Primary and old-growth forests generally have received increased attention internationally as natural climate solutions (DellaSala et al., 2020; IUCN, 2020; Law et al., 2021), including from policy makers[1] (e.g., March 22, 2022) and conservation non-governmental organizations (NGOs) in the United States[2]; [3] (accessed May 15, 2022). Article 5.1 of the Paris Climate Agreement calls on governments to protect and enhance "carbon sinks and reservoirs," while Article 21 of the UNFCCC COP26 Glasgow Climate Pact emphasizes "the importance of protecting, conserving and restoring nature and ecosystems, including forests… to achieve the long-term global goal of the Convention by acting as sinks and reservoirs of greenhouse gases and protecting biodiversity…" (UNFCCC, 2021). Furthermore, the United States was one of 140 nations at COP26 that pledged to end forest degradation and deforestation by 2030 (United Nations Climate Change, 2021). Also, the Summary for Policy Makers (SPM.D.4) in the Intergovernmental Panel on Climate Change [IPCC] (2022) report mentions safeguarding biodiversity and ecosystem integrity as fundamental to climate resilient developments. Attention to mature and old-growth forests can inform implementation of these policy commitments.

Large-scale conservation proposals for all land and waters have increasingly relied on 30 percent (i.e., 30% protected by 2030 or 30 × 30; Dinerstein et al., 2019; Carroll and Noss, 2021; Carroll and Ray, 2021; Law et al., 2021, 2022; One Earth Global Safety Net[4]; accessed May 28, 2022) and 50 percent (Half Earth) protection targets that involve triage approaches (Noss et al., 2012; Wilson, 2016). Large-scale target setting also has policy relevance, as exemplified by President Joe Biden's January 2021 executive order directing federal agencies to develop 30 × 30 targets for all lands and waters in the United States (White House, 2021). An April 2022 executive order from the President also directed federal agencies to inventory and assess threats to both mature and old-growth forests nationwide for possible protections (White House, 2022). Moreover, regionally specific proposals, such as the 79M ha of proposed protected areas in a five state area (OR, WA, ID, MT, and WY; Bader, 2000), a portion of which includes congressionally proposed wilderness additions in the Northern Rockies Ecosystem Protection Act (S.1276), have not assessed the amount of mature and old-growth forests nor its management status (i.e., how much protection is needed?). In all cases, it is vital that these forests are clearly defined, assessed, and mapped at multiple spatial scales (regional to national) to advise decision makers and NGOs on how best to meet climate and biodiversity policies and conservation targets.

Our objectives are to examine the contribution of mature and old-growth forests in the conterminous United States to: (1) conservation of at-risk forest ecosystems and species based on IUCN Red List criteria (Comer et al., 2022); (2) source catchments for drinking water (Mack et al., 2022); and (3) above-ground living biomass (Harris et al., 2021). We also applied conservation target setting developed for continental scale assessments to determine the contribution these forests could make to 30% (i.e., 30 × 30, Dinerstein et al., 2019) (lower bound), 50% (i.e., Half Earth; Noss et al., 2012; Wilson, 2016) (mid bound), and 100% (upper bound) protections. For our study, we are using estimates of forest structure that correlate with stand development collectively referred to as mature-old growth forests (MOG) to capture both the mature stage that is approaching old growth condition and the most advanced old growth stage as well. We also consider old growth a subset of primary forest defined as any forest stage lacking commercial logging or other industrial-scale developments that impairs ecosystem functions (Mackey et al., 2014). To our knowledge, this is the first comprehensive and spatially explicit assessment of MOG in the conterminous United States.

Materials and methods

Forest structure mapping

We mapped the relative level of forest structural maturity using three published spatial data sets that include forest canopy cover, canopy height, and above-ground living biomass derived from modeled satellite data (**Table 1**). These data were stratified by United States Ecoregions Level III ($n = 28$) (Omernik and Griÿt h, 2014) and Forest Types Groups ($n = 85$) (Ruefenacht et al., 2008) to account for the influences of variation in life history traits governing tree longevity and local environmental conditions on plant growth and ecosystem processes, as well as differing human and natural disturbance regimes. We used field measurements of canopy height and biomass from the Forest Inventory and Analysis plot database (FIA, 2022) to compare with our modeled forest maturity map and to aid in the interpretation of the map. We used a time series of available spatial data to examine the extent to which forests that were mapped as relatively less structurally advanced coincided with the footprints of severe natural disturbances. Further details on the methodology are provided in the Supplementary.

Expert workshops

A series of regional zoom workshops were conducted from September to November 2021 to consult with ecological and forest conservation experts (Supplementary). In total, 40 experts attended with each workshop focused on a major forested region within their region of interest. Key workshop objectives are listed in the Supplementary, including using participants to provide feedback on the initial modeling results for fine tuning. Expert consensus was that the appropriate level of forest

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[1] https://ktvz.b-cdn.net/2022/02/2022-02-17-DOI-and-USDA-Old-Growth.pdf

[2] https://www.climate-forests.org/

[3] https://forestcarboncoalition.org/

[4] https://www.oneearth.org/the-global-safety-net-a-blueprint-to-save-critical-ecosystems-and-stabilize-the-earths-climate/

ecosystem classification was the 28 Forest Types Groups—which comprise aggregations of more finely defined forest types—spatially modeled from FIA inventory plot data at a 250-m pixel resolution (Ruefenacht et al., 2008) and for Level III ecoregions (Omernik and Griÿt h, 2014).

Spatial analysis

The three spatial structural data layers of forest cover, canopy height, and above-ground living biomass were made available for the conterminous United States (**Table 1**). Spatial analyses were undertaken using Google Earth Engine (Gorelick et al., 2017). As the three data layers were generated using the Global Land Analysis and Discovery's (GLAD) Landsat Analysis Ready Data (ARD), they shared the same 30-m pixel resolution.

An overview of the workflow to create a seamless conterminous-United States wide spatial data layer of relative forest maturity is provided in **Figure 1**. This included creating a spatial vector file of each Forest Type Group for each Level III Ecoregion. Spatial data layers were generated based on spatial coverage for the Forest Type Groups found in each Level III Ecoregion, resulting in a total of 782 unique combinations. For each pixel, we quantified quartile values for the three structural variables (canopy cover, canopy height, and biomass) within each of the 782 combinations. A score was then calculated for each pixel as follows: (a) the lowest quartile value for each metric was given a score of 0 and the highest a score of 3; then (b) the three metric scores were summed giving a range in possible values from 0 (lowest quartile for the three variables) to 9 (highest quartile for the three variables), representing 10 ordinal forest maturity classes. Based on expert feedback, we then produced a simplified structural class map by classifying pixels with a score of 0 as "indeterminant, those with scores of 1–3 as "Young," scores 4–6 "Intermediate" and scores of 7–9 as "Mature." Using a global spatial data set (Petersen et al., 2016), we analyzed the modeled forest maturity map to identify how much of each maturity class was plantation rather than naturally regenerating forest and excluded plantations from analysis.

Calibration analysis

We used FIA plot data as an independent data source for calibration off the modeled forest maturity structure map. Of the three variables, only canopy height could be used for validation as the input biomass layer used FIA biomass data. The spatial units of analysis (SUA) for comparison with the FIA plot data were generated from the intersection of the map of 85 United States Ecoregion Level III with the maps of the 28 Forest Type Groups. Those SUAs were analyzed for which there were at least 10 FIA plots for each of the three FIA Structural Stage Classification levels (Pole, Mature, Late) (n = 41). For each of these 41 SUAs, we calculated aggregate statistics from the quartiles and median values for canopy height and biomass from a random sample of pixels within each of the three modeled structure levels (Young, Intermediate, MOG) with 1.5–5% of pixels sampled. Further details are provided in the Supplementary.

Land ownership and gap analysis project status

The extent and management status of MOG was assessed using spatial data provided by government agencies. We used the forest ownership dataset produced by Sass et al. (2020) for the USDA Forest Service based on 2017 data. Each ownership

TABLE 1 Details for the spatial data layers used in the forest maturity modeling and the attribution and validation analyses.

Layer	**Description**	**Data type and scale/resolution**	**Calibration data/validation approach**	**Source**
Tree canopy cover	Percent tree canopy cover where trees defined as all vegetation taller than 5 m. forest extent in the year 2000 similarly to Hansen et al., that is, any 30-m Landsat pixel that met a tree canopy threshold of at least 30% with trees taller than 5 m.	Raster (30 m)	Training data to relate to the Landsat metrics were derived from very high resolution image interpretation methods	Hansen et al. (2013) updated to 2010 (GLAD)
Forest height	Forest canopy height	Raster (30 m)	Vegetation structure data collected using airborne lidar instruments (ALS) and GEDI field plots	Potapov et al., 2021
Forest biomass	Modeled estimates of above-ground living biomass	Raster (30 m)	Based on machine learning of satellite band ratios, plot measurements of biomass, and environmental variables	Harris et al., 2021
Ecoregions (Levels III)	Areas of similar ecosystems	vector data layer (at or above 1:24,000 scale)	Field verification trips across 30 United States	Omernik and Griÿt h, 2014
Forest Type Groups	Aggregation of forest types into 28 categories	Raster (250 m)	Spatial distribution models based on correlations between FIA inventory plot data (2022) and spatial environmental data layers	Ruefenacht et al., 2008

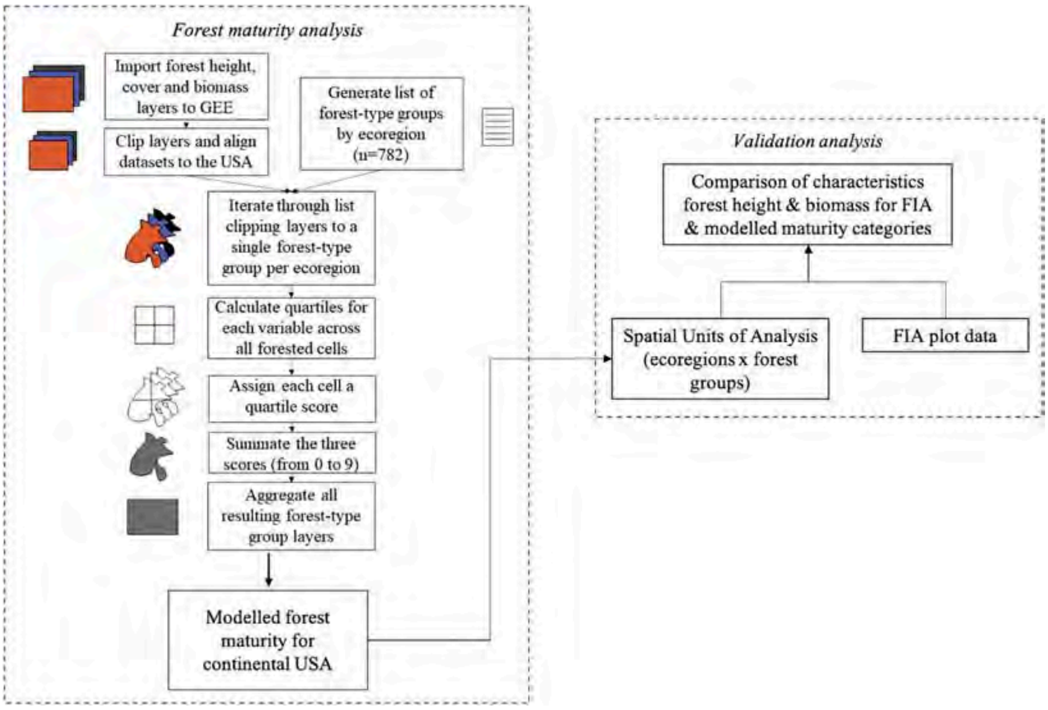

FIGURE 1
Workflow showing main steps in the calculation of the forest maturity structure model for conterminous United States, along with the validation analysis. The three 30-m resolution spatial data sets for forest cover, canopy height, and biomass were analyzed within 872 spatial units of analysis (SUA) defined by the intersection of ecoregions and major forest types. Forest Inventory Analysis (FIA, 2022) plot data were used for a validation analysis. Further details in **Supplementary Information**—Methods.

category was used as a mask to determine the extent of MOG within different tenures across the conterminous United States. The only additional aggregation made was the combination of the two FIA 41 categories, TIMO/REIT and private that were combined into a single masking layer. The Gap Analysis Project (GAP) management status codes (GAP1–4) was applied to MOG using the PAD-US Spatial Analysis Data provided by U.S. Geological Survey [USGS], and Gap Analysis Project [GAP] (2020). GAP 1 (e.g., Wilderness, National Parks) and GAP2 (e.g., National Monuments) were considered protected lands. GAP3 was multiple use management and GAP4 was no protection. The flattened version of the dataset was an important component of the analysis for determining the protected status of MOG. Inventoried roadless areas (IRAs) were filtered from the dataset and classified in our study as GAP2.5—that is—even though IRAs are given GAP3 status in the PAD-US dataset, we gave some credit to IRAs for administrative protections from most forms of logging. To ensure consistency among datasets, we compared the IRA layer to the 2001 Roadless Rule Feature layer provided by the USDA[5] for cross validation. We also assessed additional ownership and management of MOG including National Forests (National Forest System Land Units[6]), National Parks[7] and BLM (Derived from PAD-US[8]). The metadata[9] for landownerships did create some minor overlap problems where IRAs were inadvertently present in the dataset as within other ownerships even though this designation applies only to national forests. Those are recognized in each of the applicable tables as IRA misclassifications. The five western state regional example (79 M ha) that includes the Northern Rockies Ecosystem Protection Act was mapped after Bader (2000).

Biomass calculation

To determine the estimated amount of above-ground living biomass stored within MOG, spatial data produced by Harris et al. (2021) was used as an input layer. Calculating the

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[5] https://data.fs.usda.gov/geodata/edw/datasets.php?xmlKeyword=roadless

[6] https://data.fs.usda.gov/geodata/edw/datasets.php

[7] https://irma.nps.gov/DataStore/Reference/Profile/2224545?lnv=True

[8] https://www.usgs.gov/programs/gap-analysis-project/science/pad-us-data-download

[9] https://www.fs.usda.gov/rds/archive/products/RDS-2020-0044/_metadata_RDS-2020-0044.html

amount of biomass involved firstly warping the dataset to ensure a 30-m pixel size using GDAL and later masking to the extent of determined mature forest. The *R* program exactextractr was then utilized to sum the total amount of biomass within the forests. Due to the discrepancy between the input data being at a 30-m resolution and scaled to Mg/ha, the total value was then converted to produce overall biomass weight in tons.

At risk forest ecosystems and species

The IUCN Red List of Ecosystems (RLE) is an emerging global standard that integrates data and knowledge to document the relative risk status of ecosystem types. RLE criteria were used to assess 655 terrestrial ecosystems in temperate and tropical North America, including 182 forest and woodland ecosystem types in the conterminous United States using the U.S. National Vegetation Classification (Comer et al., 2022). We mapped these ecosystem types nationally using inter-agency LANDFIRE (2016) map products at 30-m pixel resolution with remote sensing data from approximately 2011. The RLE indicators that gauge the probability of range wide ecosystem collapse were measured for each criterion to address: trends in ecosystem extent (A); relative restricted nature of its distribution (B); extent and relative severity of environmental degradation (C); and extent and relative severity of disruption of biotic processes (D). Based on these measures, we categorized ecosystems as Collapsed, Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern, Data Deficient, or Not Evaluated. Some 119 (65%) of the 182 United States forest ecosystem types were listed as threatened in some form (i.e., either Critically Endangered (CR) [6.5%], Endangered (EN) [24%], Vulnerable (VU) [24%], or Near Threatened (NT) [10%]).

We also overlaid our MOG map with the modeled distributions of the threatened forest and woodland types to quantify their relative representation within managed and protected lands.

At-risk forest-associated species

We used a database containing an analysis of the habitat requirements for species of conservation concern, including their co-occurrence with standard ecosystem classification units and vegetation structural attributes (Reid et al., 2016). This database includes over 6,000 plant and animal taxa known to occur throughout the conterminous United States. At-risk status was provided using both NatureServe conservation status ranks (Stein et al., 2000) and for listing status under the United States Endangered Species Act (i.e., for species listed as Threatened or Endangered, as well as Candidate or Proposed). We documented relationships through map overlays of species locations with mapped ecosystem type distributions. While incomplete, mapped distributions of forest types provide an initial indication of where MOG may support at-risk forest-associated species.

Drinking water source areas

The USDA Forest to Faucets assessment provides a relative index summarizing the importance of forested land for the provision of surface drinking water based on biophysical and demographic data (Mack et al., 2022). These data were available at the scale of subwatersheds delineated by the USGS, of which there were approximately 100,000 in the United States (USGS et al., 2013). We masked these data by the MOG pixels to provide a spatial layer showing the relative importance of MOG to surface drinking water. We also calculated MOG area for four classes representing each quartile of the relative importance to surface drinking water index and summarized by area for each GAP status and land tenure. Classes ranged from 1 (lowest importance, 0–25% relative importance) to 4 (highest importance, 76–100% relative importance) based on the relative importance to surface water index defined by the USDA Forest Service.

Results

Forest structure classes

Three categories of structural development were identified based on the ten ordinal i.e., ranked categorical classes: young—or least advanced structurally (scores of 1–3)—totaled 41.4 M ha (22.1%); intermediate (scores of 4–6) totaled 78.5 M ha (42.0%); and MOG –most advanced structurally (scores of 7–9)—totaled 67.2 M ha (35.9%) with a grand total of 187.0 M ha of mapped structural classes (**Supplementary Figure 1**). The percentage area of young, intermediate, and MOG within United States Ecoregions Level II is also detailed in **Supplementary Figure 2**. The comparisons of FIA plot based estimates of biomass, canopy height and relative structural maturity are provided in **Supplementary Figure 3** for the 41 spatial units of analysis were there were suÿcient plot data.

Mature and old-growth forests spatial extent

The spatial distribution of MOG within the conterminous United States is shown at a national scale (**Figure 2**) and with a zoom-in to eight forested regions where these forests are widely scattered, including the Pacific Northwest (1), Pacific Southwest

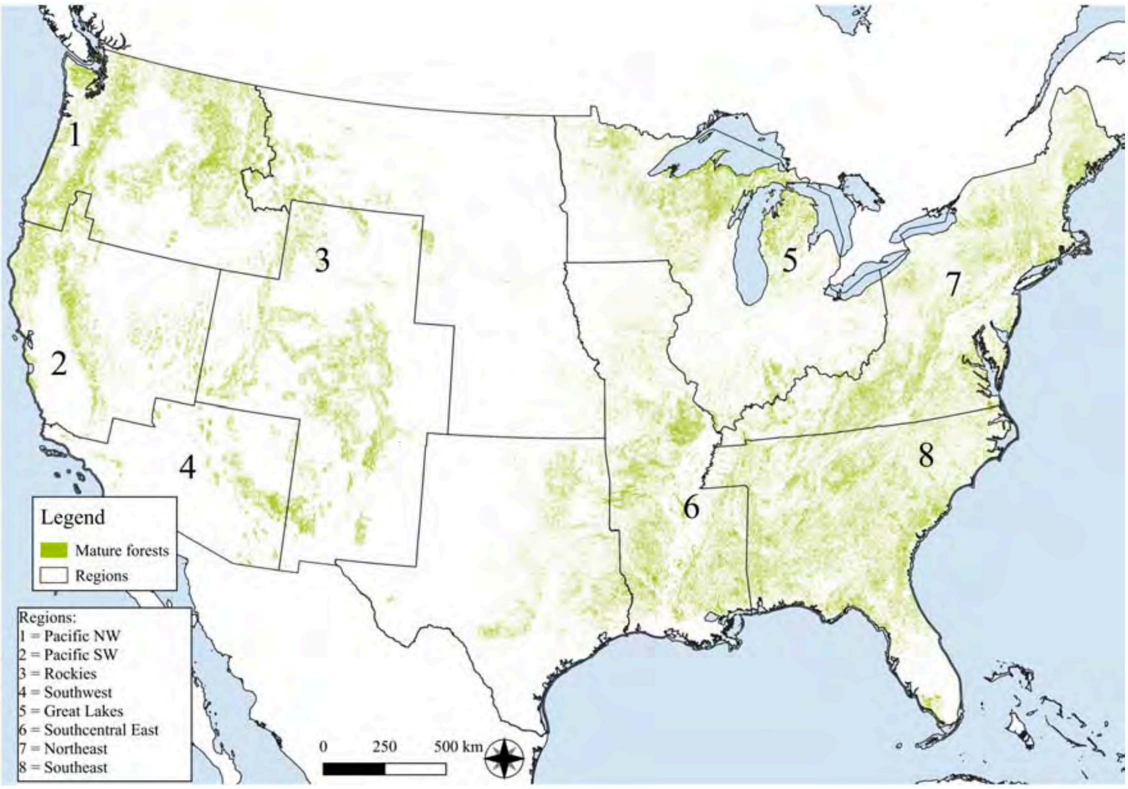

FIGURE 2
Distribution of modeled mature and old-growth forests (MOG) for the conterminous United States. Forest regions with MOG are numbered.

(2), Rockies (3), Southwest (4), Great Lakes (5), South Central (6), Northeast (7), and Southeast (8) (**Figure 3**).

Example photographs of general MOG structural features for major forest types of the conterminous United States illustrate anticipated variability in structural development of these forests (**Figures 4A–F**).

Using the western states regional MOG assessment example, MOG represent ~7.60 M ha (9.6%) of the 79.1 M ha within the five-state area that includes the Northern Rockies Ecosystem Protection Act under consideration in the United States Congress (**Figure 5**). Only 20% of MOG are in GAP1 and 2 status with 30% in IRAs having intermediate protections (GAP 2.5) (**Table 2**), meaning the vast majority of MOG in this proposal is vulnerable to development pressures.

Mature and old-growth forests major forest types

Mature and old-growth forests were located within 22 forest groups spanning conifer and hardwood types in the conterminous United States (**Table 3**). Nearly all MOG types had their greatest percentages in unprotected status (GAP3, 4; no classifications) with only 14.7% overall in GAP1 and 2 and 7.1% in GAP2.5. Only two forest types, Fir (*Abies* sp.)/Spruce (*Picea* sp.)/Mountain Hemlock (*Tsuga mertensii*) (33.1%) and Other Western Softwoods (41.3%) met the lower bound (30%) target. Percentages would improve for several forest groups if IRAs (GAP2.5 status) received higher protection status. Importantly, FIA major forest classifications inappropriately lump longleaf (*Pinus palustris*) with slash pine (*Pinus elliottii*)-dominated communities as one equivalent forest type, thereby obscuring the imperiled conservation status and biodiversity of longleaf pine wiregrass (*Aristida stricta*) communities. For instance, there are five distinct longleaf pine ecosystem types mapped nationally and assessed under the IUCN Red Listing criteria (Comer et al., 2022), with two listed as Critically Endangered, and three as Endangered that do not show up on the FIA dataset.

Mature and old-growth forests land ownership and GAP analysis project status

Federal lands (36%) have the highest proportion of MOG, of which, National Forests have most (~92%) of the federal total (**Table 4**). Approximately 24% of MOG on national forest lands

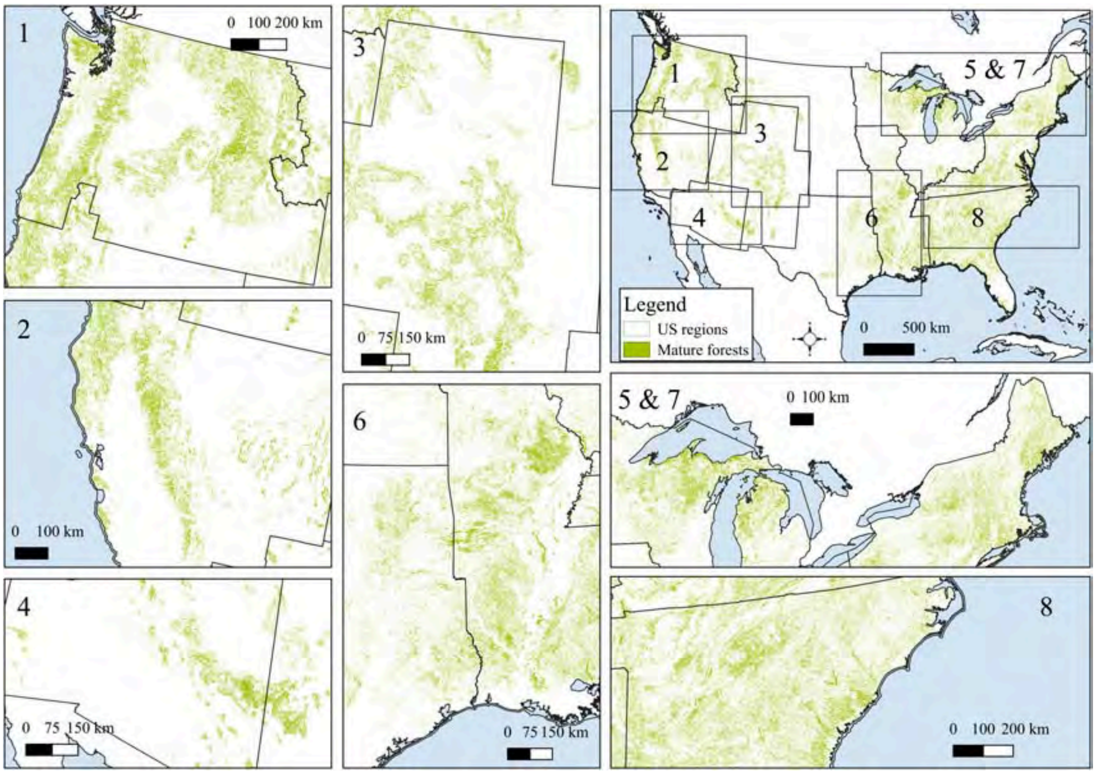

FIGURE 3
Regional zoom-ins of mature and old-growth forests of the conterminous United States. Panels show Pacific Northwest (1), Pacific Southwest (2), Rockies (3), Southwest (4), Great Lakes (5), South Central (6), Northeast (7), and Southeast (8).

are in GAP1 and 2 (**Table 4**). An additional 22% of MOG is within IRAs (GAP2.5). If IRAs received elevated conservation status, that would increase MOG protections in National Forests to 46%, which is within reach of the mid-level 50% target. **Supplementary Table 1** has a breakdown of MOG by GAP status for every national forest.

The rest of MOG on federal lands are held by the National Parks (∼3%) and BLM (∼9%) (categories overlap some due to mapping errors in the datasets). BLM lands in particular are mostly non-forested with some notable exceptions such as in southwest Oregon. However, like National Forests, only ∼24% of MOG on BLM lands have GAP1 and 2 status (**Table 4**). Of non-federal lands, MOG were highest on family private (55%) and lowest on tribal (∼4%). Interestingly, state lands (41%) were the only non-federal category where a lower bound 30% target was met but they did not have much MOG overall. All other non-federal tenures were well below even the lowest 30% target.

Mature and old-growth forests above-ground living biomass

Aggregate above-ground living biomass values in MOG are by far highest on national forests, which contain 45% of the total above-ground living biomass for all ownerships (**Table 5**). For non-federal lands, family private has the most (52%) above-ground living biomass and tribal (4%) the least. The ratio of carbon to above-ground living biomass is typically taken to be 0.5 (i.e., about 50% of the dry weight of biomass is carbon) though globally the ratio can range from 0.4–0.6 (Keith et al., 2010).

Mature and old-growth forests red list of ecosystems

Of the 182 forest and woodland ecosystem types assessed with criteria from the IUCN RLE in the United States, 119 (65%) were categorized from near threatened (NT) to critically endangered (CR); collectively considered here as "threatened" (**Figure 6**). The 102 types categorized as vulnerable (VU) through critically endangered (CR) occurred on 38% of current forest area. Critically endangered and endangered forest ecosystems were concentrated in the eastern states; mostly in areas with the longest and most intensive land use histories. Types found there included Southeastern Interior Longleaf Pine Woodland, Atlantic Coastal Plain Fall-line Sandhills Longleaf Pine Woodland, and West Gulf Coastal Plain Sandhill Oak and

FIGURE 4
Examplary photographs of mature and old-growth forests in the United States. **(A)** Mixed-conifer forest, Sequoia National Park, CA, United States (B. Bryant). **(B)** Mature Eastern Hemlock (*Tsuga canadensis*) stand, Huron Mountain Club Upper Peninsula, MI, United States (B. Boucher). **(C)** Bottomland hardwood forest, Congaree National Park, SC, United States (J. Maloff, Old Growth Network). **(D)** North-Central Interior Dry-Mesic Oak Forest and Woodland (B.S. Slaughter). **(E)** Hardwood hammock forest, Starkey Park, FL, United States (D. DellaSala). **(F)** Top ten largest bald cypress (*Taxodium distichum*) in Florida, Upper Pithlachascotee River Preserve (D. DellaSala). Nearly all old growth cypress was logged in the 1930s.

Shortleaf Pine Forest and Woodland (Supplementary Table 2). Forest type descriptions are maintained for public access on NatureServe Explorer[10] (accessed September 4, 2022).

Large proportions of MOG under GAP1 to GAP 3 status include types categorized by the IUCN RLE as Least Concern (Table 6). About 39.4 M ha (394,000 km^2) of all at-risk (NT-CR) forests and woodlands occurred within area mapped as MOG. While current area of critically endangered forests was quite limited overall, most at-risk forest mapped as MOG was categorized as Near Threatened, Vulnerable, or Endangered. These were commonly located on either federal land, predominately national forests, or family private (Table 6). Importantly, ~12.1 M ha (18%) of MOG with threatened status were located within GAP3 status

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[10] https://explorer.natureserve.org/

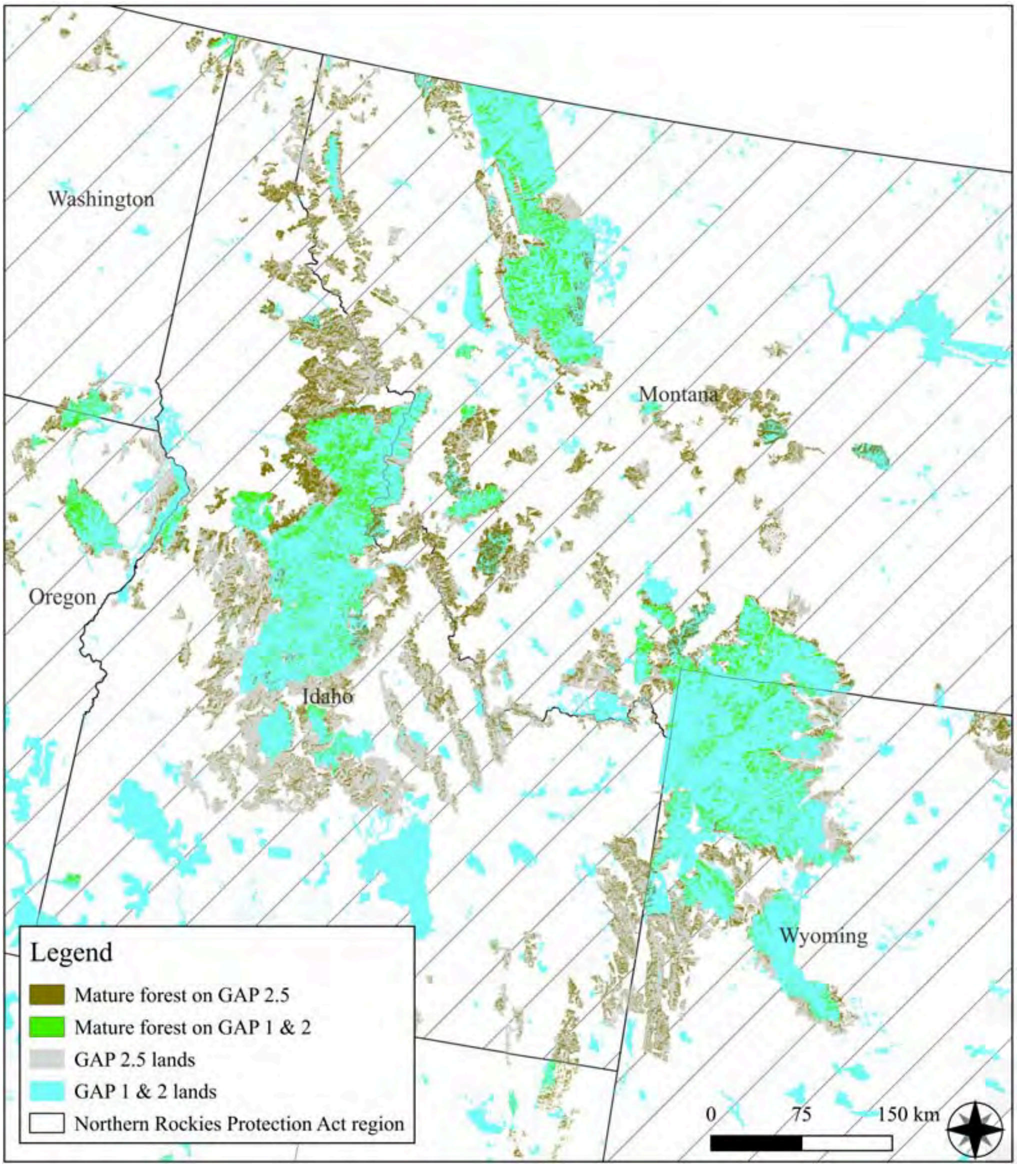

FIGURE 5
Distribution of mature and old-growth forests within the proposed five state protection area (OR, WA, ID, MT, and WY) including the Bader (2000) and Northern Rockies Ecosystem Protection Act (2021) by GAP classifications. GAP2.5 refers to Inventoried Roadless Areas (IRAs) that are not fully protected.

under multiple use management. These were, for example, North Pacific Maritime Mesic-Wet Douglas-fir (*Pseudotsuga menziesii*)-Western Hemlock (*Tsuga heterophylla*) Forest (VU) in the Pacific Northwest, and Southern Rocky Mountain Ponderosa Pine Woodland (VU) in the southern Rocky Mountains (**Figure 6**). The other large proportion of threatened MOG occurred on family private land, mostly throughout the eastern states (**Figure 6**). Examples included Ozark-Ouachita Dry Oak Woodland (EN), Allegheny-Cumberland Dry Oak Forest and Woodland (EN [VU-EN]), or Southern Piedmont Mesic Forest (EN [VU-EN]).

Mature and old-growth forests and at-risk species

Using documented relationships between species of concern and forests, there were 97 mapped forest ecosystem types known to support at-risk species (**Supplementary Table 2**) and the listed species are maintained for public access on the NatureServer Explorer (see text footnote 10; accessed September 5, 2022) under individual forest type summaries. MOG was present in 29.2 M ha of these mapped forest ecosystem types. Species considered "at-risk" within forest types using

TABLE 2 Mature and old-growth forests area (%) within the proposed five state protection area (OR, WA, ID, MT, and WY) that includes Northern Rockies Ecosystem Protection Act by GAP status.

GAP status	Area (ha)	Area (%)
GAP 1	1 174 117	15.4
GAP 2	342 516	4.5
GAP 2.5	2 331 074	30.7
GAP 3	5 033 750	66.2
GAP 4	295 733	3.9
Outside of GAP	755 909	9.9
Total area of mature forest	7 602 025	100
Total project area	79 173 694	–

Outside of GAP are areas with no GAP status, mostly on private lands.

NatureServe conservation status ranks included Vulnerable (G3), Imperiled (G2) or Critically Imperiled (G1) (Stein et al., 2000). From 1 to 64 of these at-risk species were associated with the 97 mapped forest types. Forest types with the most MOG that also included at-risk species were, for example, Laurentian-Acadian Northern Hardwood Forest (37,644 km^2 and 12 at-risk species), South-Central Interior Mesophytic Forest (16,046 km^2 and 50 at-risk species), and Southern Appalachian Oak Forest (10,190 km^2 and 48 at-risk species). Using United States Endangered Species Act (i.e., Threatened or Endangered, as well as Candidate or Proposed) as another measure of at-risk species status, 1 to 15 at-risk species were documented for their association with these 97 forest types. Among those supporting >1 at-risk species and with the extensive area in MOG were, for example, North Pacific Maritime Dry-Mesic Douglas-fir-Western Hemlock Forest (10,370 km^2 and 4 at-risk species), East Gulf Coastal Plain Large River Floodplain Forest (4,295 km^2 and 13 at-risk species), and Atlantic Coastal Plain Blackwater Stream Floodplain Forest (2,417 km^2 and 8 at-risk species).

Of the 97 forest ecosystem types with habitat relationships documented for at-risk species, 70 were considered threatened (IUCN NT, VU, EN, or CR) themselves. Threatened forest types support at-risk species (based here on NatureServe Conservation status ranks) with the most extensive area mapped as MOG in South-Central Interior Mesophytic Forest (EN) (16,046 km^2 and 50 at-risk species), Northeastern Interior Dry-Mesic Oak Forest (EN) (15, 327 km^2 and 12 at-risk species), and Southern Appalachian Oak Forest (VU) (10,190 km^2 and 48 at-risk species) (**Supplementary Table 2**).

TABLE 3 Area (×1000 hectares) and percent (%) of mature and old-growth forest within each Forest Inventory and Analysis (FIA) forest type group.

Forest type group	GAP 1	GAP 2	GAP 2.5	GAP 3	GAP 4	Outside of GAP	Total
Alder/Maple	1.1 (0.7)	5.9 (3.5)	0.8 (0.5)	46.3 (27.6)	7.9 (4.7)	106.4 (63.5)	167.6
Aspen/Birch	84.8 (2.5)	629.5 (18.9)	288.3 (8.7)	864.5 (26)	221.3 (6.6)	1 528.8 (45.9)	3 328.9
California Mixed Conifer	185.7 (13.8)	58.4 (4.3)	139.9 (10.4)	783.9 (58.3)	10.7 (0.8)	304.9 (22.7)	1 343.6
Douglas-fir	654.3 (11.1)	217.6 (3.7)	1 112.9 (18.9)	3 946.9 (67)	235.1 (4)	840 (14.3)	5 893.9
Elm/Ash/Cottonwood	11.7 (1.2)	139.9 (13.8)	1 (0.1)	46.1 (4.6)	75 (7.4)	738.9 (73)	1 011.6
Fir/Spruce/Mountain Hemlock	1 308.2 (29.6)	154.8 (3.5)	1 298.5 (29.4)	2 688.9 (60.8)	86.3 (2)	182.2 (4.1)	4 420.4
Hemlock/Sitka Spruce	127 (26.2)	15.8 (3.3)	55.3 (11.4)	287.6 (59.4)	12.5 (2.6)	41 (8.5)	483.9
Loblolly/Shortleaf Pine	41.5 (0.6)	555.8 (8.1)	9.7 (0.1)	562 (8.2)	229.3 (3.3)	5489 (79.8)	6 877.6
Lodgepole Pine	413.5 (22)	101.4 (5.4)	681.8 (36.3)	1 258.7 (67)	38.3 (2)	67.9 (3.6)	1 879.8
Longleaf/Slash Pine	19.3 (1)	90 (4.8)	3.2 (0.2)	308.7 (16.6)	72.7 (3.9)	1 365.5 (73.6)	1 856.2
Maple/Beech/Birch	65.6 (1.3)	868.6 (16.6)	29.2 (0.6)	523.7 (10)	302 (5.8)	3 484.3 (66.4)	5 244.2
Oak/Gum/Cypress	126.9 (4.1)	398.6 (13)	1.5 (0)	303.1 (9.9)	108.2 (3.5)	2138.7 (69.5)	3 075.5
Oak/Hickory	280.8 (1.6)	1173.9 (6.9)	153.2 (0.9)	1 810.3 (10.6)	1 363.4 (8)	12 421.7 (72.9)	17 050.1
Oak/Pine	23.1 (1.1)	147.6 (7)	7.1 (0.3)	167.6 (7.9)	66.3 (3.1)	1 711 (80.9)	2 115.6
Other Western Hardwoods	28.1 (23.4)	5.2 (4.4)	31.7 (26.4)	61.8 (51.5)	5.5 (4.6)	19.5 (16.2)	120.1
Other Western Softwood	86.9 (35.2)	15 (6.1)	102.1 (41.3)	119.3 (48.3)	16.7 (6.8)	9.1 (3.7)	247
Pinyon/Juniper	405.5 (10.5)	346 (9)	483.6 (12.5)	2 076.4 (53.7)	552.4 (14.3)	485.3 (12.6)	3 865.6
Ponderosa Pine	135.1 (4.2)	103 (3.2)	174.2 (5.4)	1817.3 (56.7)	412.6 (12.9)	738.2 (23)	3 206.2
Redwood	7.2 (9.4)	8.3 (10.9)	0.1 (0.1)	7 (9.2)	11.7 (15.3)	42.1 (55.2)	76.3
Spruce/Fir	31.4 (2)	312.7 (20.1)	16.9 (1.1)	264.5 (17)	153.6 (9.9)	790.9 (50.9)	1 553.1
Tanoak/Laurel	12 (5.9)	17.2 (8.4)	5.7 (2.8)	46.5 (22.6)	23.1 (11.2)	106.6 (51.9)	205.4
Tropical Hardwoods	1 (5)	4.7 (22.3)	0 (0)	7.4 (35.4)	0.3 (1.5)	7.5 (35.9)	20.9
Total	4 212.6	5 632.4	4 751	18 610.1	4 125.5	33 425.3	67 183

GAP2.5 refers to Inventoried Roadless Areas (IRAs). IRAs outside national forests are classification errors in the database. Outside of GAP are areas with no GAP status, mostly on private lands. Percentages are calculated by totaling each forest type group across rows.

TABLE 4 Total area of mature and old-growth forests (×1000 ha) and percent (parenthesis) for the conterminous United States by GAP and ownership.

Ownership and tenure	GAP 1	GAP 2	GAP 2.5	GAP 3	GAP 4	Total per owner
National Parks	822.3 (96.1)	24.5 (2.9)	0.7 (0.1)	3.3 (0.4)	4.4 (0.5)	855.6 (100)
National Forests	2 995.1 (13.7)	2 322.5 (10.6)	4 775.1 (21.9)	14 120.5 (64.7)	137.2 (0.6)	21 834.3 (100)
BLM	161.1 (7.1)	394.5 (17.4)	29.9 (1.3)	1 706.9 (75.4)	0.1 (0)	2262.6 (100)
State	11 5 (2.2)	2 086.3 (39)	4.9 (0.1)	2 054.9 (38.5)	430 (8)	5 343.7 (100)
Federal	4 014.9 (17.1)	2 906.7 (12.4)	4 756.2 (20.2)	15 731.6 (66.9)	402.4 (1.7)	23 514.5 (100)
Corporate private	13.5 (0.1)	215.4 (1.9)	3 (0)	232.4 (2.1)	645.2 (5.7)	11 223.5 (100)
Family private	32.5 (0.1)	296 (1.3)	5.2 (0)	350 (1.6)	1 067.7 (4.8)	22 467 (100)
Tribal	0.4 (0)	13.2 (0.8)	0.2 (0)	7.6 (0.5)	1 481.2 (94.6)	1 566 (100)
Total per GAP	4 239 (6.3)	5 686.8 (8.5)	4 784.2 (7.1)	18 736.3 (27.9)	4 198.1 (6.2)	67 183 (100)

Percentages are calculated across rows. GAP2.5 refers to Inventoried Roadless Areas (IRAs). IRAs outside national forests are classification errors of input datasets.

TABLE 5 Total-above ground living biomass within mature and old-growth forests (×1 M tons) by GAP and ownership.

Ownership and tenure	GAP 1	GAP 2	GAP 2.5	GAP 3	GAP 4	Total per owner
National Parks	281 (94.9)	10 (3.4)	0 (0)	1 (0.3)	3 (1)	296 (100)
National Forests	933 (15.7)	425 (7.1)	1 203 (20.2)	4 095 (68.8)	26 (0.4)	5 956 (100)
BLM	31 (5.3)	64 (11)	7 (1.2)	484 (83.4)	0 (0)	580 (100)
State	17 (1.9)	295 (33.4)	1 (0.1)	397 (45)	74 (8.4)	883 (100)
Federal	1 241 (19.3)	509 (7.9)	1203 (18.7)	4 539 (70.5)	60 (0.9)	6 441 (100)
Corporate private	3 (0.2)	35 (1.8)	0 (0)	42 (2.1)	89 (4.5)	1 970 (100)
Family private	6 (0.2)	47 (1.4)	0 (0)	56 (1.7)	123 (3.7)	3 325 (100)
Tribal	0 (0)	3 (1.1)	0 (0)	1 (0.4)	254 (93.4)	272 (100)
Total per GAP	1 285 (9.6)	920 (6.9)	1 203 (9)	5 091 (38.1)	626 (4.7)	13 351 (100)

Percentages (in brackets) are calculated across rows. GAP2.5 refers to Inventoried Roadless Areas (IRAs). IRAs outside national forests are classification errors of input datasets.

TABLE 6 Area of land (×1000 ha) and percentage area (parentheses) for each of the identified Red Listed Ecosystem (RLE) risk status by GAP and landowner.

	Not evaluated	Data deficient	Least concern	Near threatened	Vulnerable	Endangered	Critically endangered	Total by GAP
GAP status								
GAP 1	1.9 (0)	28.4 (0.5)	3 129.2 (60.3)	1 220.9 (23.5)	623 (12)	181.9 (3.5)	5.1 (0.1)	5 190.4 (100)
GAP 2	1.8 (0)	74.5 (1.5)	1 685.4 (35)	616.6 (12.8)	1 340.4 (27.9)	1 026.4 (21.3)	67.3 (1.4)	4 812.4 (100)
GAP 2.5	0 (0)	0.4 (0.1)	247.1 (81)	46.5 (15.2)	11.2 (3.7)	0 (0)	0 (0)	305.2 (100)
GAP 3	10.4 (0)	139 (0.6)	9 198.4 (42.9)	6 875.9 (32.1)	3 874.3 (18.1)	1 268.1 (5.9)	86.3 (0.4)	21 452.3 (100)
GAP 4	1.4 (0)	76.6 (1.8)	1 040.5 (24.2)	550.5 (12.8)	2 073.2 (48.3)	538.9 (12.5)	13.3 (0.3)	4 294.4 (100)
Landowner								
National Parks	1.5 (0.2)	8.3 (0.8)	558.4 (57.1)	195.2 (19.9)	200.1 (20.4)	15 (1.5)	0 (0)	978.6 (100)
National Forests	12 (0)	93.9 (0.4)	11 963.5 (46.6)	7 327.5 (28.5)	4 359.2 (17)	1 762.5 (6.9)	175.5 (0.7)	25 694 (100)
BLM	0 (0)	5.8 (0.2)	520.3 (19.9)	1 456.9 (55.7)	631.9 (24.1)	2.1 (0.1)	0 (0)	2 617.1 (100)
State	2.8 (0.1)	105.7 (2.6)	1 390.2 (34.4)	326 (8.1)	1 252.2 (30.9)	948.8 (23.5)	20.1 (0.5)	4 045.9 (100)
Federal	11.3 (0)	115 (0.4)	12 454.2 (45.1)	8 369 (30.3)	4 869.4 (17.6)	1 677.8 (6.1)	148.4 (0.5)	27 645.1 (100)
Corporate private	3.6 (0)	419.8 (5.3)	1 618 (20.3)	969.3 (12.1)	2 651.3 (33.2)	2 111.4 (26.4)	213.9 (2.7)	7 987.4 (100)
Family private	15 (0.1)	450.8 (2.7)	2 701.1 (16)	827.7 (4.9)	7 176.4 (42.5)	5 493.9 (32.5)	224.1 (1.3)	16 889 (100)
Tribal	0 (0)	16.4 (1)	738.3 (43.9)	447.1 (26.6)	457.4 (27.2)	21.2 (1.3)	0.2 (0)	1 680.6 (100)
Total by risk status	34.5 (0.1)	1 152.9 (1.9)	19 513.9 (32.4)	11 055 (18.4)	17 009.3 (28.3)	10 762.5 (17.9)	630 (1)	67 183 (100)

Percentages are calculated across rows. GAP2.5 refers to Inventoried Roadless Areas (IRAs). IRAs outside national forests are classification errors of input datasets.

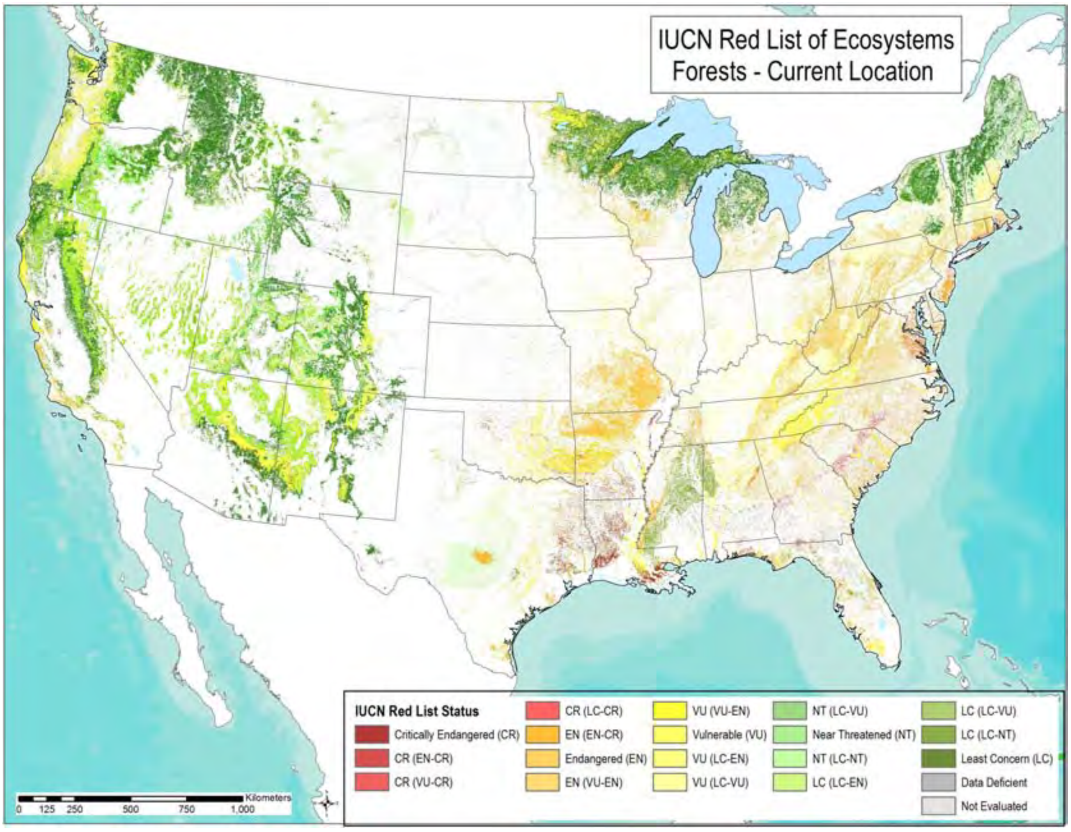

FIGURE 6
Current distribution of 182 forest and woodland ecosystem type categories under the IUCN Red List of Ecosystems (Comer et al., 2022). Nearly all these distributions include mature and old-growth forests (**Supplementary Table 2**).

TABLE 7 Mature forest area (ha) in each relative importance to surface drinking water class by GAP status and land tenure, with percentage of total mature and old-growth forest in the respective GAP/Tenure.

	Class 1 (0–25%)	Class 2 (26–50%)	Class 3 (51–75%)	Class 4 (76–100%)	Total
GAP Status					
GAP 1	1,188,095 (28.2)	1,021,604 (24.2)	1,218,859 (28.9)	790,612 (18.7)	4,219,170 (100)
GAP 2	1,804,722 (31.8)	915,163 (16.1)	1,541,173 (27.2)	1,411,752 (24.9)	5,672,810 (100)
GAP 2.5	1,646,869 (34.4)	1,220,674 (25.5)	1,355,166 (28.3)	561,520 (11.7)	4,784,229 (100)
GAP 3	5,922,561 (31.6)	4,494,644 (24)	4,720,470 (25.2)	3,598,512 (19.2)	18,736,188 (100)
GAP 4	1,178,791 (28.1)	773,969 (18.4)	1,370,386 (32.7)	873,587 (20.8)	4,196,733 (100)
Outside GAP	6,077,230 (20.6)	3,883,699 (13.2)	7,433,106 (25.2)	12,130,797 (41.1)	29,524,833 (100)
Land Tenure					
National Forests	5,713,619 (26.2)	5,498,207 (25.2)	6,119,473 (28)	4,501,227 (20.6)	21,832,525 (100)
National Parks	257,648 (30.1)	145,354 (17)	214,784 (25.1)	237,857 (27.8)	855,644 (100)
Federal Land	7,144,748 (30.4)	5,709,127 (24.3)	6,217,105 (26.5)	4,421,747 (18.8)	23,492,727 (100)
State Lands	1,704,860 (32.0)	803,361 (15.1)	1,360,235 (25.5)	1,463,130 (27.4)	5,331,587 (100)
Family Private Lands	4,381,601 (19.5)	3,208,018 (14.3)	6,200,135 (27.6)	8,666,291 (38.6)	22,456,045 (100)
Corporate Private Lands	3,081,796 (27.5)	1,815,543 (16.2)	2,672,084 (23.8)	3,653,002 (32.6)	11,222,425 (100)
Tribal Lands	611,203 (39)	384,502 (24.6)	517,106 (33)	53,000 (3.4)	1,565,810 (100)
BLM Lands	1,245,174 (55.6)	415,190 (18.5)	358,263 (16)	220,752 (9.9)	2,239,379 (100)
Total	17,818,269	12,309,753	17,639,160	19,366,781	67,133,962

Mature and old-growth forests and drinking water

Based on the USDA drinking water source area dataset, MOG with the highest drinking water value (Class 4) were mostly on Federal lands with surprising large areas on family private and corporate private (**Table 7**). Importantly, a substantial (4.5 M ha, >39%) amount of the highest quality drinking water comes from MOG within GAP3 and 4 status, and much more (12.1 M ha) is outside GAP status all together. Any loss of these forests due to logging and development would potentially impact drinking water supplies.

Discussion

Mature and old-growth forest structure and spatial analysis

Forest age and level of stand development are typically measured through tree ring analysis (e.g., core drill samples from living trees) and diameter distributions of dominant trees but can also be assessed using models based on measurements of forest structure—canopy height, canopy cover, biomass, as in our study. Other forest structural development characteristics indicative of the later stages of forest development include vertical vegetation layering and coarse woody debris (not measured in our study). Differences in the longevity, life history traits and niche requirements of tree species means that in many ecosystem types, the taxonomic composition of the dominant canopy species can reflect stages progressing from early to late seral. Gap-phase dynamics are diagnostic of the most structurally advanced old-growth. Furthermore, environmental factors that regulate plant growth, ecosystem processes rates and site productivity—thermal, moisture, radiation and nutrient regimes—result in variation within the ecosystem type of forest structure classes in terms of tree height, canopy density, and above-ground woody biomass.

Pan et al. (2011) used 2006 FIA plot data and remote sensing data at 1-km resolution to produce an age class distribution map in discrete age intervals of North American forests. Our inventory provides an updated and continuous-based structure map at 30-m resolution for tracking future changes in ecological development and management of MOG that can be updated as new datasets and advancements in monitoring technologies become available. We estimate 67.2 M (∼36% of all structural classes) of MOG are scattered across eight geographic regions in the conterminous United States that provide options for stepped up national and regional conservation. With the exception of IRAs, MOG are mostly not large contiguous blocks as they are nested within a highly fragmented matrix that has contributed to edge effects and diminished ecosystem functions (see Heilman et al., 2002).

Federal lands

Combined federal lands represented ∼35% of the total MOG structural classes with most (∼92%) on national forests and a fraction managed by National Parks (∼3%) and BLM (9%) (some overlap in mapping datasets). MOG on federal lands have the highest conservation values reflective of their above-ground living biomass, at-risk ecosystems and species, and drinking water source areas. However, only 24% of MOG on national forest and BLM lands each are fully protected, which is below even the lowest bound 30% target. Our analysis supports 100% of federal MOG for inclusion in protected areas based on their superior climate, water, and biodiversity associated values. We note that adding ∼20.8 M ha of unprotected federal MOG to the United States protected areas network would still fall far short of the 30% target for all lands and waters given only 12% of all types are protected nationally. To achieve a near tripling of protections nationally on top of 20.8 M ha of proposed MOG protections would still require another 125 M ha of new protections from all types and landowners (National Geographic, 2021).

An alternative scenario is that the unprotected federal MOG in GAP2.5, 3, and 4 status is logged and then regrown. The consequences of this logging on exacerbating climate change can be assessed in terms of the projected emissions and their effect on the atmospheric CO_2 concentration. A comparison of protected vs. logged federal MOG allows the mitigation benefit of protecting MOG to be further evaluated in terms of carbon emissions avoided. The area of 20.8 M ha at-risk MOG on federal lands currently stores ∼5.8 Gt of above-ground living biomass (Federal land GAP 2.5 + 3 + 4; **Table 5**), which is equivalent to 10.64 Gt CO_2. It is assumed that 50% of the carbon that had been stored in the biomass of logged MOG is emitted to the atmosphere due to combustion or decomposition of waste and short-lived wood products (Brown et al., 1997; Keith et al., 2014). This represents a carbon stock loss from the biosphere and a stock gain by the atmosphere. Logging emissions would remain in the atmosphere for decades and are partially removed by sinks. This can be calculated as the fraction of the airborne CO_2 from each pulse of emissions that decreases over time by removals from the natural land and ocean sinks and the regrowth of the forest (Keith et al., 2022). Carbon stock remaining in the atmosphere as the airborne fraction of the emissions was estimated for 2030 (after 8 years) and 2050 (after 28 years) to comply with global emissions reduction targets and for assessing the mitigation potential of full protection. By 2030, 74% of logging emissions would remain in the atmosphere, and by 2050, 54% would remain (Keith et al., 2022). This carbon stock remaining in the atmosphere also can be converted to parts per million by volume (ppm) as the common unit to express atmospheric CO_2 concentration (1 ppm = 7.8 Gt CO_2) (CIDAC, 1990). If 74% of the CO_2 emitted remains in the atmosphere by 2030, then 10.54 Gt CO_2 emissions are required to raise the atmospheric CO_2 concentration by 1 ppm. Logging emissions would consequently result in 0.5 ppm increase in atmospheric CO_2 concentration by 2030 and 0.37 ppm by 2050.

The quantity of logging emissions also can be compared with the total United States emissions that were 5.8 Gt CO_{2e} in 2020[11] (accessed September 5, 2022), which would be 0.532 Gt CO_2 from MOG logging per year, the equivalent to 9.2% of the total annual United States emissions.

We note while such an accelerated increase in logging may be logistically unrealistic due to a number of factors (e.g., clearcut vs. selection logging, congressional appropriations, timber sale economics) not the least of which is accessibility of remaining MOG that becomes increasingly costly as easy to access sites are initially logged. However, the Trump administration issued an executive order in 2019 designed to greatly ramp up logging by 72% on national forests.[12] According to conservation groups, at least some of those sales under the Trump administration are ongoing[13] (accessed September 5, 2022). Additionally, legislation is routinely introduced in Congress to greatly increase federal lands logging at the expense of forest protections[14]. Logging unprotected MOG would also contribute to total United States emissions and make President Biden's stated goal of emissions reduction of 50–52% by 2030 far more difficult to achieve. Conversely, not logging these unprotected MOG would avoid the decadal logging equivalent of ∼0.5 ppm CO_2 (5.32 Gt CO_2) or ∼9% of United States total annual emissions, which would make a meaningful mitigation contribution to the world as natural climate solutions (Griscom et al., 2017; Moomaw et al., 2019; Keith et al., 2022). It is this current decade that is critical for mitigation actions to avoid emissions and not to add to the atmospheric CO_2 concentration, including those from the land-use sector.

The IRA component of MOG represents what remains of intact blocks on national forests. Elevating the conservation status of IRAs to GAP2 would increase MOG protections on national forests to that approaching the mid-bound (50%) target. However, that would take either an act of Congress or administrative changes that remove exemptions for logging and other development projects (e.g., hydroelectric development, mining) along with new regulations making it difficult to overturn roadless protections in general. The national roadless conservation rule has sustained 14 legal challenges upheld in appellate courts, was overturned twice on the Tongass National Forest in Alaska by pro-development administrations (i.e., George W Bush and Donald Trump), and was substantially changed by state petitions to the federal government in Idaho and Colorado. Increasing administrative or congressional IRA protections is key to elevating the conservation status of IRAs so they can be considered GAP2. While there is no comparable roadless policy for BLM lands, MOG could be nominated to the National Landscape Conservation System[15] (accessed May 15, 2022). The BLM oversees 14 M ha of mostly iconic lands and waterways designated by Congress or presidential executive order mainly for conservation purposes that includes national monuments and other protective designations.

Regional

Federal forests in the Eastern region are maturing from logging that eliminated all but a fraction (1–2%) of the old-growth forests over a century ago (Davis, 1996). Most mature forest types in this region lack protections, many are not on federal lands, and most are fragmented especially given that large IRAs are mostly in western regions. Additionally, the USDA Forest Service (2022) revised its 20-year forest management plans for the 416,000 ha Nantahala and Pisgah National Forest in western North Carolina claiming that they needed to log mature forests to create a diversity of seral stages even though classic old-growth forests are still well below historical levels (Davis, 1996). A combination of federal protections, improved forestry practices, and conservation incentives on non-federal lands are needed in this region to meet conservation targets for MOG.

Under the Trump administration, the USDA Forest Service removed protections for large diameter (>50 cm dbh, up to 150 years old) trees on national forests in eastern Oregon and Washington that were in place for over two decades, even though large trees remain below historical levels (Mildrexler et al., 2020). We recommend restoring those protections. The five state western proposal that includes the Northern Rockies Ecosystem Protection Act also contains nearly 11 M ha of MOG with only 20% in GAP1 and 2 status and another 30% in IRAs (GAP2.5). Recent policy and management decisions underscore the importance of increasing MOG protections in this region as well.

Non-federal lands

Family forest owners are a group of nearly 10 million families, trusts, and estates representing the largest landowner category in the United States with one-third of the total forest ownership (vonHedemann and Schultz, 2021). Substantial area of at-risk ecosystems, at-risk species, and drinking water also occur on these lands mostly in the eastern states where federal lands are scarce. Family landowners generally tend to manage their forests for aesthetics, wildlife, conservation, and family ownership legacy providing opportunities for conservation investments (Butler et al., 2016).

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[11] https://www.epa.gov/climate-indicators/climate-change-indicators-us-greenhouse-gas-emissions

[12] https://www.usda.gov/sites/default/files/documents/usda-strategic-plan-2018-2022.pdf

[13] https://www.climate-forests.org/worth-more-standing

[14] https://www.congress.gov/bill/115th-congress/house-bill/2936/text/ih?overview=closed&format=txt

[15] https://www.blm.gov/programs/national-conservation-lands

State lands are under state regulatory authorities and these vary widely in the extent to which they have as either policy or practice the protection of MOG. Aside from state parks, most forested states grant preference to intensive forest management over forest protections. Large corporate landowners manage forests mainly to maximize their return-on-investment by cutting trees when they approach culmination of mean annual increment (just before they reach maturity). MOG therefore are often looked at as a financial liability to be converted into fast growing monocultural plantations on short-timber rotation cycles. Many tribal lands also have timber objectives. In the Great Lakes, however, larger Indian reservations contain more MOG, higher biomass, and better sustain biodiversity than surrounding public lands (Waller and Reo, 2018).

In general, for all non-federal lands, a combination of regulatory improvements and incentives could retain more MOG (Dreiss and Malcolm, 2022). This might include conservation easements, fee-title acquisitions, and carbon offsets that result in verifiable conservation gains over *status quo* management. Our MOG assessment may also provide procurement guidance to the private sector regarding avoiding logging in older forests, as, for example, a recent shareholder resolution at the Home Depot chain to purchase wood not coming from old-growth forests[16] (accessed May 20, 2022).

Data and model limitations

A limitation of our modeled forest structural maturity is that it does not directly provide a measure of forest stand age. Such an effort would need to cross-walk our modeled MOG areas with on-the-ground forest plot metrics derived from the FIA dataset. However, our structural maturity levels (Young, Intermediate, and MOG) overlap well with the FIA Structural Stage Classification levels (Pole, Mature, and Late) and are reasonably indicative of forest age classes.

We assumed that for a given Forest Type Group in a given ecoregion, the level of maturity would be monotonically related to increasing canopy cover, canopy height and biomass. An initial visual inspection of the modeled forest maturity map identified two landscape settings where the forest was likely erroneously assigned a younger structural class. One was forests bordering the alpine zone that naturally have a sparser and shorter canopy and support lower biomass stocks compared to a similar type at a lower elevation. Less obviously, are forests in climatically drier ecoregions on exposed topographic positions that naturally would be sparser, shorter and have less biomass than similar forest types nearby with higher site productivity (McKenney and Pedlar, 2003). The Oak/Hickory Forest Type Group also had some anomalous results with lower-than-expected areas of Young forest. This is likely the result of substantial wildfire suppression in these fragmented forests across their range (Nowacki and Abrams, 2008).

The Forest Type Groups, stratified by United States Ecoregions Level III, were used to represent the major differences in forest ecosystems. However, as these Groups are only intended to indicate broad distribution patterns of forest cover in the United States, modeled with an overall accuracy of 65% (Ruefenacht et al., 2008). They represent a highly generalized level of ecological organization within which resides a rich forest biodiversity that encompasses a range of natural variability in tree growth rates due to local physical environmental conditions that means in some locations there can be a mismatch between stand development and forest structure.

Discretion should be taken when interpreting the MOG water overlay given the differing spatial scale of input datasets. The relative importance to surface drinking water dataset is provided at the scale of subwatersheds, which vary in size and shape as their bounds are largely determined by topographic and hydrologic features of the landscape (USGS et al., 2013). So, while we presented the water importance overlay at 30-m resolution, the masked values are from the coarser dataset, meaning there may be some fine-scale variation missed. There may also be some correlation between MOG area and areas highly valuable for surface drinking water, as the layer incorporates forest metrics including forest cover, forest ownership and insect and disease risk (Mack et al., 2022). Given that the index incorporates many other non-forest variables, the impact of this correlation is likely minimal.

Finally, we did not assess the critical landscape and climate refugia role that larger and more continuous MOG (e.g., IRAs) play in a rapidly changing climate, including enabling species movements (i.e., connectivity up and down elevation, northern latitudinal shifts) and providing minimum critical areas for apex predators and other area and climate sensitive species.

Conservation recommendations

President Biden's Executive Order (White House, 2022) for forests aims to "institutionalize climate-smart management and conservation strategies that address threats to mature and old-growth forests on Federal lands." Mature forests, which include the old-growth forest class, provide superior values compared to logged forests as natural climate solutions (Griscom et al., 2017; Moomaw et al., 2019) in meeting both White House (2021, 2022) executive orders. Moreover, the 30 × 30 executive order includes all lands and waters—and not just federal—that require a combination of conservation measures to achieve this target (e.g., in regions with little federal lands such as the eastern region). However, the current *status quo* management of MOG and low protection levels on all lands presents unacceptable risks at a time when the global community is seeking ways to reduce the rapidly accelerating biodiversity and climate

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[16] https://ir.homedepot.com/~/media/Files/H/HomeDepot-IR/2022/2022%20Proxy%20Statement%20-%20Final.pdf

crises (Ripple et al., 2021). While our analysis presented three target scenarios of 30, 50, and 100% protection, there are climate, biodiversity, and drinking water benefits for choosing the upper bound 100% target for MOG on federal lands with additional measures on non-federal lands to compliment a federal reserve system anchored in MOG. The IRA component of MOG includes remaining relatively intact forest blocks that would benefit from elevating the GAP status of IRAs through enhanced protective measures. One way to do this would be to introduce national rulemaking that protects all remaining federal MOG in and out of IRAs. We note that the White House (2022) also calls for prioritizing the restoration of old-growth forests as "climate-smart forest stewardship." In our view, this can include allowing mature forests to grow into old growth structurally over time as in the Eastern region in order to begin restoring the national and regional deficits in old-growth forests. It can also mean restoring the beneficial role of wildfires in maintaining diverse understories in fire-adapted older forests such as many dry mixed conifer, oak-hickory, and open pine systems (e.g., long-leaf pine wiregrass). Typically, MOG that have experienced severe natural disturbance are logged, including within administrative reserves (such as late-successional reserves under the Northwest Forest Plan in the Pacific Northwest) and even within IRAs. However, we recommend protections extend through post-disturbance successional stages to allow forests to recover carbon stocks (proforestation, Moomaw et al., 2019) and because most carbon in severe disturbances simply transfers from live to dead pools and soils (Law et al., 2021).

A large-scale effort to protect MOG nationwide, including all primary and old-growth forests within the highest end of the mature forest spectrum, would help the United States meet a range of multilateral commitments related to protecting and restoring ecosystem integrity. Ecosystem integrity has long been a bedrock principle in the United Nations, recognized in both the Rio Declaration and Agenda 21, and were agreed to in 1992 at the United Nations Conference on Environment and Development (UNCED) (the 'Earth Summit'). The UNFCCC's Paris Agreement (UNFCCC 1/CP.21), agreed in 2015, carried forward the concept of ecosystem integrity in its preamble, and more recently the Intergovernmental Panel on Climate Change's 6th Assessment Report made numerous references to the fundamental importance of primary forests, ecological restoration and ecosystem integrity (Intergovernmental Panel on Climate Change [IPCC], 2022). Similarly, the Convention on Biological Diversity also recognizes the importance of primary forests and ecosystem integrity *via* decisions 14/5 and 14/30 agreed in 2018 at its 14th Conference of the Parties. The United Nations Strategic Plan for Forests 2030 (ECOSOC Resolution 2017/4), which builds on the 2007 UN Forest Instrument (A/RES/62/98 and A/RES/70/199), emphasizes ending deforestation and preventing forest degradation as key globally priorities. The United Nations global decade on restoration was launched in 2021, following on the 2011 Bonn Challenge, with a target of 350 million ha of restoration, including a pledge of 15 million ha from the United States. The UN Sustainable Development Goals also has a goal of halting and reversing land degradation (United Nations, 2022). Finally, 95 nations, including the United States, recently agreed to support the 30 × 30 initiative as part of their COP15 Convention on Biological Diversity obligations in June 2022. Mature and old-growth forest inventories (White House, 2022) provide a foundation for introducing much needed policies that are based on the upper bound full protection for MOG, which would allow the United States to fulfill its international obligations as a leader in the global effort to end forest degradation and deforestation.

Data availability statement

The datasets presented in this study can be found in online repositories and on matureforests.org; accessed September 9, 2022. The names of the repository/repositories and accession number(s) can be found in the article/**Supplementary material**.

Ethics statement

Written informed consent was obtained from the individual(s) for the publication of any identifiable images or data included in this article.

Author contributions

BR contribute to the development of the article's methods that were added per reviewers request for more on the methodology – the methods were greatly expanded in the article and the online **Supplementary material**. All authors contributed to its completion.

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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

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.979528/full#supplementary-material

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Article

An Ecoregional Conservation Assessment for the Southern Rocky Mountains Ecoregion and Santa Fe Subregion, Wyoming to New Mexico, USA

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Abstract: We conducted a multi-scaled Ecoregional Conservation Assessment for the Southern Rockies (~14.5 M ha) and its trailing edge, the Santa Fe Subregion (~2.2 M ha), from Wyoming to New Mexico, USA. We included a representation analysis of Existing Vegetation Types (EVTs), mature and old-growth forests (MOG), and four focal species—Canada lynx (*Lynx canadensis*), North American wolverine (*Gulo gulo luscus*), Mexican spotted owl (*Strix occidentalis lucida*), and northern goshawk (*Accipiter gentilis*)—in relation to 30 × 30 and 50 × 50 conservation targets. To integrate conservation targets with wildfire risk reduction to the built environment and climate change planning, we overlaid the location of wildfires and forest treatments in relation to the Wildland–Urban Interface (WUI) and included downscaled climate projections for a lower (RCP4.5) and higher (RCP8.5) emission scenario. Protected areas were highly skewed toward upper-elevation EVTs (most were >50% protected), underrepresented forest types (<30% protected), especially MOG (<22% protected) and riparian areas (~14% protected), and poorly represented habitats (<30%) for at least three of the focal species, especially in the subregion where nearly all the targets underperformed compared to the ecoregion. Most (>73%) forest-thinning treatments over the past decade were >1 km from delineated WUI areas, well beyond the distance at which vegetation management can effectively reduce structure ignition risk (<50 m from structures). Extreme heat, drought, snowpack reductions, altered timing of peak stream flows, increasing wildfires, and potential shifts in the climate, favoring woodlands over conifer forests, may impact forest-dependent species, while declining snowpack may impact wolverines that den at upper elevations. Strategically targeting the built environment for fuel treatments would improve wildfire risk reduction and may allow for expansion of protected areas held up in controversy. Stepped-up protection for roadless areas, adoption of wilderness proposals, and greater protection for MOG and riparian forests are critical for meeting representation targets.

Keywords: biodiversity; climate change; ecoregion; conservation; Santa Fe; Southern Rockies

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1. Introduction

The Southern Rocky Mountains Ecoregion (SRME) spans ~14.5 M ha of a rugged terrain characterized by abrupt transitions from many of the tallest peaks (>3660 m) in North America to expansive lowland valleys, primarily within portions of southern Wyoming, central and western Colorado, and northern New Mexico, USA [1,2]. A prominent feature is the Continental Divide that splits the Pacific (to the west) and Atlantic (to the east) drainages. The beta diversity of fauna and flora is especially pronounced across elevational life zones, with distinct shifts in species assemblages traversing lower montane/foothills, upper montane, subalpine, and alpine areas [1,3]. The World Wildlife Fund considered the ecoregion the Colorado Rockies Forests (Ecoregion #45) and ranked it "bioregionally outstanding" and "relatively stable" due mainly to large intact areas, including national parks, wilderness areas, and Inventoried Roadless Areas (IRAs) [1,4]. NatureServe listed the ecoregion as the Southern Rocky Mountain Montane Forest & Woodland Macrogroup [M022] [5]. The USDA Forest Service identified five distinct subsections, including the Northern Parks and Ranges, South-Central Highlands, Northern-Central Highlands and Rocky Mountains, Southern Parks and Rocky Mountain Ranges, and Northern Rio Grande Basin [3]. Within the SRME, some 184 plant and animal species are endemic, 100 are globally imperiled (G1–G2), 23 are listed under the Endangered Species Act, and 7 have been extirpated [1,3]. Importantly, species reintroductions have taken place in portions of the ecoregion, including the Mexican gray wolf (*Canis lupus*), bison (*Bison bison*), black-footed ferret (*Mustela nigripes*), river otter (*Lutra canadensis*), and Canada lynx (*Felis lynx canadensis*, in Colorado), with a wolverine (*Gulo gulo luscus*) reintroduction program recently approved in Colorado that will begin soon (Colorado Senate Bill 24-171; https://leg.colorado.gov/bills/sb24-171 (accessed on 25 May 2024)).

Large-scale conservation proposals (e.g., 30% protected by 2030, "30 × 30"; 50% protected by 2050, "50 × 50") [6] are a cornerstone of conservation biology approaches worldwide [7], as well as of long-standing conservation efforts in this ecoregion [1,3,8,9]. For instance, The Nature Conservancy identified 188 conservation priority areas, totaling 50% of the SRME, to meet conservation goals of targeted species and natural and ecological systems [3]. In the Southern Rockies, protected areas may function as important climate refugia with relatively low climate velocities compared to their developed surroundings [9], especially where there are large roadless area complexes, wilderness areas, and national parks [1,8].

Notably, the trailing edge of ecoregions may be especially vulnerable to higher climate velocities because species assemblages and climatic conditions are at their margins. A case in point is the Santa Fe Subregion (SFSR) at the southern edge of the SRME that climatically differs from most of the ecoregion via seasonal monsoons that affect natural disturbance dynamics. Climate change-related shifts in monsoon delivery may affect the onset and length of the wildfire season [10]. The SFSR also includes a dense population center nearby, Santa Fe, that has experienced periodic wildfires in the surroundings, with some wildfires spilling into nearby communities that abut the two primary national forests in this subregion: the Santa Fe and Carson (a small portion of the Rio Grande National Forest in Colorado is also included in the SFSR). The Santa Fe National Forest is close to numerous homes in harm's way of wildfires. The overwhelming response by the USDA Forest Service has been unprecedented: aerial fire suppression, along with expansive forest thinning and burning proposed by researchers (e.g., prescribed fire and pile burning), [11–14] as well as road building to access sites for vegetation management.

There is scientific debate and public controversy about whether such aggressive fuel-reduction treatments are an effective strategy in a changing climate [15], particularly considering the cumulative ecosystem damages associated with some of the treatments [16], whether too much forest biomass is being removed and too frequently [17], or whether fire-risk reduction for communities should instead target areas closest to homes [18,19], the smoke and human health risks of frequent and extensive prescribed burns, and prescribed fires that sometimes escape containment (e.g., Calf Canyon/Hermit's Peak fire of 2022) [20]. Importantly, The Nature Conservancy identified ~46% of the Santa Fe National Forest as a priority for coarse and fine-filter conservation [21]. However, little progress has been made toward these broader conservation targets, mainly due to the controversy over forest management and wildfires.

Our objective is to present a multi-scaled Ecoregional Conservation Assessment (ECA) that incorporates the conservation needs of both the larger SRME and the SFRS nested within it. Multi-scaled ECAs are necessary to ensure that a particular area of interest (subregion) is contextually analyzed for its relative conservation contributions within the backdrop of climate change, forest management, and wildfires. It is also necessary to demonstrate that large-scale conservation (e.g., priority areas, focal species distributions) can be compatible with wildfire risk reduction in the built environment and climate change planning.

We selected the Canada lynx, a federally threatened species under the U.S. Endangered Species Act; wolverine, federally threatened; northern goshawk (*Accipiter gentilis*), a USDA Forest Service "sensitive species;" and Mexican spotted owl (*Strix occidentalis lucida*), federally threatened, to represent a mixture of forest conservation and landscape connectivity needs at the two spatial scales (ecoregion, subregion), and to compare levels of protection of these focal species between the two scales using 30% and 50% targets. ECAs that include both landscape and focal species can be useful in advancing conservation proposals in regions facing multiple threats from development, wildland fires affecting towns, climate change, and controversial forest management practices. Our ECA approach to the SRME builds on a related ECA for the Mogollon Highlands in Arizona, just to the southeast, which are facing some of the same conflicts over protection vs. forest management and wildfire risks [22]. ECAs like these may provide a means to advance conservation in high fire-risk environments where protected area proposals have stalled due to land-management agencies and/or elected official calls for increased forest management via logging, burning, and road building.

2. Materials and Methods

2.1. Study Area

We used the Environmental Protection Agency (EPA) Level III ecoregional classifications, as others have used [2], to map the SRME study area (i.e., EPA Ecoregion 21) and overlaid a climate change projection boundary based on the study area's grid coordinates in the Climate Toolbox online portal (climatetoolbox.org (accessed on 3 May 2024)) (Figure 1). The study area boundary was confirmed by regional experts in a May 2024 workshop. For the purpose of a continuous ecoregional analysis, we did not include small, isolated fragments in Utah that are, despite their discontinuity, considered part of EPA Ecoregion 21.

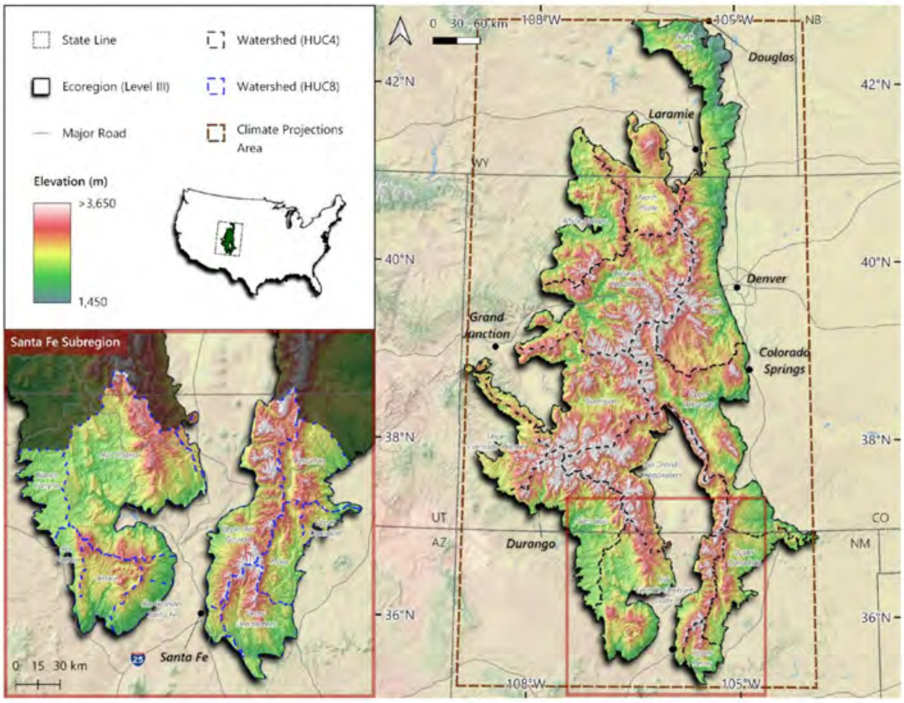

Figure 1. Southern Rocky Mountains Ecoregion showing elevation, HUC4 watersheds at the ecoregion scale, HUC8 watersheds at the Santa Fe subregion scale, and the climate change projection area rectangle derived using the Climate Toolbox (https://climatetoolbox.org (accessed on 3 May 2024)). See Table S1 for HUC8 watersheds.

Watershed boundaries were overlaid on the study area using 4-digit Hydrologic Unit Codes [HUCs] [23] for the ecoregion and 8-digit HUCs for the SFSR in order to provide the necessary detail for a scaled analysis. We delineated the SFSR as the 10 southernmost 8-digit HUCs in the SRME (Table S1) (Figure 1). All spatial analyses were conducted at both the SRME and SFSR scale. Based on our mapping approach, the SRME totaled 14,475,519 ha and the SFSR totaled 2,188,050 ha (~15% of the SRME) (Figure 1).

We clipped all spatial datasets to the study area and re-projected to a CONUS Albers projection (EPSG:5070) using QGIS version 3.36 (https://qgis.org; accessed on 10 May 2024). To reduce processing time, we converted most of our vector datasets to 30 m raster datasets aligned with LANDFIRE (2022, LF 2.3.0) rasters, such as the elevation dataset that we used to create Figure 1. This allowed us to combine rasters representing different metrics, each having a set of unique pixel values corresponding to surface ownership, vegetation type, forest structure class, etc. The only exceptions to this raster approach were our analyses involving wolverine habitat connectivity as well as the analyses involving USDA Forest Service thinning activities, which were both conducted using clipped vector datasets.

2.2. Landowners and GAP Status

For the Wyoming and New Mexico portions of the SRME, we used surface landowner data from the PAD-US 3.0. For the Colorado portion of the SRME (which comprises the majority of the ecoregion), we extracted landowner data from the Colorado Ownership Management and Protection Map (COMaP, v20230223), as it has greater accuracy than the PAD-US across the state. We grouped landowner polygons into nine ownership categories for all analyses that involved surface ownership. We also included the National Forest Boundaries from the USDA Forest Service Enterprise Data Warehouse, as described in DellaSala et al. [22].

We extracted U.S. Geological Survey (USGS) GAP Analysis Project (GAP) status codes 1–4 from the USGS Protected Areas Database (PAD), supplemented with data from the National Conservation Easement Database (NCEDB). USGS Gap Status Codes are assigned status codes based on degrees of protection, with GAP 1 (permanent protection, e.g., designated wilderness and national parks) and GAP 2 (maintained primarily in natural state, e.g., national monuments and wildlife refuges) having the highest protection vs. GAP 3 (extractive use) and GAP 4 (private lands with no protections) (see https://d9-wret.s3.us-west-2.amazonaws.com/assets/palladium/production/s3fs-public/atoms/files/GAP%20Status%20Code%20Assignment_2021.pdf (accessed on 1 August 2024)). We combined USDA Forest Service IRA data from the national dataset (2001 Roadless Area Conservation Rule) for IRAs in New Mexico and Wyoming and from the 2012 Colorado Roadless Rule dataset for IRAs in Colorado (https://www.fs.usda.gov/main/roadless/coloradoroadlessrules (accessed on 10 May 2024)). The Colorado Roadless Rule differs from the 2001 national rule as it classified portions of IRAs as either "upper tier" or "non-upper tier". Upper-tier IRAs have even greater protection than those under the national rule (e.g., in Wyoming or New Mexico), so we assigned upper tiers as GAP 2. We assigned IRAs in Wyoming and New Mexico as well as non-upper-tier IRAs in Colorado as GAP 2.5, as these areas have enhanced protection beyond what is typical for GAP 3 lands (see [22]). Because the PAD-US data combined with IRA and NCEDB data include overlapping polygons, our final GAP status dataset represents the lowest GAP status code (i.e., the highest level of protection) for any given area. Any areas outside of this combined dataset were assigned GAP 4. We combined the final GAP status rasters with rasters for the metrics below to determine the proportion of each area (e.g., Canada lynx suitable habitat) in each GAP status.

We obtained wilderness area boundaries in several proposed federal legislation efforts that we had spatial data for, including the Colorado Wilderness Act, Colorado Outdoor Recreation and Environment Act, Gunnison Outdoor Resources Protection Act, and the Sarvis Creek Wilderness Completion Act (a total of 210,486 ha proposed as wilderness in these bills). We created a separate GAP status dataset with existing wilderness boundaries adjusted and new wilderness areas added, assuming all these bills were signed into law. We then calculated the GAP status distribution across the SRME and SFSR under this scenario.

2.3. Existing Vegetation Types (2020 Update)

We accessed Existing Vegetation Type (EVT) data for the study area using LANDFIRE (2022, LF 2.3.0), which represents the current distribution of terrestrial ecological systems, developed by NatureServe for the western hemisphere. There were 97 EVTs within the SRME (Table S2), which we grouped into 19 broader categories, with a focus on the forest types most likely used by our focal species, including alpine, aspen (*Populus* spp.) and mixed-conifer forest, aspen forest and woodland, lodgepole pine (*Pinus contorta)* forest, mixed-conifer forest, pinyon (*Pinus* spp.)–juniper (*Juniperus* spp.), ponderosa pine, and subalpine forest. The EVTs within the SFSR were generally similar to those of the ecoregion described by Vander Lee et al. [21], with some noted exceptions such as the lack of lodgepole pine forest and limber pine woodland.

Characteristic tree species in the study area include Engelmann spruce (*Picea engelmannii*), blue spruce (*Picea pungens*), subalpine fir (*Abies lasiocarpa*), Rocky Mountain Douglas fir (*Pseudotsuga menziesii var. glauca*), Rocky Mountain white fir (*Abies concolor subsp. concolor*), Rocky Mountain bristlecone pine (*Pinus aristata*), limber pine (*Pinus flexilis*), lodgepole pine, ponderosa pine (*Pinus ponderosa*), Colorado pinyon pine (*Pinus edulis*), Rocky Mountain juniper (*Juniperus scopulorum*), and gambel oak (*Quercus gambelii*). Interestingly, southwestern white pine (*Pinus strobiformis*) and limber pine commingle at or near the limits of their geographical ranges to form a unique hybrid zone in the SFSR [24]. Riparian areas are characterized by abundant forbs and shrubs (when not grazed by cattle), narrowleaf cottonwood (*Populus angustifolia*), quaking aspen (*Populus tremuloides*), plains cottonwood (*Populus deltoides*), peachleaf willow (*Salix amygdaloides*), Rocky Mountain maple (*Acer grandidentatum*), and thinleaf alder (*Alnus tenuifolia*) (see [4]). Alpine zones (above tree line) support a variety of shrubs, wildflowers, krummholz (stunted trees) and many non-vascular plants on exposed rocks [2].

2.4. Mature and Old-Growth Forests (MOG)

We obtained spatial datasets on mature and old-growth (MOG) forest distributions from DellaSala et al. [25], who used three proxies to define MOG forests at 30 m resolution: tree height, canopy coverage, and above-ground biomass. As in DellaSala et al. [25], we grouped the nine forest structure classes in this dataset into three broader categories: young, intermediate, and mature forests. Because some of the proxy data used to create the original MOG dataset were obtained several years prior, we determined that the dataset needed to be screened for relatively recent high-severity fire events to ensure that we did not consider areas with greater than about 75% tree mortality from fire as MOG. We extracted high-severity fire data from the four-class composite burn index (CBI-4) annual mosaics, 2012 through 2023, in the USDA Forest Service Rapid Assessment of Vegetation Condition after Wildfire (RAVG) database and censored out any overlapping MOG pixels from our final analyses and maps (https://burnseverity.cr.usgs.gov/ravg/data-access (accessed on 14 April 2024)).

Using the RAVG mosaics allowed us to include fire severity data from the 2022 Hermits Peak/Calf Canyon Fire, which burned a substantial portion of the SFSR but which was not yet included in the Monitoring Trends in the Burn Severity (MTBS) dataset. Data for some fires in the earlier years of the annual mosaic range were affected by the Landsat 7 Scan Line Corrector error. Any areas within the mosaics that were within the swaths lacking data due to this well-known error were also censored from the final MOG dataset.

2.5. Focal Species

2.5.1. Wolverine

Wolverines occupy isolated subalpine areas at low population densities and have been used to model metapopulation dynamics and landscaped connectivity with dispersing animals following low-resistance pathways that connect high-quality habitats [26]. We used a habitat connectivity dataset provided by Carroll et al. [26] via Data Basin, who used Circuitscape 4.0 to produce habitat connectivity scores for the western USA at an approximately 25 km resolution. We clipped this raster dataset to the SRME, then extracted the raster pixels with connectivity scores at the 90th percentile or above and again at the 95th percentile or above for the ecoregion. We converted these two sets of extracted pixels to vector formats and then clipped our GAP vector layer to them and calculated the GAP distribution for each dataset (GAP refers to the U.S. Geological Survey Gap Analysis Project; https://www.usgs.gov/programs/gap-analysis-project (accessed on 1 August 2024)). We repeated this again for the SFSR, but the 90th and 95th percentile values were still based on the entire SRME.

2.5.2. Canada Lynx, Northern Goshawk, and Mexican Spotted Owl

Canada lynx use mid-elevation boreal and subalpine zones with deep snowpack, selecting forests with a high proportion of beetle-killed large trees and with extensive horizontal cover, used by its principal prey species, the snowshoe hare (*Lepus americanus*) [27]. Northern goshawks select mature forests with large trees and extensive canopy closure [28] and in parts of their range will nest in dense aspen and lodgepole pine forests [29]. The Mexican spotted owl typically uses forests with extensive canopy cover in mixed-conifer and pine-oak forests and woodlands and is known to be sensitive to habitat fragmentation [30].

We used the 2001 GAP Analysis Project habitat suitability dataset (30 m resolution) for each of the three species. Because of the age of these datasets, we censored out any suitable habitat pixels that had experienced high-severity fire from 2001 to 2023, which is a conservative approach that ensures suitable habitat distribution was not overestimated. We extracted high-severity pixels from RAVG annual mosaics for the 2012–2023 period, as described in the MOG section above. We then extracted the high-severity class of pixels from the MTBS annual fire severity raster mosaics for the 2001–2011 period (RAVG data were not available for the region prior to 2012) and combined these with the high-severity fire pixels from the RAVG dataset to create a mask layer that we used to censor out any suitable habitat pixels in the 2001 GAP Analysis datasets. We combined our censored habitat suitability datasets with the GAP status datasets for both the SRME and SFSR to calculate the GAP status distributions for each species' total area of suitable habitat.

2.6. Wildland–Urban Interface/Intermix (WUI), Wildfires, and Forest Thinning

We extracted the six 2020 categories of WUI areas from the national WUI dataset produced by Radeloff et al. [31]: low-density intermix, medium-density intermix, high-density intermix, low-density interface, medium-density interface, and high-density interface. We rasterized the dataset as we had with the other datasets above and combined it with our GAP status raster for both the SRME and SFSR.

We extracted all wildfires from the MTBS national dataset from 1984 to 2022, amended with the final fire perimeter for the 2022 Hermits Peak/Calf Canyon Fire, and then dissolved these perimeters to delineate the portions of the SRME and SFSR that burned at least once during that time period. We did not analyze fire severity distributions as that was beyond the scope of this study. We rasterized the fire footprint data as described previously and combined it with our GAP status raster as well as our WUI raster. We also created a raster denoting existing wilderness, upper-tier IRAs in Colorado, and non-upper-tier Colorado IRAs, as well as IRAs in Wyoming and New Mexico, and then combined this with the fire footprint raster.

To determine where mechanical thinning operations have been taking place on national forest land in the SRME and SFSR relative to WUI areas, we extracted from the USDA Forest Service's Forest Activities Tracking System (FACTS) database (https://data.fs.usda.gov/geodata/edw/datasets.php (accessed on 18 April 2024)) all activity polygons with a completion date during or after 2014 and before 2024 and which had a treatment type of "thinning" in the hazardous fuels dataset in FACTS, or an activity name of "commercial thinning" in the timber harvest dataset in FACTS, or an activity name of "precommercial thinning" in the timber stand improvement dataset in FACTS. We merged and dissolved these polygons to delineate the 2014–2023 mechanical thinning footprint in national forests across the SRME and SFSR. Next, we dissolved our WUI dataset and added to it four buffer zones at 250 m increments from the edge of any WUI outer boundary. We then intersected our thinning footprint vector dataset with these buffer zones to determine the area and percentage that was conducted within 250 m, 500 m, 750 m, 1 km, and >1 km of a WUI area.

2.7. Downscaled Climate Projections

The extreme topographic relief of the Rockies (Figure 1) drives much of the climatic variability within the SRME. The climate is considered a temperate semiarid steppe regime with annual average temperatures ranging from 1.6 °C to 7.2 °C, reaching 10 °C in low-lying valleys [3]. Eastern slopes are much drier due to the montane rain-shadow. Late-summer monsoonal precipitation is characteristic of the SFRS [10]. Overall annual precipitation ranges from <254 mm at the base of mountains to >1.4 m at higher elevations, primarily as snowfall [3].

We used the Climate Toolbox online portal (https://climatetoolbox.org (accessed on 3 May 2024)), which includes a collection of web tools visualizing past and present climate and vegetation of the contiguous USA, to project potential climate change scenarios for the study area. Methods, data, and sources for the many different tools are available on the Climate Toolbox website. We calculated historical trends using the "Historical climate tracker" tool, delineated with a rectangle that encompassed the entire study area (see Figure 1). For future climate trend projections across the study area, we input a custom shapefile in the Climate Toolbox portal. In general, future projections were more precisely delineated than historical climate assessment.

Historical values were calculated using the gridMET dataset, which is a gridded surface meteorological dataset covering the continental USA from 1979 to the present, mapping surface weather variables at ~4 km spatial grain [32]. Future projections were produced using a Multivariate Adaptive Constructed Analogs (MACA) version 2 output, based on an ensemble of 20 GCMs (bcc-cs1-1, bcc-csm1-1-m, BNU-ESM, CanESM2, CCSM4, CNRM-CN5, CSIRO-Mk3-6-0, GFDL-ESM2M, GFDL-ESM2G, HADGem2-CC365, HADGem2-ES365, inmcm4, IPSL-CM5A-LR, IPSL-CM5A-MR, IPSL-CM5B-LR, MIROC5, MIROC-ESM, MIROC-ESM-CHEM, MRI-CGCM3, NorESM1-M) and 2 scenarios (RCP 4.5 and 8.5) that were downscaled to a ~4 km resolution for compatibility with the gridMET data [32].

We accessed output from the MC2 dynamic global vegetation model [33,34] through the Climate Toolbox Future Vegetation web tool. MC2 was forced with downscaled MACAv2-PRISM data. Historical and future vegetation data, which are sourced from the Integrated Scenarios Project (https://d2k78bk4kdhbpr.cloudfront.net/media/content/files/Integrated_Scenarios_Draft_Final_Report_2014-06-30_V2-1_1.pdf (accessed on 23 March 2024)) were used to simulate potential vegetation changes based on climate variables. The high uncertainty of these projections stems from numerous non-modeled factors such as species dispersal capabilities, competition among species, and natural successional dynamics.

We accessed streamflow projections through the Climate Toolbox Future Streamflows web tool, also sourced from the Integrated Scenarios Project (https://d2k78bk4kdhbpr.cloudfront.net/media/content/files/Integrated_Scenarios_Draft_Final_Report_2014-06-30_V2-1_1.pdf (accessed on 3 May 2024)). Streamflow data were generated from the non-regulated stream routing of VIC (version 4.1.2) hydrologic outputs, utilizing a large-scale river-routing scheme [35] and forced with MACAv2-LIVNEHv13 downscaling of the CMIP5 global climate model outputs.

3. Results

3.1. Landownerships and Gap Status

Nearly half (48.5%) of the 14.5 M ha SRME is managed by the USDA Forest Service; 34% is private surface ownership, 8.2% is managed by the U.S. Bureau of Land Management (BLM), 3.9% is by various state agencies, 2.9% is by Native American tribes, 1.3% is by the National Park Service, and the remainder is managed by multiple agencies and entities (Figure 2, Table 1). Landownership distribution is similar in the SFSR (e.g., 46.3% is managed by the USDA Forest Service), with the exception of distinctly more tribal ownership (12.1%) and the complete lack of BLM land (Table 1 vs. Table 2).

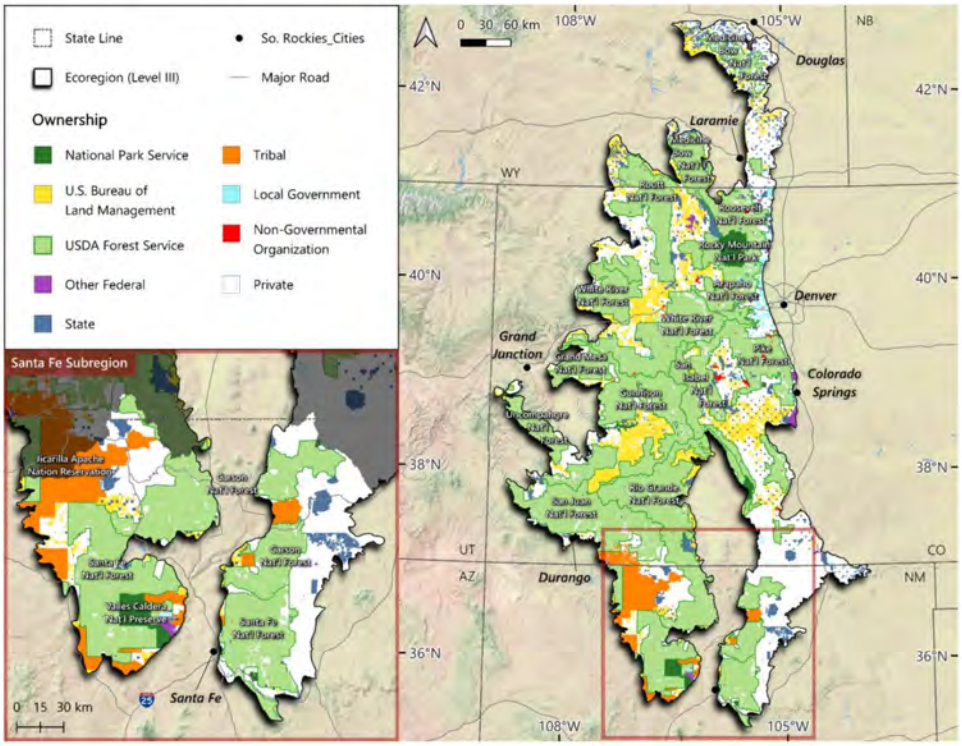

Figure 2. Surface ownership distribution across the Southern Rocky Mountains Ecoregion and Santa Fe Subregion, Wyoming to New Mexico.

Table 1. Landownerships and GAP status for the Southern Rocky Mountains Ecoregion.

	Southern Rocky Mountains Ecoregion					
Owner Category	**GAP ha**					**Total Owner Category ha**
	(%)					
	1	**2**	**2.5**	**3**	**4**	**(%)**
National Park Service	139,643 (72.3)	40,539 (21.0)	1 (0.0)	8684 (4.5)	4302 (2.2)	193,170 (1.3)
U.S. Bureau of Land Management	20,911 (1.8)	104,967 (8.8)	143 (0.0)	1,059,753 (88.8)	7847 (0.7)	1,193,622 (8.2)
USDA Forest Service	1,486,778 (21.2)	510,940 (7.3)	1,396,938 (19.9)	3,614,900 (51.5)	9478 (0.1)	7,019,033 (48.5)
Other Federal [1]	20 (0.0)	10,866 (21.6)	0 (0.0)	497 (1.0)	39,025 (77.4)	50,408 (0.3)
State	79 (0.0)	52,332 (9.4)	353 (0.1)	303,385 (54.3)	202,997 (36.3)	559,145 (3.9)

Table 1. *Cont.*

	Southern Rocky Mountains Ecoregion					
Owner Category	**GAP ha**					**Total Owner Category ha**
	(%)					
	1	**2**	**2.5**	**3**	**4**	**(%)**
Local Government	1284 (1.5)	24,838 (28.3)	43 (0.0)	8924 (10.2)	52,801 (60.1)	87,889 (0.6)
Tribal	1 (0.0)	274 (0.1)	64 (0.0)	174 (0.0)	413,551 (99.9)	414,064 (2.9)
Non-Governmental Organization	128 (0.4)	22,579 (70.2)	10 (0.0)	2263 (7.0)	7185 (22.3)	32,165 (0.2)
Private	2326 (0.0)	209,099 (4.2)	2174 (0.0)	108,796 (2.2)	4,603,628 (93.5)	4,926,023 (34.0)
Total GAP ha (%)	1,651,170 (11.4)	976,433 (6.7)	1,399,726 (9.7)	5,107,376 (35.3)	5,340,813 (36.9)	14,475,519

[1] Includes U.S. Army Corps of Engineers, U.S. Bureau of Reclamation, U.S. Department of Agriculture (non-Forest Service), U.S. Department of Defense, U.S. Department of Energy, U.S. Department of Interior (non-Bureau of Land Management, non-National Park Service, non-Fish and Wildlife Service), and U.S. Fish and Wildlife Service.

Table 2. Landownerships and GAP status for the Santa Fe Subregion.

	Southern Rocky Mountains Ecoregion					
Owner Category	**GAP ha (%)**					**Total Owner Category ha**
	1	**2**	**2.5**	**3**	**4**	**(%)**
National Park Service	12,605 (24.6)	38,609 (75.4)	0 (0.0)	0 (0.0)	0 (0.0)	51,214 (2.3)
U.S. Bureau of Land Management	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
USDA Forest Service	162,852 (16.1)	10,581 (1.0)	99,897 (9.9)	740,343 (73.0)	36 (0.0)	1,013,710 (46.3)
Other Federal [1]	1 (0.0)	8003 (13.3)	2 (0.0)	41,924 (69.6)	10,287 (17.1)	60,217 (2.8)
State	0 (0.0)	31,818 (44.7)	1 (0.0)	8781 (12.3)	30,634 (43.0)	71,234 (3.3)
Local Government	0 (0.0)	2 (0.3)	1 (0.1)	0 (0.0)	893 (99.6)	897 (0.0)
Tribal	1 (0.0)	274 (0.1)	64 (0.0)	45 (0.0)	264,245 (99.9)	264,630 (12.1)
Non-Governmental Organization	0 (0.0)	215 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	215 (0.0)
Private	86 (0.0)	1272 (0.2)	380 (0.1)	7311 (1.0)	716,884 (98.8)	725,933 (33.2)
Total GAP ha (%)	175,546 (8.0)	90,775 (4.1)	100,345 (4.6)	798,404 (36.5)	1,022,980 (46.8)	2,188,050

[1] Includes U.S. Army Corps of Engineers, U.S. Bureau of Reclamation, U.S. Department of Agriculture (non-Forest Service), U.S. Department of Defense, U.S. Department of Energy, U.S. Department of Interior (non-Bureau of Land Management, non-National Park Service, non-Fish and Wildlife Service), and U.S. Fish and Wildlife Service.

Notably, only 18.2% and 12.1% of the SRME and SFSR, respectively, are within designated protected areas (GAP 1 and 2) (Tables 1 and 2). With stepped-up protection for

IRAs (i.e., IRAs+), protection levels would rise to 27.8% for the SRME, which is close to the 30 × 30 target but considerably below the 50 × 50 target (Table 1). The SFRS is even further below both targets with just 16.8% if IRAs+ were added (Table 2). Even if all currently proposed wilderness (210,486 ha) areas in Colorado were signed into law, protection levels would only marginally increase across the SRME (18.9% or 28.2% with IRA+ added). The SFSR would not see any changes as none of the lands are included in any of the wilderness proposals for which we had spatial datasets.

The USDA Forest Service, the major landowner within the SRME, has protected just 28.5% of its lands across the ecoregion, with an additional 19.9% within IRAs+, which would approach (48.4% total) the 50 × 50 target. In contrast, the agency has protected just 17.1% of national forest lands within the SFSR, with an additional 9.9% within IRAs+, which would fall below (27%) even the 30 × 30 target.

3.2. Existing Vegetation Type Representation Analysis

Not surprisingly, for both the SRME and SFRS, only the upper-elevation areas (sparse, subalpine forest, snow–ice, barren, and alpine) met either the 30 × 30 or 50 × 50 targets (Tables 3 and 4). By contrast, none of the low–mid-elevation forest types, where forest management and development are concentrated, were even close to the targets. For example, 65.9% of the alpine habitat already has GAP 1 or 2 status across the SRME, despite accounting for only 1.3% of the entire ecoregion. Similarly, 40.4% of the subalpine forest in the SRME has GAP 1 or 2 status, and this would increase to 57% with IRA+ added. However, only 5.4% of the ponderosa pine forest—which accounts for about 15.2% of the SRME—is within designated protected areas, and this number would only increase to 10.5% with IRA+ added (Table 3). Such low levels of protection for lower-elevation forests are even more apparent in the SFSR, where only 5.1% of ponderosa pine forests has GAP 1 or 2 status, despite accounting for 30.2% of the total area of the SFSR (Table 4).

Table 3. GAP status of Existing Vegetation Type categories (see Table S2 for definition of categories) for the Southern Rocky Mountains Ecoregion.

Southern Rocky Mountains Ecoregion						
Existing Vegetation Type (EVT) Category	**GAP ha (%)**					**Total EVT Category ha**
	1	**2**	**2.5**	**3**	**4**	**(%)**
Agricultural	269 (0.1)	11,263 (4.4)	1008 (0.4)	22,927 (8.9)	221,516 (86.2)	256,983 (1.8)
Alpine	90,446 (49.9)	29,059 (16.0)	22,827 (12.6)	29,109 (16.1)	9781 (5.4)	181,223 (1.3)
Aspen and Mixed-Conifer Forest	5177 (7.5)	2484 (3.6)	17,949 (26.1)	33,109 (48.2)	9966 (14.5)	68,684 (0.5)
Aspen Forest and Woodland	107,598 (8.4)	92,004 (7.2)	236,841 (18.5)	500,609 (39.1)	343,511 (26.8)	1,280,563 (8.8)
Barren	52,872 (39.6)	13,289 (10.0)	18,192 (13.6)	26,440 (19.8)	22,601 (16.9)	133,395 (0.9)
Developed	1443 (0.7)	4819 (2.2)	541 (0.2)	42,593 (19.6)	167,541 (77.2)	216,938 (1.5)
Grassland	80,727 (5.6)	95,578 (6.6)	71,477 (5.0)	386,897 (26.8)	807,428 (56.0)	1,442,106 (10.0)
Limber Pine Woodland	4 (0.1)	237 (6.1)	26 (0.7)	2165 (55.2)	1489 (38.0)	3921 (0.0)
Lodgepole Pine Forest	114,905 (13.8)	64,508 (7.8)	137,148 (16.5)	408,600 (49.2)	106,138 (12.8)	831,299 (5.7)

Table 3. *Cont.*

Southern Rocky Mountains Ecoregion						
Existing Vegetation Type (EVT) Category	**GAP ha (%)**					**Total EVT Category ha**
	1	**2**	**2.5**	**3**	**4**	**(%)**
Mixed-Conifer Forest	91,210 (7.6)	87,846 (7.3)	154,977 (12.9)	506,968 (42.1)	362,187 (30.1)	1,203,189 (8.3)
Pinyon–Juniper	18,355 (1.9)	50,682 (5.3)	36,605 (3.8)	386,388 (40.4)	463,682 (48.5)	955,712 (6.6)
Ponderosa Pine	35,994 (1.6)	83,489 (3.8)	112,688 (5.1)	842,012 (38.2)	1,130,986 (51.3)	2,205,170 (15.2)
Riparian	21,052 (8.6)	13,503 (5.5)	17,583 (7.2)	80,563 (32.8)	113,188 (46.0)	245,889 (1.7)
Shrubland	67,705 (2.7)	127,211 (5.2)	118,569 (4.8)	904,887 (36.7)	1,250,583 (50.7)	2,468,954 (17.1)
Snow–Ice	41,221 (67.2)	8151 (13.3)	2358 (3.8)	7225 (11.8)	2348 (3.8)	61,304 (0.4)
Sparse	162,830 (54.8)	35,553 (12.0)	39,627 (13.3)	43,009 (14.5)	16,005 (5.4)	297,024 (2.1)
Subalpine Forest	747,527 (30.6)	240,071 (9.8)	405,574 (16.6)	836,305 (34.3)	211,538 (8.7)	2,441,016 (16.9)
Water	3725 (5.9)	5335 (8.5)	1698 (2.7)	21,600 (34.4)	30,441 (48.5)	62,799 (0.4)
Wetland	8111 (6.8)	11,349 (9.5)	4037 (3.4)	25,971 (21.8)	69,883 (58.6)	119,351 (0.8)
Total GAP ha (%)	1,651,170 (11.4)	976,433 (6.7)	1,399,726 (9.7)	5,107,376 (35.3)	5,340,813 (36.9)	14,475,519 (100%)

Table 4. GAP status of Existing Vegetation Type categories (see Table S2 for definition of categories) for the Santa Fe Subregion.

Santa Fe Subregion						
Existing Vegetation Type (EVT) Category	**GAP ha (%)**					**Total EVT Category ha**
	1	**2**	**2.5**	**3**	**4**	**(%)**
Agricultural	40 (0.1)	455 (1.5)	101 (0.3)	1833 (6.2)	27,075 (91.8)	29,505 (1.3)
Alpine	453 (22.6)	141 (7.0)	25 (1.2)	182 (9.1)	1208 (60.1)	2009 (0.1)
Aspen and Mixed-Conifer Forest	306 (7.9)	371 (9.6)	172 (4.4)	890 (23.0)	2136 (55.1)	3875 (0.2)
Aspen Forest and Woodland	9814 (12.7)	4648 (6.0)	3495 (4.5)	30,877 (39.9)	28,563 (36.9)	77,397 (3.5)
Barren	4045 (46.2)	438 (5.0)	290 (3.3)	799 (9.1)	3185 (36.4)	8757 (0.4)
Developed	223 (0.8)	668 (2.5)	97 (0.4)	4544 (16.8)	21,545 (79.6)	27,077 (1.2)
Grassland	6756 (5.6)	11,666 (9.7)	4544 (3.8)	30,197 (25.0)	67,543 (56.0)	120,706 (5.5)

Table 4. *Cont.*

Santa Fe Subregion						
Existing Vegetation Type (EVT) Category	**GAP ha (%)**					**Total EVT Category ha (%)**
	1	**2**	**2.5**	**3**	**4**	
Limber Pine Woodland	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Lodgepole Pine Forest	0.1 (4.3)	1 (39.1)	1 (52.2)	0.1 (4.3)	0 (0.0)	2 (0.0)
Mixed-Conifer Forest	40,613 (11.2)	20,745 (5.7)	26,675 (7.4)	159,960 (44.2)	113,726 (31.4)	361,719 (16.5)
Pinyon–Juniper	13,342 (3.5)	8390 (2.2)	20,138 (5.3)	145,166 (37.9)	196,042 (51.2)	383,078 (17.5)
Ponderosa Pine	16,241 (2.5)	17,185 (2.6)	21,711 (3.3)	298,328 (45.1)	308,192 (46.6)	661,657 (30.2)
Riparian	948 (4.8)	1146 (5.8)	495 (2.5)	4920 (24.9)	12,284 (62.1)	19,793 (0.9)
Shrubland	15,066 (5.8)	13,315 (5.2)	10,137 (3.9)	64,256 (24.9)	155,022 (60.1)	257,795 (11.8)
Snow–Ice	9 (43.9)	0 (0.0)	0 (0.0)	0 (0.0)	12 (56.1)	21 (0.0)
Sparse	1206 (35.5)	146 (4.3)	271 (8.0)	650 (19.1)	1122 (33.1)	3395 (0.2)
Subalpine Forest	66,104 (31.1)	8037 (3.8)	12,129 (5.7)	53,830 (25.3)	72,629 (34.1)	212,730 (9.7)
Water	91 (1.9)	351 (7.2)	3 (0.1)	118 (2.4)	4298 (88.4)	4860 (0.2)
Wetland	289 (2.1)	3072 (22.5)	60 (0.4)	1855 (13.6)	8397 (61.4)	13,673 (0.6)
Total GAP ha (%)	175,546 (8.0)	90,775 (4.1)	100,345 (4.6)	798,404 (36.5)	1,022,980 (46.8)	2,188,050 (100.0)

Other EVT categories also have surprisingly low representation in designated protected areas. Only 7.2% and 5.7% of pinyon–juniper forests in the SRME and SFSR, respectively, have GAP 1 or 2 status (Tables 3 and 4). Shrubland habitats account for 17.1% of the SRME, but only 7.9% of these habitat types is within designated protected areas (Table 3). And importantly, only 14.1% and 10.6% of riparian EVTs in the SRME and SFSR, respectively, have a GAP status of 1 or 2 (Tables 3 and 4). With IRAs+, riparian protection would increase to 21.3% and 13.1% in the SRME and SFSR, respectively, which are still well below even the 30 × 30 target.

3.3. Mature and Old-Growth Forest Representation Analysis

The SRME contains some 2,760,948 ha and the SFRS has 601,322 ha of MOG forests (21.8% of the ecoregion MOG), with the rest in structurally younger forest classes (Table 5). Notably, only 21.5% and 16.1% of MOG forests at the ecoregional and subregional scale, respectively, are protected with GAP 1 and 2 status (Table 5). With the inclusion of IRAs+, MOG forest protection levels would rise to 37.9% and 22.9%, respectively, but these are still below most conservation targets.

Table 5. Forest structure classes (based on [25]) and GAP status within the Southern Rocky Mountains Ecoregion and Santa Fe Subregion.

Southern Rocky Mountains Ecoregion						
Forest Structure Class	**GAP ha** **(%)**					**Total Forest Structure Class ha**
	1	**2**	**2.5**	**3**	**4**	**(%)**
Young	214,080 (14.1)	110,619 (7.3)	189,426 (12.5)	618,906 (40.9)	381,940 (25.2)	1,514,970 (22.9)
Intermediate	274,961 (11.8)	160,632 (6.9)	302,829 (13.0)	967,726 (41.5)	625,263 (26.8)	2,331,411 (35.3)
Mature	387,317 (14.0)	206,024 (7.5)	438,769 (15.9)	1,078,196 (39.1)	650,641 (23.6)	2,760,947 (41.8)
Total GAP ha	876,358 (13.3)	477,275 (7.2)	931,024 (14.1)	2,664,829 (40.3)	1,657,843 (25.1)	6,607,329 (100.0)
Santa Fe Subregion						
Forest Structure Class	GAP ha (%)					Total Forest Structure Class ha
	1	2	2.5	3	4	(%)
Young	16,957 (8.8)	10,126 (5.2)	9021 (4.7)	78,272 (40.5)	78,996 (40.9)	193,372 (15.9)
Intermediate	33,504 (7.9)	18,373 (4.4)	19,557 (4.6)	182,556 (43.3)	167,959 (39.8)	421,949 (34.7)
Mature	74,385	22,007	41,420	275,932	187,588	601,332
	(12.4)	(3.7)	(6.9)	(45.9)	(31.2)	(49.4)
Total GAP ha	124,846 (10.3)	50,505 (4.2)	69,999 (5.8)	536,760 (44.1)	434,542 (35.7)	1,216,653 (100.0)

3.4. Focal Species Distributions and GAP Status

3.4.1. Wolverine

Wolverine habitat connectivity spans the SRME, providing potentially suitable north–south and east–west linkage zones to varying degrees (Figure 3). The highest connectivity scores are clustered in the center of the SRME (around Gunnison, Colorado, dark purple area) and along northwest portions of the SRME southwest of Laramie, Wyoming (Figure 3), as well as within the southeastern section of the SFSR (Figure 3 inset).

Areas in the upper tiers of connectivity scores across the SRME are meeting the 30% but not the 50% targets (32.2% and 31% of areas with 90th percentile and 95th percentile of connectivity scores, respectively; Table 6). With the inclusion of IRAs+, approximately 49% of each tier would be protected, which nearly meets the 50% target. For the SFSR, only 14.7% and 26.5% of the 90th percentile and 95th percentile connectivity tiers, respectively, are protected. With the inclusion of IRAs+, 16.7% and 28.6% of each tier, respectively, would be protected, which are below the 30% target (Table 6).

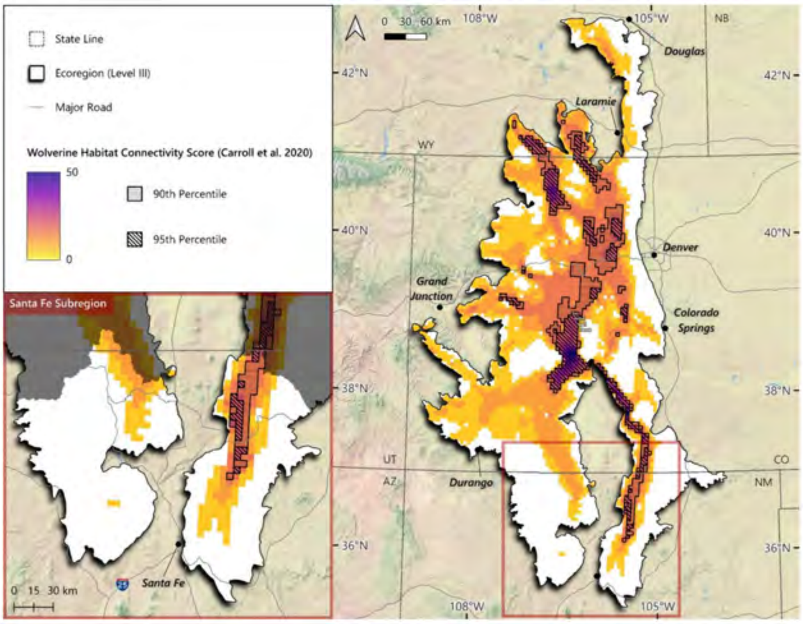

Figure 3. Wolverine connectivity scores for the Southern Rockies Ecoregion and Santa Fe Subregion based on Carroll et al. [26]. Note the clustering of dark colors that may act as important linkage zones for connectivity and dispersal of wolverine across the ecoregion.

Table 6. GAP status of upper tiers of wolverine habitat connectivity across the Southern Rocky Mountains Ecoregion and Santa Fe Subregion.

Southern Rocky Mountains Ecoregion						
Wolverine Habitat Connectivity Tier	**GAP ha**					**Wolverine Habitat Connectivity Tier ha**
	(%)					
	1	**2**	**2.5**	**3**	**4**	**(%)**
90th Percentile	370,568 (23.2)	142,632 (8.9)	259,856 (16.3)	565,749 (35.5)	255,199 (16.0)	1,594,004 (66.7)
95th Percentile	186,999 (23.5)	59,476 (7.5)	145,152 (18.3)	299,470 (37.7)	104,002 (13.1)	795,099 (33.3)
Total GAP ha	557,567 (23.3)	202,108 (8.5)	405,008 (17.0)	865,219 (36.2)	359,201 (15.0)	2,389,103
Santa Fe Subregion						
Wolverine Habitat Connectivity Tier	GAP ha					Wolverine Habitat Connectivity Tier ha
	(%)					
	1	2	2.5	3	4	(%)
90th Percentile	16,567 (14.7)	4 (0.0)	2224 (2.0)	45,033 (39.9)	49,005 (43.4)	112,833 (73.9)
95th Percentile	10,559 (26.5)	2 (0.0)	809 (2.0)	13,624 (34.2)	14,807 (37.2)	39,801 (26.1)
Total GAP ha	27,126 (17.8)	6 (0.0)	3033 (2.0)	58,657 (38.4)	63,812 (41.8)	152,634

3.4.2. Mexican Spotted Owl and Northern Goshawk Representation Analysis

Both the Mexican spotted owl and northern goshawk overlap in old forest habitats across the SRME, with the goshawk using mature forests for both the summer and winter range and the Mexican spotted owl more limited in its distribution (Figure 4). Thus, we combined the analyses of representation on the same figure for these two forest raptors.

For the Mexican spotted owl, the SRME contains 344,789 ha of suitable habitat, while the SFRS contains 193,419 ha (56% of the total) (Table 7). Levels of protection range from

5.8% in the SFSR to 7.4% in the SRME. The addition of IRAs+ would approximately double their protection levels (12 and 17% in the SFSR and SRME, respectively), but these would still be well below the conservation targets.

Table 7. Suitable habitat for Mexican spotted owl, northern goshawk, and Canada lynx, along with their GAP status within the Southern Rocky Mountains Ecoregion and Santa Fe Subregion.

Southern Rocky Mountains Ecoregion						
Focal Species	**GAP ha**					**Total Focal Species Suitable Habitat ha**
	(%)					
	1	**2**	**2.5**	**3**	**4**	**(%)**
Mexican Spotted Owl	7912 (2.3)	17,767 (5.2)	32,989 (9.6)	181,424 (52.6)	104,697 (30.4)	344,789 (2.7)
Northern Goshawk	995,417 (10.3)	637,456 (6.6)	1,041,847 (10.7)	3,732,433 (38.5)	3,299,723 (34.0)	9,706,876 (75.2)
Canada Lynx	558,604 (19.6)	258,103 (9.0)	520,036 (18.2)	1,163,796 (40.7)	356,529 (12.5)	2,857,068 (22.1)
Total GAP ha	1,561,934 (12.1)	913,326 (7.1)	1,594,872 (12.4)	5,077,653 (39.3)	3,760,949 (29.1)	12,908,733
Santa Fe Subregion						
Focal Species	GAP ha					Total Focal Species Suitable Habitat ha
	(%)					
	1	2	2.5	3	4	(%)
Mexican Spotted Owl	7218 (3.7)	4054 (2.1)	11,312 (5.8)	112,238 (58.0)	58,596 (30.3)	193,419 (9.9)
Northern Goshawk	130,313 (7.4)	65,243 (3.7)	83,743 (4.7)	684,744 (38.8)	800,875 (45.4)	1,764,918 (90.1)
Canada Lynx	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Total GAP ha	137,531 (7.0)	69,297 (3.5)	95,056 (4.9)	796,982 (40.7)	859,471 (43.9)	1,958,337

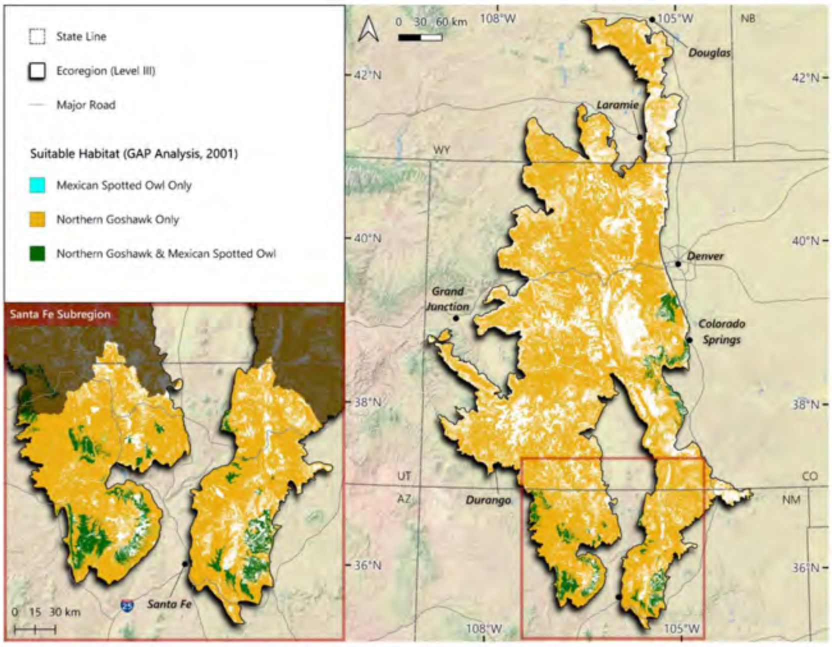

Figure 4. Suitable habitat for both the Mexican spotted owl and northern goshawk in the Southern Rocky Mountains Ecoregion and Santa Fe Subregion.

3.4.3. Canada Lynx Representation Analysis

The SRME contains ~2.9 M ha for Canada lynx habitat with no existing habitat identified in the SFSR (Table 7). Nearly 29% of suitable lynx habitat is protected, and IRAs+ would increase that to 46.8%, which is near the 50 × 50 target. While the historic range of the lynx includes northern New Mexico according to Thornton and Murray [36], no extant habitat was identified in the SFRS according to the 2001 GAP Analysis data (see Discussion).

3.5. WUI, Wildfires, and Forest Thinning

From 1984 to 2022, ~1.27 M ha (8.8%) of the SRME and 366,839 ha (16.8%) of the SFRS experienced a wildfire, with a substantially lower proportion of the total wildfire footprint intersecting the WUI within the SRME (2.3%) and the WUI in the SFRS (1.5%) (Figure 5, Table 8). Most of the WUI in the SRME is considered low-density intermix (75.6%) and medium-density intermix (12.7%). The same general pattern was observed within the SFSR, with 77% and 11.1% of the WUI being considered low-density and medium-density intermixes, respectively. Of the WUI that intersected the total fire footprint, 88.5% and 90.9% were a low-density intermix in the SRME and SFSR, respectively (Table 8).

Table 8. Wildland–Urban Interface/Intermix class distribution across the SRME and SFSR and the relative proportions that were intersected by at least one fire between 1984 and 2022.

Wildland–Urban Interface/Intermix (2020) Class	**Southern Rocky Mountains Ecoregion**		**Santa Fe Subregion**	
	All ha	**Burned ha**	**All ha**	**Burned ha**
	(%)	**(%)**	**(%)**	**(%)**
Low-Density Intermix	410,361 (75.6)	25,685 (88.5)	51,441 (77.0)	4909 (90.9)
Medium-Density Intermix	69,114 (12.7)	1442 (5.0)	7392 (11.1)	166 (3.1)
High-Density Intermix	237 (0.0)	2 (0.0)	26 (0.0)	1 (0.0)
Low-Density Interface	25,640 (4.7)	1536 (5.3)	5086 (7.6)	165 (3.1)
Medium-Density Interface	31,149 (5.7)	295 (1.0)	2495 (3.7)	113 (2.1)
High-Density Interface	6097 (1.1)	78 (0.3)	357 (0.5)	48 (0.9)
Total ha (%) [1]	542,599 (3.8)	29,037 (2.3)	66,797 (3.1)	5402 (1.5)

[1] The first and third columns are the percentages of the SRME and SFSR, respectively. The second and fourth columns are the percentages of the total burned area within the SRME (1,270,603 ha) and SFSR (366,839 ha), respectively.

We also found that 12.6% (160,046 ha) of the total fire footprint in the SRME overlapped existing wilderness, with 11.4% (41,844 ha) overlapping in the SFSR. Upper-tier IRAs in Colorado represented only about 3.4% (43,244 ha) of the total fire footprint in the SRME. Non-upper tier-IRAs in Colorado and IRAs in Wyoming and New Mexico represented 14% (177,324 ha) and 8% (29,507 ha) of the total fire footprint in the SRME and SFSR, respectively.

Notably, 73.5% of the total area thinned by the USDA Forest Service between 2014 and 2023 in the SRME (47,174 ha) and 79.7 of the total area thinned in the SFSR (16,874 ha) were >1 km away from the WUI. Only 8.1% of the thinned area in the SRME (2813 ha) and 4.4% in the SFSR (746 ha) were within 250 m of a WUI area.

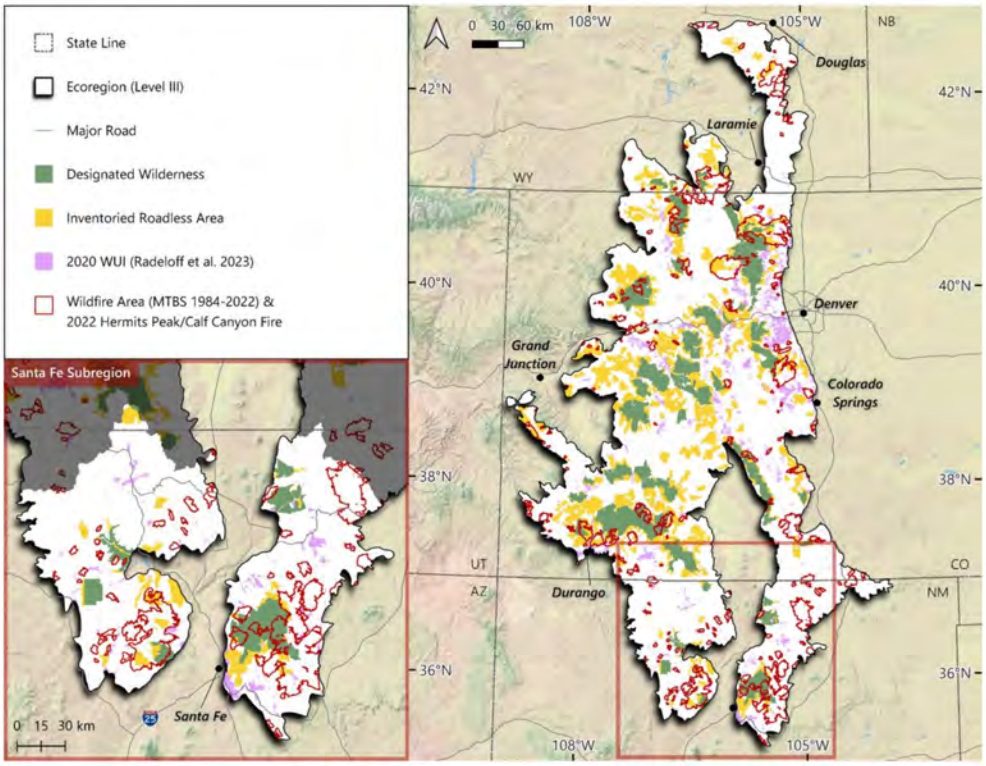

Figure 5. Wildfires within the Southern Rocky Mountains Ecoregion and Santa Fe Subregion (1984–2022) in the Wildland–Urban Interface [31], wilderness, and Inventoried Roadless Areas. IRAs and designated wilderness are shown.

3.6. Climate Change

3.6.1. Historical Trends

From 1979 to 2023, the average temperature across the study area increased by 1.2 °C, as obtained from the Climate Toolbox (Table 9). The minimum temperature increased by 1.5 °C, while the maximum temperature increased by 0.8 °C, on average. Additional historical changes have included a longer frost-free season, declining average annual precipitation, more drought, and reduced snowpack (Table 9).

Table 9. Historical (1979–2023) climate changes for the Southern Rocky Mountains Ecoregion [1].

Average Annual Temperature	+1.2 °C
Maximum Temperature	+0.8 °C
Minimum Temperature	+1.5 °C
Frost-Free Season	+29 days longer frost-free season
Annual Precipitation	−15%
Drought [2]	Increasing frequency
Snowpack [3]	<20% at most sites

[1] GridMET gridded surface meteorological dataset accessed from https://climatetoolbox.org; accessed on 4 April 2024. [2] Palmer Drought Severity Index (PDSI) accessed from https://climatetoolbox.org; accessed on 4 April 2024. [3] EPA 2023. https://www.epa.gov/climate-indicators/climate-change-indicators-snowpack (accessed on 10 May 2024) [37].

3.6.2. Future Projections under Two Emission Scenarios

Temperature Projections. The lower-emissions trajectory (RCP4.5) indicates that average warming in the SRME could be limited to 3.0 °C (range from 1.7° to 4.3 °C) by the end of the century (Figure 6). The higher-emissions trajectory (RCP8.5) indicates a more extreme average annual temperature increase of 5.2 °C (range from 3.5° to 7.2 °C) by the end of the century when compared to the historical average from 1951 to 1980 (Figure 6).

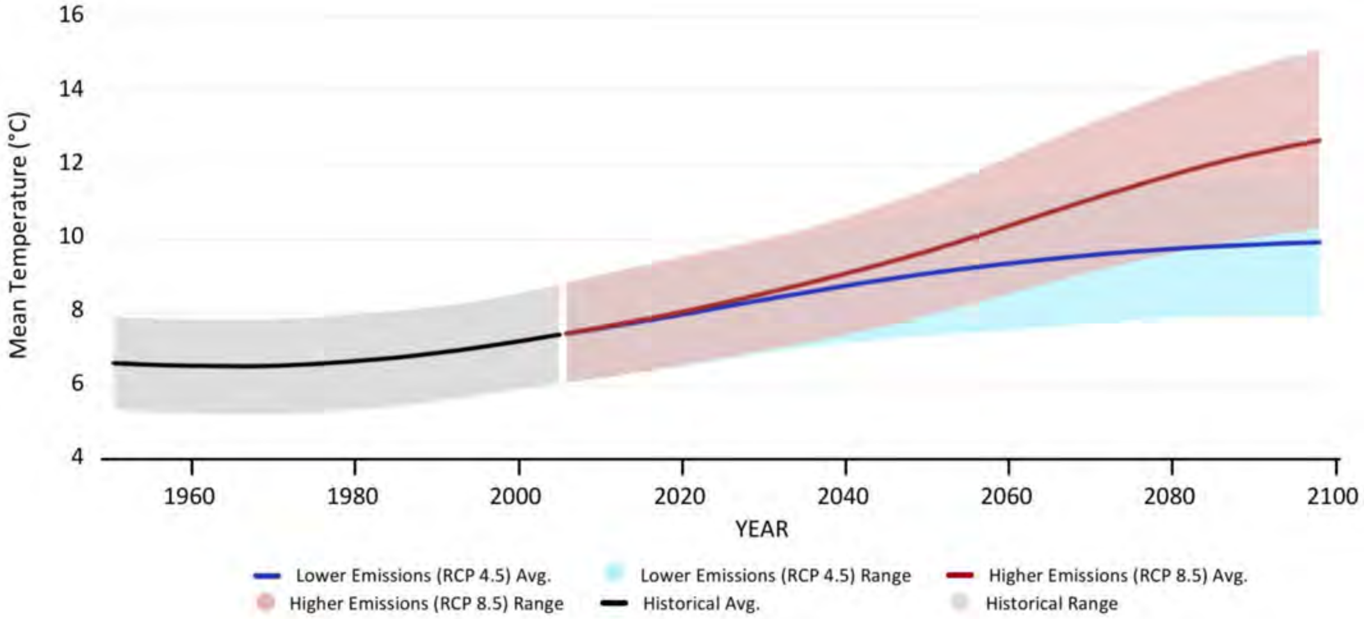

Figure 6. Mean temperature across the study area from 1950 to 2100 under the lower (blue) and higher (pink) emissions scenarios. Graph created with Climate Toolbox Future Time Series web tool [38].

Heat Wave Projections. More frequent days of high heat are expected in the SRME as climate change intensifies over the century (Table 10). An additional 40 days/yr with extreme heat >32 °C are projected by the end of the century if emissions continue unabated (RCP8.5). However, if emissions are reduced, additional severe heat days could be limited to approximately 15 days/yr, on average, by the end of the century.

Table 10. Estimated number of additional days per year over 32 °C, 38 °C, and 41 °C across the Southern Rocky Mountains Ecoregion based on continued high emission (RCP8.5) vs. low emission (RCP4.5) scenarios for two time periods (2040–2069, 2070–2099). Data accessed from Climate Toolbox Future Box Plots web tool [38].

Years	RCP8.5			RCP4.5		
	>32 °C	>38 °C	>41 °C	>32 °C	>38 °C	>41 °C
2040–2069	+19.6	+1.3	+0.1	+12.3	+0.4	+0.0
2070–2099	+39.3	+6.4	+1.1	+15.2	+0.7	+0.0

Precipitation Projections. High year-to-year variation in annual precipitation (Figure S1) makes long-term trends more difficult to assess (Figure S2), and thus we have placed these results in the Online Supplementary Material. The study area could experience a range of future precipitation trends, from a potential increase of ~26% to a decline of ~20% (Figure S2). Average precipitation change is projected at +6%, while uncertainty in the precipitation projections is quite high. However, both evapotranspiration and the Climatic Water Deficit (CWD), a measure of water stress based on the evaporative demand in plants, are expected to increase (Figures S3 and S4). Thus, even if annual precipitation increases, the hotter temperatures mean that more plant stress and evaporative losses would occur. Further, as warming of the SRME intensifies, precipitation is expected to increasingly fall as rain instead of snow, leading to continued declines of 40–92% in snowpack if emissions continue unabated and 22–72% if emissions are reduced (Figures S5 and S6).

Streamflow Projections. Streamflow in the Southern Rockies generally peaks in June when the snowpack recedes. Gradual snowmelt at higher elevations continues through the summer months, feeding summer streamflow. Continued warming is expected to reduce snowpack and cause faster runoff from rainfall in the winter, leading to earlier peak flows (Figure S7). With less snow, lower summer flows and more extreme conditions are expected.

Vegetation Projections. As climate change intensifies, dominant vegetation types are expected to shift, affecting wildlife habitat suitability and wildfire behavior. Uncertainties in vegetation response to changes in climate are related to many factors, including insect outbreaks, wildfires, drought response, plant dispersal mechanisms, plant establishment, and species competition. Results from the functional vegetation model indicate that the distribution of conifer forests may constrict while woodland and shrubland distributions expand (Figure S8) (MC2 model) [33,34].

4. Discussion

4.1. Representation and Importance of Protected Areas

Our ECA builds on prior conservation plans for the SRME and SFSR that are over two decades old with little success toward initial target setting [1,3]. One of the interesting findings of our ECA is that while landownership patterns were very similar between the two scales (e.g., USDA Forest Service manages 46%–48% of the area in both cases), there were striking differences in protection levels between the ecoregion and subregion. In nearly all of the representation analyses, the SFSR underperformed not only in the 30 × 30 and 50 × 50 targets but also in comparison with the SRME. This underscores the contextual importance of the subregion relative to its larger surroundings, and it highlights the need for greater conservation attention to begin closing the noted gaps in protection. Current wilderness proposals (which are concentrated in the Colorado portion of the SRME), while important, are not enough to increase relative protection levels. This is because most of the total area proposed for wilderness is already GAP 2 or 2.5. Our analysis also highlights the need for policymakers and land-management agencies to explore additional ways to increase the protection level for GAP 3 or 4 lands across the ecoregion.

Additionally, the protected-area network was highly skewed toward upper-elevation EVTs (alpine, barren, sparse, rock, and ice), which is no surprise given this had also been previously reported [1]. In contrast, montane forest, woodland, pinyon–juniper, and riparian areas where wildlife concentrates, including three of our focal species (goshawk, Mexican spotted owl, Canada lynx), were poorly represented. Ponderosa pine forests, particularly, have low levels of protection across both the SRME and SFSR despite accounting for a large proportion of the EVT area. This forest type is also heavily targeted for fuel reduction, involving intensive thinning projects in both the SRME and SFSR. Importantly, there is some evidence suggesting that the white pine–limber pine hybrid zone is moving north in response to climate disruption [39,40]. Nutritious white pine seeds are eaten by a wide diversity of wildlife and have coevolved a mutualistic relationship with Clark's nutcrackers (*Nucifraga columbiana*) to disperse their large, wingless seeds. A high level of genetic resistance to the exotic white pine blister rust *Cronartium ribicola*, a significant stressor to white pines throughout the West, is found within the SFSR [41]. However, despite the need to preserve uniquely resistant populations, the Santa Fe and Carson national forest management plans provide no protection for white pines that are vulnerable when clearing vegetation for fuel reduction.

4.2. Focal Species Conservation

We identified the important habitats for four focal species (Canada lynx, northern goshawk, Mexican spotted owl, and wolverine) at both spatial scales. Other than the wolverine, protection levels for the three other focal species underperformed, and were improved by the addition of IRAs+, but still remained below the conservation targets. Three of the four (all but wolverine) focal species use dense forests—mostly MOG forests—although

Canada lynx forage on snowshoe hares using forest openings [27]. The MOG forest' protection's underperformance was striking for the SFSR, where MOG was concentrated but poorly represented in protected areas. For northern goshawks and Mexican spotted owls, their dependence on older forests may put them in conflict with much of the USDA Forest Service's fuel reduction projects that, at least for the spotted owl, can degrade habitat [42], although this is currently debated among researchers [43]. Interestingly, the GAP Analysis 2001 habitat suitability dataset did not delineate any Canada lynx habitat within the SFSR. This may have been due to assumptions at the time about the species' historical range. Thornton and Murray [36], however, found that the Canada lynx was historically more widespread than typically thought, with a significant amount of suitable habitat located in the higher elevations of the SFSR. That study also found that Canada lynx suitable habitat across the region will diminish by 2050 and 2070 under a moderate-emissions scenario [36]. Such habitat changes will need to be accounted for when determining where Canada lynx should be reintroduced in the SRME, and our results show that even this relatively high-elevation species would still benefit from increased protection levels.

The situation for wolverines is better overall in terms of habitat protection; however, even high-elevation areas are experiencing recreation pressures [44]. Based on the wolverine connectivity score [26], we identified several linkage zones that may connect portions of the wolverine range, potentially allowing for movements in relation to climate shifts and expansion of wolverine into the southern trailing edge. These include linkage zones around Gunnison, Colorado (central portion of the region), just southwest of Laramie, Wyoming (northern edge), along the spine of the Rockies, and on the eastern flanks of the Santa Fe National Forest (again poorly represented). Additionally, although not modeled here, at mid-elevations, linkage zones are also known to be important for the movements of lynx from their northern to southern range in the Rockies [27].

4.3. Wildfires, Wilderness, and the Wildland–Urban Interface

Fire regimes of the SRME have been described as moderate–high frequency and low–mixed severity at lower elevations (e.g., foothills) with infrequent, high-severity fires in upper montane areas [45–48]. Wildfires tend to peak prior to the arrival of midsummer monsoons in the SFRS. Historically, there have been very large fires (hundreds of thousands to millions of hectares) during drought years in Colorado [47] and New Mexico [48]. Variability in fire regimes throughout the SRME creates the conditions for a mixture of open and closed canopy forests; however, forest densities have been affected by fire suppression (mostly foothills) [47], and logging and livestock grazing in places. Notably, wildfire regimes in large, protected areas across the Rockies seem to be operating within historic bounds [47], possibly due to their highly skewed upper-elevation locations that are difficult to access for fire suppression and vegetation treatments and differences in vegetation types at higher elevations [1]. This is in contrast to areas with less protection and more exposure to logging, which tend to burn more severely [49]. Additionally, outbreaks of bark beetles (*Scolytinae*) and western spruce budworm (*Choristoneura freemani*) have been widespread since the 1990s [50] and linked to global overheating, especially during the winter [51]. Importantly, outbreaks can lower forest canopy fuel profiles, rendering affected areas less prone to subsequent fires [50,52–55]. Outbreaks also tend to be highly concentrated in areas where extensive monoculture forestry has reduced host-tree species variability, simplified structural complexity (e.g., older forest age classes, large trees, snags), and degraded habitat for insectivorous species [56].

Approximately 1.27 M ha of the SRME and 366,839 ha of the SFSR experienced wildfires at least once over the four decades for which we have fire data. Interestingly, existing wilderness and IRAs represented 19.5% to 30% of the total fire footprint in the SFSR and SRME, respectively, despite these designations accounting for 12.8% (281,110 ha) to 24.3% (3,523,888 ha) of the total area in each region. While IRAs were not designated until at least 2001, the disproportionate occurrence of fire in the wilderness and IRAs is still worth noting and may be due to a number of factors. Wilderness areas in the SRME skew toward upper-elevation areas (the average elevation of the wilderness in the SRME is 3249 m) where subalpine and lodgepole forests dominate, both of which have fire regimes characterized by long fire rotations and large stand-replacing fires. For example, 13.4% (21,414 ha) of the wilderness that burned in the SRME was due to the 2020 Cameron Peak Fire alone. Existing wilderness represents 11.1% of the total land area in the SRME and 12.6% of the total fire footprint, indicating that fire occurrence was also disproportionate in IRAs. These areas tend to be located at lower elevations (the average elevation of upper-tier and non-upper-tier IRAs is 3126 m and 2893 m, respectively) compared to the existing wilderness, and therefore have a greater proportion of forest types with shorter fire rotations such as mixed-conifer and ponderosa pine forests. While we did not conduct an analysis of fire severity distributions, the greater occurrence of fire in IRAs may represent a restorative trajectory toward pre-suppression historical conditions.

The WUI, in particular, represented 2.3% and 1.5% of the total area burned in the ecoregion and subregion, respectively. Most of the wildfire area that intersected the WUI occurred in the low-density intermix class (~90% of the total WUI area burned between 1984 and 2022). This class is also the most abundant WUI type across both the SRME and SFSR. Interestingly, 73.5% to 79.7% of the total area thinned in the SRME and SFSR, respectively, was >1 km away from the WUI. That is, despite the wide distribution of the WUI (542,599 ha across the ecoregion), the vast majority of thinning activities on USDA Forest Service land are occurring at substantial distances from at-risk communities.

Additionally, while the U.S. Forest Service has conducted hundreds of prescribed burns over the past few decades, there have been four controversial prescribed burns since 2000 that escaped containment and destroyed dozens of homes, including the Cerro Grande Fire, the Cerro Pelado Fire, the Hermits Peak, and the Calf Canyon Fire, within the subregion. Based on an analysis of the USDA Forest Service's Fire History Occurrences and Perimeters dataset for Region 3, Hyden [20] estimated that the total area burned since 2014 in the Santa Fe National Forest area by escaped prescribed fires was ~154,830 ha, about 94% of all wildfires. While prescribed burning along with cultural burning practices have many ecological benefits, the substantially large relative area impacted by escaped prescribed fires that do so under extreme fire weather could be a limiting factor in forest recruitment in a changing climate, especially for important habitat types such as MOG forests. Even one escaped burn can shelf all prescribed fires at least temporarily due to controversy with the affected communities and human health issues regarding smoke inhalation (https://www.fs.usda.gov/about-agency/newsroom/releases/usda-forest-service-chief-randy-moores-statement-announcing-actions (accessed on 10 May 2024)).

4.4. Climate Change

The Southern Rocky Mountains Ecoregion has already experienced elevated temperatures, increased drought, and reduced snowpack. The velocity of climate change across the ecoregion will depend on the particular emission pathway (RCP4.5 vs. RCP 8.5); however, the current trajectory more closely follows RCP8.5, as emissions continue to rise to unprecedented levels [57]. Climate change may also interact with land use (although not modeled here) to limit the adaptive capacity of focal species and important habitat types. Most notably, projected increases in wildfires would reset forest succession from MOG to complex early seral forests [58], resulting in broad shifts in species assemblages. Further, MC2 model projections indicate that conifer distribution may shrink while woodlands expand and this may affect at least the three focal species using conifer forests in our study area (lynx, spotted owl, goshawk). Continued reductions in snowpack will affect stream flows, with impacts to aquatic species and riparian obligates (e.g., beaver, *Castor canadensis*). At higher elevations, wolverines will be affected due to their propensity to den in snowfields [44].

5. Conclusions and Conservation Recommendations

The biodiversity of the SRME varies across topo-edaphic gradients (e.g., life zones) and is particularly vulnerable to unprecedented land uses and climate change. The protected-areas network, while important in potentially slowing climate change effects [9], poorly represents most EVTs, MOG forests, and suitable habitats for focal species, especially along the trailing edge within the SFRS that might be more vulnerable to higher climate velocities.

We reaffirmed the conservation value of IRAs [1], especially if bumped up in protection status from GAP 2.5 to GAP 2, in helping to meet 30 × 30 and 50 × 50 targets. IRAs could be upgraded to IRAs+ by adopting enhanced protective measures ("upper-tier roadless") of the 1.7 M ha Colorado Roadless Rule applied throughout the ecoregion. IRAs+ could also be advanced to wilderness protection through congressional legislation as proposed in Colorado (e.g., H.R. 803) and New Mexico (Pecos Wilderness Protection Act (not analyzed here, S. 3033, due to lack of spatial data). President Biden's Executive Order 14,008 pertains to 30 × 30 [59] and representation targets in this ecoregion could help inform the nation's overall 30 × 30 efforts. Notably, all 128 national forest plans are proposed for revision in relation to a nationwide MOG forest draft environmental impact statement in response to President Biden's Executive Order 14,008 [60]. Our target-setting for MOG forests helps inform the importance of this process underway and the need for strict protections from logging [26] given their pivotal conservation importance.

Our ECA provides an integrated approach to conservation, wildfire risk reduction, and climate change planning in reaffirming the importance of broad conservation targets [1,3,21] and integrating them with effective wildfire risk reductions aimed at the built environment. Most notably, the Forest Service is conducting controversial forest management and fuel-reduction treatments >1 km from the nearest structures, while at least some scientists are calling for wildfire risk reduction targeting the home ignition zone [18,19,61]. A more targeted use of fuel-reduction treatments [61] might allow protected area proposals to advance in association with climate change planning for more fires. Additionally, increased habitat protection for three of the four focal species in our study area (Canada lynx, Mexican spotted owl, and northern goshawk) that utilize forests might improve their chances of surviving climate change and land-use stressors, while additional restrictions are needed on recreation access in high elevation areas to protect wolverines and allow them and lynx to reoccupy the trailing edges of their historic range in search of climate refugia. Intact areas protected from development have the best chance of serving as climate refugia and important linkage zones [8]. Moreover, effective road closures and road obliterations would help in rewilding efforts across the region [62], reduce fragmentation of linkage zones, and lower unwanted human-caused wildfire ignitions [63].

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/land13091432/s1. Figure S1. Annual precipitation (mm) across the study area, from 1979–2023, showing precipitation lower than the overall mean (441 mm) in red and higher than the mean in blue. The trendline shows an overall decline in precipitation of −16mm/decade ($r = -0.36$, $p = 0.02$). Graph created with gridMET data from Climate Toolbox Historical Climate Tracker web tool (Hegewisch and Abatzoglou, 2023) [38]. Figure S2. Projected future mean precipitation for the study area varies substantially compared to the historical average (1950–2005). Graph created with Climate Toolbox Future Time Series web tool based on MACAv2-METDATA CMIP5 model ensemble (Hegewisch and Abatzoglou, 2023) [38]. Figure S3. Evapotranspiration is projected to increase by 17–37% with higher emissions (RCP8.5) and by 8–23% with lower emissions (RCP4.5). Graph created with Climate Toolbox Future Time Series web tool based on MACAv2-METDATA CMIP5 model ensemble (Hegewisch and Abatzoglou 2024, 2023) [38]. Figure S4. Increasing Climatic Water Deficit (mm), based on continued higher emissions (RCP8.5). Data from 20 GCMs shown, including median (blue line), 5th and 95th percentiles (box), and highest/lowest values (green lines or "whiskers"). Graph downloaded from Climate Toolbox Future Box Plots web tool (Hegewisch and Abatzoglou, 2023) [38]. Figure S5. Winter (Dec-Feb) snow water equivalent (mm) across the study area is projected to decline by 40–92%, as compared to the historical period, by the end of the century. Graph downloaded from Climate Toolbox Future Box Plots web tool (Hegewisch and Abatzoglou, 2023) [38]. Figure S6. Observed changes in April snowpack across the Western U.S. from 1955–2020. Map by NOAA Climate.gov based on USDA Natural Resources Conservation Snow Data (EPA 2023). Figure S7. MC2 vegetation model results compare modeled 1971–2000 vegetation types (left) to projected vegetation types in 2070–2099 (right) based on ensemble average across 20 GCMs and continued higher emissions (RCP8.5). Limited shifts in dominant vegetation type are expected across the study area by the end of the century, primarily as a loss of subalpine forest, and expansion of shrublands. Graphic downloaded from Climate Toolbox Future Vegetation web tool using MC2-MACAv2-Prism, without fire suppression. Figure S8. Projected streamflow (m^3/s) on the Colorado River at the Glenwood Springs Gauge Station from 2070–2099, as compared to historical flows (1950–2005). Historical flows (dark blue) show a peak in June and lowest flows during winter, while future. Table S1. The 10 southernmost watersheds (8-digit Hydrologic Unit Code) of the Southern Rocky Mountains Ecoregion (SRME), which we used to delineate the Santa Fe Subregion (SFSR). Table S2. Existing Vegetation Types (EVT) as defined by LANDFIRE 2022 within the SRME and the broader categories we created from them. References [37,38] are cited in the Supplementary Materials.

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Article

The Tongass National Forest, Southeast Alaska, USA: A Natural Climate Solution of Global Significance

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Abstract: The 6.7 M ha Tongass National Forest in southeast Alaska, USA, supports a world-class salmon fishery, is one of the world's most intact temperate rainforests, and is recognized for exceptional levels of carbon stored in woody biomass. We quantified biomass and soil organic carbon (C) by land use designation, Inventoried Roadless Areas (IRAs), young and productive old-growth forests (POGs), and 77 priority watersheds. We used published timber harvest volumes (roundwood) to estimate C stock change across five time periods from early historical (1909–1951) through future (2022–2100). Total soil organic and woody biomass C in the Tongass was 2.7 Pg, representing ~20% of the total forest C stock in the entire national forest system, the equivalent of 1.5 times the 2019 US greenhouse gas emissions. IRAs account for just over half the C, with 48% stored in POGs. Nearly 15% of all C is within T77 watersheds, >80% of which overlaps with IRAs, with half of that overlapping with POGs. Young growth accounted for only ~5% of the total C stock. Nearly two centuries of historical and projected logging would release an estimated 69.5 Mt CO_2e, equivalent to the cumulative emissions of ~15 million vehicles. Previously logged forests within IRAs should be allowed to recover carbon stock via proforestation. Tongass old growth, IRAs, and priority watersheds deserve stepped-up protection as natural climate solutions.

Keywords: carbon emissions; carbon stores; inventoried roadless areas; old-growth forest; southeast Alaska; temperate rainforest; Tongass National Forest; natural climate solutions

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1. Introduction

The 6.7 M ha Tongass National Forest (TNF) in southeast Alaska, USA, is the largest national forest managed by the USDA Forest Service in the 77.2 M ha national forest system. The region's productive old-growth forests (POGs; wood standing volume >46.6 m^3/ha; forests $\geq$150 years old) [1,2] contain far more old growth than any other national forest, providing opportune settings for large-landscape conservation in one of the world's most relatively intact temperate rainforests [2,3]. The TNF also has been the focus of logging debates for decades with pro-conservation presidential administrations enacting forest protections and pro-development ones allowing increased timber removals. Under President Bill Clinton, the National Roadless Conservation Rule of 2001 [4] protected from development 23.4 M ha of federally Inventoried Roadless Areas (IRAs $\geq$ 2000 ha) across the entire national forest system, 3.7 M ha of which was in the TNF, the largest such expanse. Roadless areas tend to have higher levels of biodiversity and intact ecosystem services than logged and roaded areas [5–7].

To date, there have been 14 legal attempts to overturn roadless protections as they apply to the Tongass; none have invalidated the conservation rule in appellate courts (e.g., https://earthjustice.org/features/timeline-of-the-roadless-rule; accessed on 15 April 2022). However, both the George W. Bush and Donald Trump administrations used executive powers to roll back roadless protections on the Tongass in favor of old growth logging and development. The Joe Biden administration is set to "repeal or replace" the Trump reversal [8], and thus it is imperative that roadless values are well documented, particularly as conservation outcomes are ostensibly tied to political parties changing hands.

Industrial-scale POG logging began ramping up on the Tongass with passage of the Tongass Timber Act of 1947 that authorized two federally subsidized fifty-year pulp contracts [9]. The contracts expired in 2000 and, in 2016, the Barack Obama administration amended the Tongass Land Management Plan (TLMP) of 2008 with the intent to transition logging out of POGs and into suitable young-growth forests (previously logged, naturally reforested, and now commercially viable) [10]. Professional fish and wildlife societies and many scientists have repeatedly called for stepped-up protections for all POGs and IRAs on the TNF (e.g., https://conbio.org/policy/scb-and-other-science-societies-call-on-president-obama-to-save-tongass-rai; accessed on 12 February 2022). Conservation groups also have proposed 77 priority watersheds for salmon and wildlife known as the "Salmon Forest Proposal" or the "Tongass 77" (herein T77) [11]. Notably, POG logging was prohibited within the T77 under the 2016 TLMP transition amendment; however, that too was reversed by the Trump administration shortly thereafter. On 15 July 2021, the Biden administration announced plans to end all "large-scale old-growth logging" on the TNF, thereby providing de facto protections once again for most POGs, IRAs, and T77 priority areas while restarting the transition to timber harvests focused on young growth (https://www.whitehouse.gov/briefing-room/presidential-actions/2021/01/27/executive-order-on-tackling-the-climate-crisis-at-home-and-abroad/; accessed on 12 April 2022). Some small-scale POG logging would be permitted in transition.

Carbon (C) stocks have been quantified previously on the TNF [12] and recognized as nationally significant by USDA Forest Service researchers [13–15] and in congressional policy reviews [16]. However, the USDA Forest Service has undervalued the C stock importance of the TNF by routinely dismissing stock change from logging as inconsequential to total US greenhouse gases (GHGs) [10,17]. Further, the agency believes that logging emissions are simply offset by the storage of C in harvested wood product (HWP) pools and natural reforestation [10,17,18]. The significance of the region to the development of US forest policy around natural climate solutions demands that spatially explicit data on Tongass carbon stocks be updated and an assessment of stock change be attributable to historical, contemporary, and anticipated logging levels.

It follows that our objectives are to: (1) quantify current biomass and soil carbon stocks within land cover (POG, young growth) and land use categories (IRAs, T77 watersheds); and (2) estimate C emissions spanning ~2 centuries of logging on the TNF. Our analysis is key to shedding light on the importance of IRA protections and policy options for both old growth and young-growth forests. Given the national significance of C stocks on the TNF [12], managing forests to maximize C stock potential would demonstrate the US has made a forest-based nationally determined contribution (NDC) to the Paris Climate Agreement. Article 5.1 of the agreement recognizes the need for countries to take specific actions that conserve and enhance nature-based solutions as C sinks and reservoirs [19].

2. Methods

2.1. Study Area

The TNF in southeast Alaska is within the North Pacific Coastal Forest bioregion, which includes several WWF Global 200 ecoregions. At a finer scale, the Tongass also spans the perhumid temperate rainforest climate subzone [20], recognized as globally unique [2,3] (Figure 1). Temperate rainforests are distributed on the Alaskan mainland juxtaposed against the windward edge of the Coast Mountains, separating Alaska from British Columbia. Rainforests are scattered across an archipelago of thousands of islands from the Dixon Entrance (54° N) northward to Yakutat Bay (just north of Glacier Bay, 59° N), a distance of 835 km that includes 30,000 km of shoreline [3]. Interspersed are tree-stunted muskegs, tidewater glaciers, and deeply dissected fjords. Approximately 20% of the TNF is non-forested [10]. Importantly, about 90% of temperate rainforest on the TNF was stunted muskegs, tidewater glaciers, and deeply dissected fjords. Approximately 20% of the TNF is non-forested [10]. Importantly, about 90% of temperate rainforest on the TNF was considered POG in the early 1990s [21], among the largest such concentrations of temperate rainforests [3]. However, only 3% of forested areas include the largest old-growth trees (highest timber volumes) due to high-grade logging prior to the 1990s [1]. "Unproductive" old-growth also occurs mostly in muskegs having no commercial timber value [10].

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Figure 1. Study area (dark gray), defined as land managed by the United States Department of Agriculture Forest Service within the administrative boundary of the Tongass National Forest, southeast Alaska, and the spatial distribution of young-growth forest (light green) and productive old-growth forest (dark green).

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The Koppen Climate Classification subtype for the southeast Alaska region of our study area is "Dfc" (Continental Subarctic Climate). Mean precipitation during the winter is 642 mm (125 mm to 1473 mm range) and mean temperature in the summer is 12.5 °C (9.9 °C to 17.9 °C range), which is on the wetter, cooler side of temperate rainforests globally [3]. Due to the northern latitude and short growing seasons, treeline on the TNF is generally 300 m, declining northward. Old-growth forests are characterized by multi-layered forest canopies mainly of western hemlock (*Tsuga heterophylla*), yellow-cedar (*Callitropsis nootkatensis*), mountain hemlock (*T. mertensiana*), Sitka spruce (*Picea sitchensis*), western red cedar (*Thuja plicata*), and low-growing shore pine (*Pinus contorta*) on wetter sites such as muskegs. Rainforest understories are rich in forbs and shrubs [20,21] with dense mats of oceanic lichens and bryophytes that carpet the ground and extend into the overstory canopy.

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Prolific salmonid runs include chum (*O. keta*), coho (*O. kisutch*), king (*O. tshawytscha*), pink (*O. gorbuscha*), sockeye (*O. nerka*), and steelhead trout (*O. mykiss*) that support some of the largest concentrations of brown bears (*Ursus arctos*) and bald eagles (*Haliaeetus* *leucocephalus*) in the world [2,3]. Notably, old-growth forests and IRAs provide important refugia for salmonids and Sitka-black tailed deer (*Odocolieus hemionus sitkensis*), considered staple food sources for Alaskan tribes [2,3]

The T77 portion of the study area was based on a spatially explicit ranked-analysis performed by Trout Unlimited, the Nature Conservancy, and Audubon Alaska [11] (https://databasin.org/datasets/72977f90d25a4fcf9f455b9017f2a5e2/; accessed on 5 May 2022).

This dataset includes the highest ranked watersheds in 14 biogeograpical provinces on the TNF based on a suite of attributes, including: top-ranked habitat for the six salmonid species; habitat of the marbled murrelet (*Brachyramphus marmoratus*), a federally threatened seabird species that nests in old-growth forests from California to Washington; black bear (*Ursus americanus*) and brown bear summer habitat; Sitka black-tailed deer wintering habitat; and estuaries and riparian areas that have large-tree, old-growth forests [11]. Excluded were watersheds already protected, in non-federal ownership, managed for other values (such as urban recreation, experimental forest, or timber), and lacking public support [11]. T77 watersheds total 764,855 ha (~11% of the TNF land base); however, they have never been analyzed for C stocks.

2.2. Timber Sale Datasets

We accessed USDA Forest Service datasets on timber volume sold on the TNF and allocated them into five time periods (bins): (1) early historical (ca 1909–1951) [9]; (2) pulp (1952–2000) [22,23]; (3) post pulp (2001–2015) [9]; (4) transition (2016–2021) [10,24]; and (5) future (2022 projected to the end of century) [10].

Tongass management priorities are based on a zoning process known as Land Use Designations (LUDs). In general, there are 18 LUDs nested within three major groupings (summarized herein). LUD 1 includes strictly protected Wilderness and National Monuments; LUD 2 includes Natural Settings managed for non-motorized recreation, old-growth and watershed protections, and Research Natural Areas; and LUD 3 (Development) is managed mainly for timber and mineral extraction. This is in addition to IRAs that are a separate administrative category that precludes most development.

2.3. Carbon Datasets

Our spatially explicit gridded estimates of C density (ca. 2019) in woody plant biomass are derived from a combination of published datasets spanning the study area (Table S1). Researchers [25] combined FIA ground measurements ($n > 1000$ plots) with environmental covariates (e.g., topography, climate, and disturbance) to calibrate a machine learning algorithm producing lower and upper bound 30 m gridded estimates of C density (metric tons of carbon per hectare, t C ha^{-1}). These were grouped by woody biomass pools including live trees, roots, woody debris, seedlings/saplings, snags, and understory vegetation. C density estimates represent potential C storage, which should closely approximate current storage in old-growth ecosystems, but do not account for active or historical removals of C from logging. Thus, we applied pixel-level adjustments to estimate current (ca. 2019) C density in woody plant biomass. This was accomplished using tree cover data [26] to establish a baseline of ca. 2000 forest cover (>25% tree canopy within a 30 m grid cell), which we then used to remove (i.e., set to zero) all non-forested pixels from the ca. 2000 C density layers. Grid cells were also set to zero if they were identified in the tree cover data [26] as having lost forest cover during the 2001–2019 period. The remaining grid cells reflect the lower and upper bound estimates of current C density in all woody biomass pools. As a result of logging activities prior to 2000, these data are expected to overestimate C stock in young-growth forest.

For a small portion of the study region not included in prior work [25], we estimated C density using a multi-step approach. First, we combined the forest cover loss information for the 2001–2019 period [26] with the 30 m map of aboveground live dry woody biomass (AGB) density (ca. 2000) [27] to estimate current (ca. 2019) AGB density. Next, for grid cells in which we had estimates (ca. 2019) of both AGB ([27], modified data) and all woody biomass pools combined [25] (modified data), we computed the ratio of C in AGB to all biomass pools by forest group (using USFS data). Finally, we applied these ratios as a scaling factor—again by forest group—to the grid cells in which we had only estimates of AGB density, thus producing lower and upper bound estimates, as well as pixel-level mean estimates, of C density in all woody biomass pools Tongass-wide.

Soil C stocks were included using recently published data for the region. We used a 90 m gridded estimate of soil organic C for the top 1 m of mineral soil, including surface organic horizons [28]. We extracted the study region, resampled the grid cells to 30 m using a nearest neighbor approach and re-projected the data to the same coordinate reference system as the biomass density layers.

C stock herein refers to the total amount of C within a defined area and is generally displayed in units of millions (M) of metric tons (t) or petagrams (1 Pg = 1 billion t). Additional information on the errors and uncertainties associated with the biomass and soil C data sets incorporated here can be found in [25,26,28].

2.4. GIS Overlays

Several geospatial datasets were used to further characterize C stocks within the study area. First, the administrative boundary of the study area, land ownership information, and IRAs designated by the 2001 Roadless Area Conservation Rule were retrieved from the USFS Geodata Clearinghouse (https://data.fs.usda.gov/geodata/; accessed on 12 April 2022). Forest growth information, including spatially explicit delineations of young growth and POG—also produced by the USFS—were obtained via databasin.org. All GIS layers were acquired as Esri (polygon) shapefiles. Additional geospatial data used to identify scenarios of IRAs at risk from potential forest management plan changes were acquired from The Nature Conservancy and Audubon Alaska (18 September 2019, personal communication, D. Albert). We rasterized, re-projected, and resampled all layers to match the spatial resolution (30 m) and coordinate reference system of the C density estimates. Next, across all layers, areas outside of the study region were masked as No-Data grid cells. Areas of overlap between the young growth and POG layers were allocated to the young growth category. We then used raster-based zonal statistics to quantify the magnitude of C stored in woody biomass and soil organic matter (to a depth of 1 m) inside and outside of the areas defined by the various GIS overlays described above. All geoprocessing, analysis, and visualization were performed using R statistical software (version 3.4, https://www.r-project.org; accessed on 5 May 2020), Python (version 3.6, https://www.python.org; accessed on 5 May 2020), GDAL (version 3.2, https://gdal.org; accessed on 5 May 2020), and Esri ArcGIS Pro (version 2.9, https://www.esri.com; accessed on 5 May 2020).

2.5. Evaluating At-Risk IRA and POG Scenarios

Administrative policy changes on the TNF have mainly centered on IRAs. Therefore, using the GIS methods and spatial data sets described above, we analyzed existing C stocks and thus, the potential loss of these C stocks, as part of three policy scenarios: (1) all IRAs within the 2016 TLMP Development LUDs are vulnerable; (2) only IRAs with POGs within 2016 TLMP Development LUDs are vulnerable; and (3) all IRA POGs within the 2016 TLMP Development LUDs considered suitable for logging are vulnerable based on reversion to the 2008 TLMP plan (which could happen under a pro-development future administration).

2.6. Estimating Emissions from Harvested Wood Products

We estimated CO_2 emissions associated with past (1909–2021) and projected (2022–2100) logging for wood product pools (HWP) on the TNF following published methods [29]. Logging for wood products removes C from the forest, transferring it to a series of production phases and end uses. Some fraction of the extracted C (i.e., roundwood) is temporarily stored in wood products (e.g., lumber, plywood, paper, etc.) while they remain in use, followed by eventual disposal and emission to the atmosphere [30]. Determining the climate impacts of HWP typically involves estimating C that is temporarily stored in wood products and in solid waste disposal (SWD) sites. The difference between the amount of C in roundwood removed from the forest and that stored in products and SWD sites at any given time constitutes realized emissions [29,30].

The most common method used to estimate CO_2 emissions from HWP is the Production Approach, which tracks C in wood that was harvested in a specified area regardless of where the wood is ultimately consumed. There are several accounting options that guide this calculation [29]. Here, we estimated the amount of C from a given year's logging (annually 1909–2100) that remains stored in end uses and landfills over a subsequent 100-year period [30]. This approach approximates the annual climate impact of withholding C from the atmosphere (i.e., C temporarily stored in HWPs) by a certain amount each year for 100 years as described by a series of decay curves [29]. The 100-year disposition approach facilitates tracking the full temporal impact of harvesting and attribution from the year in which the logging occurs to the year when emissions are ultimately realized (i.e., "seen" by the atmosphere).

Figure S1 illustrates the basic set of calculations used to track C in HWP from forest removal to timber products to primary wood products to end uses and finally to disposal, applying regional estimates for product ratios and half-lives at each stage. Harvest records are used to distribute annual cut volumes among specific timber product classes (e.g., softwood, sawtimber). Timber products are further distributed to specific primary wood products (e.g., softwood lumber, softwood plywood, softwood mill residue used for non-structural panels, etc.) using default average primary product ratios from national level accounting that describe primary products output according to regional forest industry structure [31,32].

We implemented the following multi-step procedure [29] in the R software package: (1) enter roundwood harvest data for the reporting period; (2) allocate harvest to product classes (e.g., sawtimber softwood, pulpwood softwood); (3) estimate the weight of harvested wood using average specific gravities by species group; (4) calculate the weight of harvested C for each harvest year; (5) estimate the 100-year annual disposition of C as fractions of roundwood by product class; (6) calculate C stock changes in the HWP pool and emissions for the inventory period; and (7) calculate annual additions to the HWP pool and associated emissions for the inventory period.

As inputs to this procedure, we used TNF timber harvest records for the period 1909–2021 obtained from USDA Forest Service cut history reports [9]. Harvest projections (2022–2100) were based on the Tongass Forest Plan [10]. We applied the average annual proportions of Alaska region harvests distributed to timber product classes ([33]: Table 3). We established decay rates following disposition patterns contained in the literature ([29]: Table 6-A-5) for the Pacific Northwest-West (PNW-W) region. Other researchers [29] did not include comprehensive (i.e., 100-year) decay functions, but rather included disposition patterns based on a subset of points along the trajectory of each function (i.e., years 1–10 and five-year intervals thereafter beginning in year 15). We estimated decay functions for PNW-W softwood sawlog and pulpwood emissions by fitting asymptotic regression functions to these data (SSasymp) in R.

We note that our results do not reflect total gross emissions from logging; rather, they are limited to the fate of harvested roundwood removed from the forest. Other logging-related emissions, including decay of logging residue, decomposition of litter, and loss of soil organic C were not included. Similarly, the results do not reflect net emissions as they do not consider, for example, C sequestration associated with forest regrowth nor do they account for emissions reductions that might be realized through material substitution, i.e., when wood is substituted for other building materials such as concrete or steel, although wood substitution benefits have been grossly overstated [34].

3. Results

3.1. Young vs. Productive Old Growth Forests

POGs represent about 30% of the Tongass land base and 92% of the productive forests overall. The balance includes unproductive old growth mainly on muskegs as well as non-forest types (see Figure 1). About 8% of the productive forest on the TNF or 3% of the total land base is in young growth condition, almost exclusively the result of old-growth clearcut logging. POG logging and associated road building has resulted in high levels of localized fragmentation, particularly on Prince of Wales Island (*Taan* in Tlingit), the largest and most productive island in terms of POG in the archipelago (Figure 1).

3.2. Timber Volume Sold by Time Period

Annual logging levels throughout the first half of the 20th century (i.e., early historical era) were 243,000 m^3 yr^{-1}, with the lowest levels recorded in 1909 at 37,000 m^3 (Table 1, Table S2). Logging ramped up substantially in the second half of the 20th century (pulp era), averaging ~2 million m^3 yr^{-1} and peaking in 1973 at nearly 3.6 million m^3, followed by a sharp decline in the late 1990s to <900,000 m^3 yr^{-1} (Table 1, Table S2). Between 2001 and 2015 (post pulp era), average logging volume was 230,000 m^3 yr^{-1}. From 2016 to 2021 (transition), average logging fell to 132,000 m^3 yr^{-1}, with the lowest level recorded at 71,000 m^3 in 2019 (Table 1, Table S2). Projecting forward, annual logging levels are expected to rise to 279,000 m^3 yr^{-1} from 2022 to 2031, and then to 595,000 m^3 yr^{-1} from 2032 to the end of the century (Table 1, Table S2). Nearly all of the projected harvest volume would come from young-growth forests should the transition to young-growth logging hold.

Table 1. Past (1909–2021) and projected (2022–2100) timber harvest levels on the Tongass National Forest by era, including average (thousand cubic meters per year) and total (thousand cubic meters) harvest levels. Projections are based on [10]. See Table S2 for annual harvest data.

Years	Era	Average Harvest (1×10^3 m^3 yr^{-1})	Total Harvest (1×10^3 m^3)
1909–1951	Early Historical	243	10,450
1952–2000	Pulp	2041	100,018
2001–2015	Post Pulp	230	3452
2016–2021	Transition	132	789
2022–2031	Projections	279	2793
2032–2100	Projections	595	41,059

3.3. Carbon Stocks

Total C stocks on the TNF are approximately 2679 Mt C (or ~2.7 Pg C, Table 2) with C density varying spatially across the region (Figure 2). Nearly half (48%; 1283.3 Mt) of the C is stored in POGs, split nearly evenly between soil (52.7%; 676.5 Mt C) and woody biomass (47.3%; 607.3 Mt C) (Table 2, Figures 3 and S2). Young growth accounts for just 4.8% (128.8 Mt C) of the total C, with nearly all of it (96%; 124.0 Mt C) outside IRAs (Table 2, Figure 3). IRAs account for just over half (51.3%; 1373.7 Mt) of the C, with soil and woody biomass accounting for 61.5% (845.4 Mt C) and 38.5% (528.3 Mt C) of that C, respectively (Table 2, Figures 3 and S3). Nearly 15% (392.9 Mt C) of all C in the study area is within T77 watersheds, with >80% (328.1 Mt C) of that C overlapping with IRAs and half of that (163.7 Mt C) overlapping with POG (Table 2, Figure 3). As anticipated, the C density of woody biomass in POG (293.5 (259–327) t C ha^{-1}) is greater than the C density of woody biomass in young-growth forest (281.6 (249–314) t C ha^{-1}) (Table 2); however, given the source data used in our analysis [25], C density in young-growth forest is likely overestimated.

Table 2. Carbon stocks (million metric tons) in woody plant biomass and soil organic matter by forest age class (productive old growth vs. young growth) inside and outside of Inventoried Roadless Areas (IRAs) and within the T77 watersheds in the Tongass National Forest, southeast Alaska. POG = Productive Old Growth; YG = Young Growth. Values in parentheses indicate ranges (lower and upper bounds). Biomass was scaled [25] to determine lower and upper bounds using the range of ratios between the live trees measured by Forest Inventory Analysis (FIA) plot data and the other C pools (excluding soils) [12]. Soil was not scaled (see [28]), hence the lack of ranges.

	Area	**Soil**	**Woody Biomass**	**Total**
	(ha)	**(Mt C)**	**(Mt C)**	**(Mt C)**
Inside T77 Watersheds				
Inside IRAs				
POG	256,897	92.2	71.6 (63.2–79.8)	163.7 (155.4–171.9)
YG	1112	0.4	0.2 (0.2–0.3)	0.6 (0.6–0.7)
Other	429,312	117.6	46.1 (40.7–51.3)	163.7 (158.3–168.9)
Subtotal	687,321	210.2	117.9 (104.1–131.3)	328.1 (314.4–341.5)
Outside IRAs				
POG	52,143	18.8	16.1 (14.3–18.0)	35.0 (33.1–36.8)
YG	20,904	8.4	6.1 (5.4–6.8)	14.5 (13.8–15.2)
Other	35,251	10.6	4.7 (4.2–5.3)	15.4 (14.8–15.9)
Subtotal	108,298	37.8	27.0 (23.8–30.1)	64.8 (61.7–67.9)
Total				
POG	309,040	111.0	87.7 (77.5–97.8)	198.7 (188.5–208.8)
YG	22,015	8.8	6.3 (5.6–7.0)	15.1 (14.4–15.9)
Other	464,563	128.2	50.8 (44.9–56.6)	179.0 (173.1–184.8)
Total	795,619	248.1	144.8 (128.0–161.4)	392.9 (376.0–409.4)
All Tongass				
Inside IRAs				
POG	1,060,035	349.5	311.7 (275.5–347.4)	661.2 (625.0–696.9)
YG	7978	2.9	1.8 (1.6–2.0)	4.7 (4.5–5.0)
Other	2,657,417	493.0	214.8 (189.8–239.3)	707.8 (682.7–732.3)
Subtotal	3,725,431	845.4	528.3 (466.9–588.7)	1373.7 (1312.3–1434.1)
Outside IRAs				
POG	1,009,308	327.0	295.6 (261.3–329.5)	622.6 (588.3–656.5)
YG	178,473	73.3	50.7 (44.8–56.5)	124.0 (118.1–129.8)
Other	1,860,951	376.8	181.6 (160.5–202.3)	558.4 (537.3–579.2)
Subtotal	3,048,732	777.1	527.9 (466.6–588.3)	1305.1 (1243.7–1365.4)
Total				
POG	2,069,344	676.5	607.3 (536.8–676.9)	1283.8 (1213.3–1353.3)
YG	186,451	76.3	52.5 (46.4–58.5)	128.8 (122.7–134.8)
Other	4,518,369	869.8	396.5 (350.2–441.6)	1266.3 (1220.0–1311.4)
Total	6774,163	1622.6	1056.3 (933.4–1177.0)	2678.8 (2556.0–2799.5)

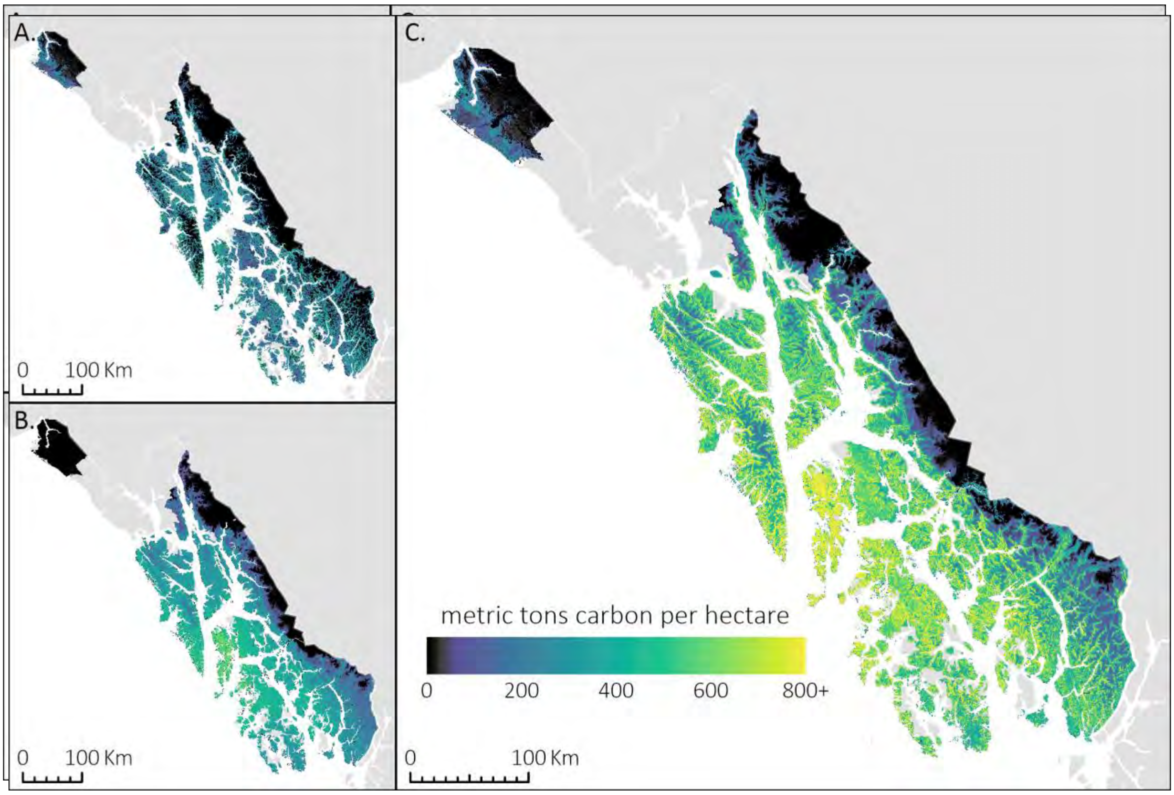

Figure 2. Spatial distribution of carbon (metric tons ha^{-1}) stored in (**A**) woody plant biomass (carbon pools include trees, roots, woody debris, seedlings/saplings, snags and understory vegetation), (**B**) soil organic matter (top 1 m of mineral soil plus surface organic horizons), and (**C**) the sum of biomass and soil in the Tongass National Forest.

Figure 2. Spatial distribution of carbon (metric tons ha^{-1}) stored in (**A**) woody plant biomass (carbon pools include trees, roots, woody debris, seedlings/saplings, dead snags, and understory vegetation), (**B**) soil organic matter (top 1 m of mineral soil plus surface organic horizons), and (**C**) the sum of biomass and soil in the Tongass National Forest.

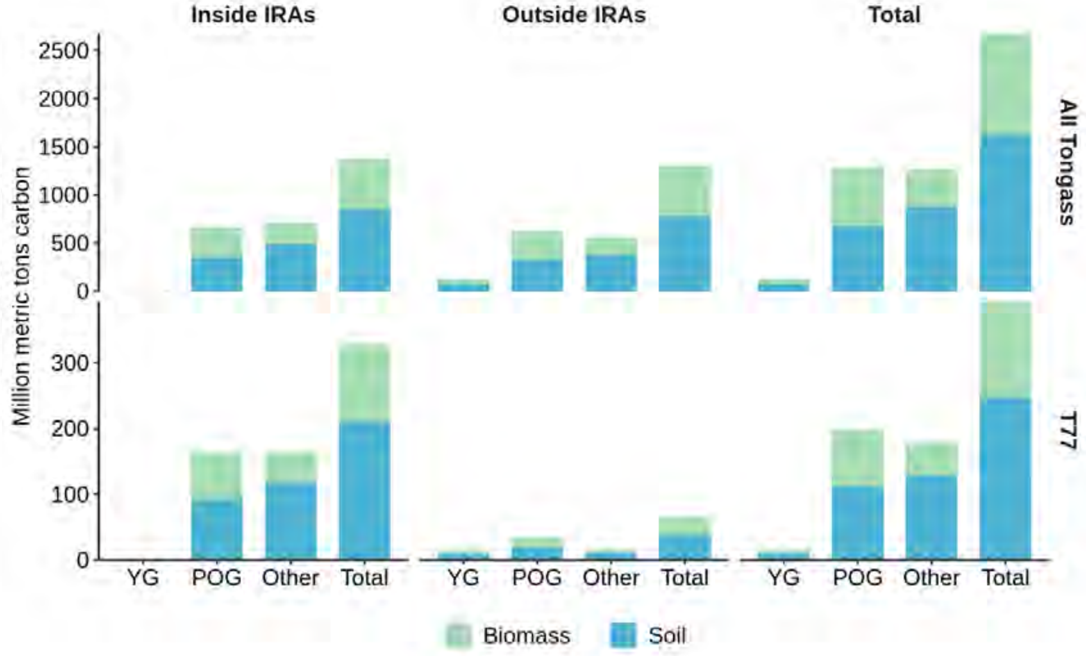

Figure 3. Carbon (million metric tons) stored in woody plant biomass and soil by forest age class (YG=young growth; POG=productive old growth) both inside and outside of Inventoried Roadless Areas (IRAs) and inside Tongass 77 watersheds (T77; bottom row) on the Tongass National Forest (top).

Figure 3. Carbon (million metric tons) stored in woody plant biomass and soil by forest age class (YG=young growth; POG=productive old growth) both inside and outside of Inventoried Roadless Areas (IRAs) and inside Tongass 77 watersheds (T77; bottom row) on the Tongass National Forest (top).

3.4. At-Risk Scenarios

About 11% of the total IRAs on the TNF are within LUDs that could be developed (Scenario 1, Table 3). Some 40% of the vulnerable IRAs and their C stock contain POG (Scenario 2, Table 3). About half those in at-risk IRAs would be exposed to development under the Trump administration's rollback of roadless protections (Scenario 3, Table 3). Notably, West Chichagof-Yakobi and Prince of Wales Island, along with several smaller islands close to the mainland, show the highest concentration of IRA vulnerabilities to development (Figure 4). Overall, our analysis illustrates the importance of retaining the protective measures of IRAs on the TNF.

Table 3. Area (hectares, ha) and carbon stocks (million metric tons) affected by three policy scenarios centered on at-risk inventoried roadless areas. See Section 2.5. for description of scenarios. Note, the areas of these regions are not mutually exclusive and are depicted visually in Figure 4. Values within parentheses are ranges (lower and upper bound). Biomass was scaled [25] to determine lower and upper bounds using the range of ratios between the live trees measured by Forest Inventory Analysis (FIA) plot data and the other C pools (excluding soils) [12]. Soil was not scaled (see [28]), hence the lack of ranges.

Scenario	Area (ha)	Soil (Mt C)	Woody Biomass (Mt C)	Total (Mt C)
1.	1,015,701	342.6	196.8 (173.9–219.3)	539.4 (516.5–561.9)
2.	408,808	148.1	117.5 (103.9–131.0)	265.6 (252.0–279.1)
3.	201,483	75.3	60.6 (53.6–67.6)	135.9 (128.8–142.8)

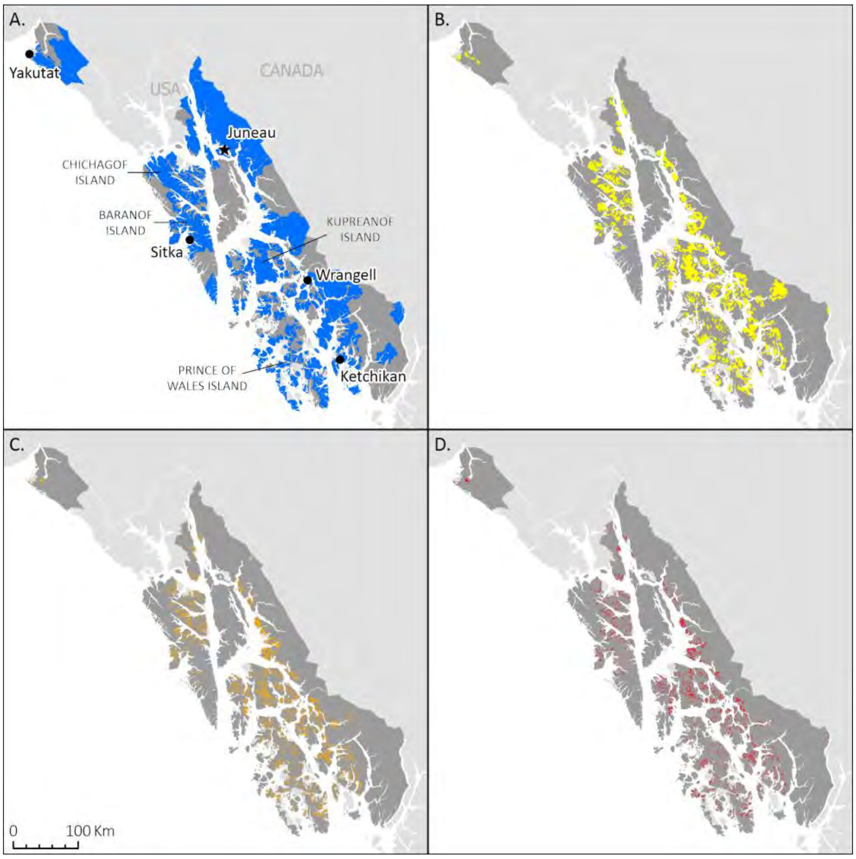

Figure 4. Spatial distribution of inventoried roadless areas based on: (**A**) all roadless areas (blue), (**B**) scenario 1 (yellow), (**C**) scenario 2 (orange), and (**D**) scenario 3 (red). Study area shown in gray. See Section 2.5. for description of scenarios.

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Our estimates of committed 100-year carbon dioxide emissions attributable to HWP (1910–2013) exhibit strong agreement with previous estimates [33] for the USFS Alaska Region (Tongass and Chugach National Forests combined; Figure S4). On the TNF, over the period 1909–2100, committed 100-year emissions track annual logging levels, rising sharply from the 1950s and peaking in the 1970s, followed by a decreasing trend into the 21st century (Figure 5). During this period (pulp era, 1952–2000), committed 100-year emissions average >900,000 t CO_2 yr^{-1}, the most of any period (Table 4). By the transition era (2016–2021), average committed emissions dropped more than 90% to 60,449 t CO_2 yr^{-1} (Table 4). With logging levels projected to rise into the future, committed emissions are anticipated to more than double to approximately 128,374 t CO_2 yr^{-1} between 2022 and 2031 and then more than double again to 273,492 t CO_2 yr^{-1} from 2032 onward (Table 4). Despite the expected increases, projected emissions should remain far below the peak emissions of the 1970s (Figure 5B, Table 4). Following a similar trend, annual realized emissions peaked during the pulp era (1952–2000), averaging >750,000 t CO_2 yr^{-1} followed by a drop to <250,000 t CO_2 yr^{-1} by the present day (Figure 5B, Table 4). Cumulative realized emissions show the fastest increase during the second half of the 20th century (Figure 5B), and over the full period of the analysis (1909–2100), we estimated 69.5 Mt CO_2 of cumulative emissions from HWP (Table S2).

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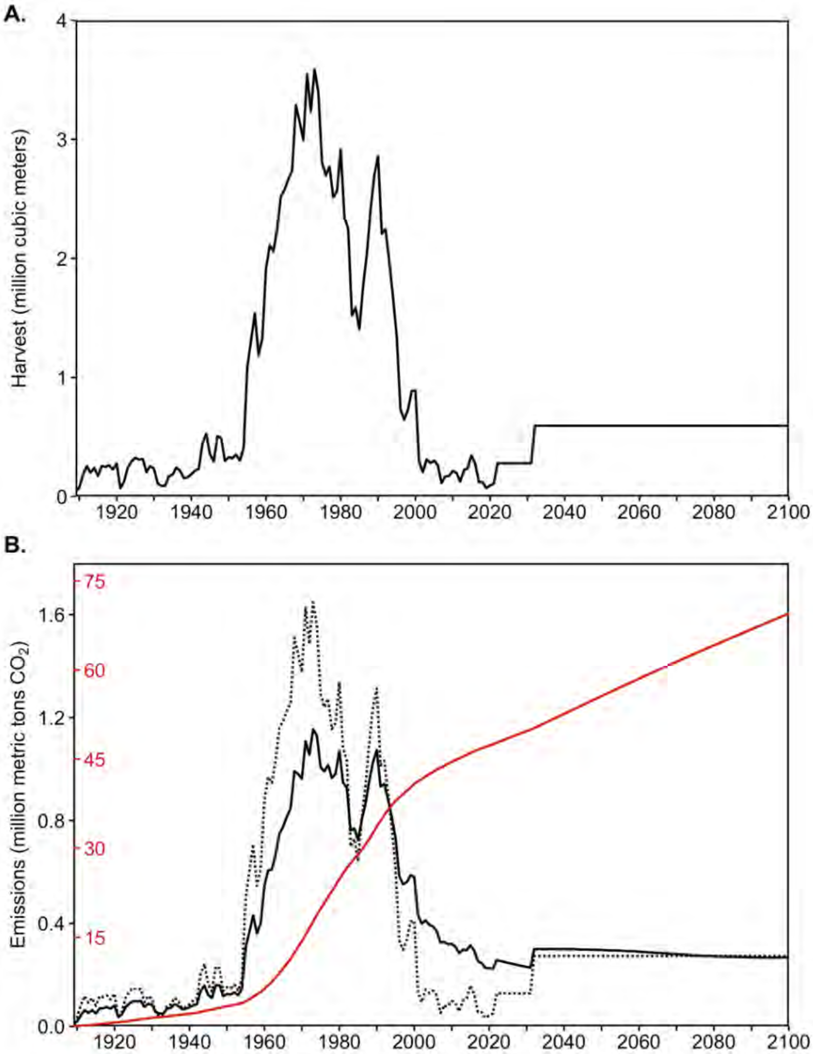

Figure 5. (**A**) Historic (1909–2021) and projected (2022–2100) annual harvest volumes (million cubic meters) for the Tongass National Forest. (**B**) Estimated 100-yr emissions from harvested wood products

(i.e., based on (**A**)), including annual committed (black dotted line), annual realized (black solid line), and cumulative realized (red line) emissions (million metric tons CO_2). Committed emissions reflect the CO_2 emissions that are annually committed to reach the atmosphere given the total harvested volume in a given year. Realized emissions model a more temporally realistic disposition of CO_2 emissions to the atmosphere following published wood product decay curves (see methods). Cumulative realized emissions track the cumulative sum of annual realized emissions through time.

Table 4. Historic (1909–2021) and projected (2022–2100) carbon dioxide emissions from harvested wood products (HWP) on the Tongass National Forest by era. Average (metric tons CO_2 per year) and total (million metric tons CO_2) annual committed and realized emissions are based on a 100-year HWP disposition period. See Table S2 for all annual-level estimates as well as cumulative realized emissions for the 1909–2100 timeframe.

Years	Era	Committed 100-Year Emissions		Realized 100-Year Emissions	
		Average ($t\ CO_2\ yr^{-1}$)	Total ($Mt\ CO_2$)	Average ($t\ CO_2\ yr^{-1}$)	Total ($Mt\ CO_2$)
1909–1951	Early Historical	111,692	4.8	81,673	3.5
1952–2000	Pulp	938,147	46.0	761,687	37.3
2001–2015	Post Pulp	105,763	1.6	346,387	5.2
2016–2021	Transition	60,449	0.4	244,912	1.5
2022–2031	Projections	128,374	1.3	242,374	2.4
2032–2100	Projections	273,492	18.9	284,168	19.6

4. Discussion

4.1. Timber Volume and Associated Impacts

Logging on the TNF can be traced back to at least 1909 with timber volume at 37,000 m^3; logging remained at relatively low levels of $\leq$243,000 $m^3\ yr^{-1}$ for decades prior to World War II. The relatively low early historical levels were mainly because Alaska was the last old growth timber frontier in the USA and the high cost of access (roads) and shipping logs overseas. However, the onset of the pulp era, and signing of two 50-year contracts in the 1950s, ushered in nearly a 15-fold increase over the early historical period, with a peak in logging volume in 1973 followed by a precipitous decline when the pulp contracts expired in 2000. During peak years, the largest tree POG forests were disproportionately targeted due to high levels of timber volume at the stand level [1]. Timber volumes hit their lowest contemporary levels in 2019, a 50-fold decrease from the 1973 peak. Logging levels are projected to increase ~8-fold from the 2019 low through the end of the century, with most of the volume anticipated from young forests (if the transition to young-growth logging holds). In general, future fluctuations in timber volumes are anticipated under the TLMP transition plan due to a range of factors, including timber demand (e.g., exports vs. domestic), political pressure (presidential administrations), forest plan amendments, and institutional factors related to the time required by the agency to fully transition.

Historical logging on the TNF has come at the expense of primary, old-growth rainforest and intact forest landscapes (roadless areas), which have been replaced by >186,451 ha of production, high road density (>2.6 km/km^2), and naturally regenerated monocultures lacking the structural complexity, C storage capacity, and biodiversity of old growth [2,3]. Much of the logging has been concentrated on Prince of Wales Island, the largest island with the most POG in the Alexander Archipelago [35]. Notably, over 8000 km of roads crisscross the TNF, 2400 km (30%) of which are on Prince of Wales Island alone (https://dot.alaska.gov/stwdplng/scenic/byways-pow.shtml, accessed on 11 February 2022). The impacts of road building can extend 1 km on either side of the road, potentially affecting sensitive taxa, water quality, C storage and sequestration among other impacts [6]. Additionally, since 1980, the timber volume sold from the TNF has generated a deficit, with administrative expenses exceeding revenues and sales proceeding regardless due to congressionally subsidized below-cost timber sales at a cost of approximately $1.7 billion (https:

//www.taxpayer.net/energy-natural-resources/cutting-our-losses-tongass-timber-2/, accessed on 11 February 2022). The TNF represents the most expensive timber program in the national forest system mainly because of road construction and maintenance costs in a remote, island-dominated region.

Despite peak logging periods and high-grade logging practices [1], 92% of productive forests on the TNF remain in old growth condition, compared to 8% in young growth (following previous clearcut logging). Earlier studies reported 90% of productive forests were POG based on USDA reports in 1991 [21]. Others [1,35] reported 88% of the entire region of southeast Alaska (state and native Alaskan corporation lands included) was POG at the time. Slight differences in POG estimates are likely due to differences in spatial extent and methods among studies. Nevertheless, the TNF is unique in that most of its forests remain POG, unlike those in the conterminous USA where nearly all old growth was logged long ago and replaced by intensively managed timber lands.

4.2. Carbon Stock (Carbon Reservoir)

Our findings underscore the significance of the C stock on the TNF. Using FIA plot data, researchers [12] reported the total Tongass C stock of 2.8 ± 0.5 Pg as compared to 2.7 Pg (upper bound 2.8) in our study. The earlier study [12] also noted that the TNF represented 8% of the total C stock in all forests in the conterminous USA. Our figure of 20% compares the Tongass C stock to that of the national forest system [36] rather than all conterminous USA forests [12], showcasing the significance of the TNF among federally managed national forests. The high C stock value of the TNF is particularly noteworthy given that the TNF represents just under 9% of the total area of the national forest system but has a relatively large share (20%) of the national forest C stock. This relative comparison speaks not only to the significance of the TNF as a C reservoir, but also as a region of conservation focus, allowing decision makers to prioritize strategically important natural climate solutions [37,38]. Notably, the 2.7 Pg C stock estimate for the TNF represents a CO_2e of 1.5 times US aggregate GHG emissions in 2019 (https://www.epa.gov/sites/default/files/2021-04/documents/us-ghg-inventory-2021-main-text.pdf?VersionId=uuA7i8WoMDBOc0M4ln8WVXMgn1GkujvD; accessed on 15 April 2022).

In this study and a prior one [12], a substantial amount of the stored C was in the soils. We reported ~53% and 47% of C in soils and woody biomass, respectively, compared to the earlier [12] estimate of 66% and 36% of C in the soil and woody biomass pools. Our findings for IRAs are closer to earlier figures [12], with 62% and 39% of C in soils and biomass, respectively. Differences in C stock estimates likely reflect the datasets used (FIA plots vs. pooled datasets in our study) and perhaps differences in site productivity among sampled areas. Importantly, our study provides a spatially explicit and updated dataset that can be publicly accessed (databasin.org).

It should be noted that we assessed only the C stock value of the TNF. Prior researchers [12] provided an estimate of the annual C sequestration rate of unlogged forests at 0.04–0.33 Tg C yr^{-1}, which would build on the C sink potential of the TNF as logging transitions out of the most C rich and biodiverse areas.

4.3. Importance of IRAs and Tongass 77 Watersheds

Inventoried roadless areas have a long history of conservation in the USA, beginning in the 1970s with the RARE I and RARE II (Roadless Area Review and Evaluation) mapping processes used for making wilderness nominations to Congress [39]. Subsequently, a lot of attention has focused on IRAs, with some areas being designated wilderness, and most others protected administratively (National Roadless Conservation Rule) because of their superior biodiversity values compared to logged areas [5–7].

The TNF is a "hot spot" of IRA values and challenges, representing 16% of the nation's total IRAs and the subject of numerous court cases. While IRA fish and wildlife habitat values have been documented on the TNF [40], our study is the first to quantify the C stock value of IRAs, which contain over half the entire C stock on the TNF. Importantly, the C stock within IRA POGs (and POGs generally) are likely to remain relatively stable compared to the interior of Alaska and the southern extent of the North Pacific coastal temperate rainforest biome subject to more extreme climate change [41–43].

The protection of IRAs also has enjoyed broad public support (>95% of thousands of comments received by the USDA Forest Service have been supportive; https://www.usda.gov/media/press-releases/2021/11/19/usda-announces-steps-restore-roadless-protections-tongass-national; accessed on 14 February 2022) from Alaskan tribes, scientists, conservation groups, and fishing and recreational interests that may benefit economically and culturally (traditional tribal values) from these intact ecosystems if they are fully protected.

The T77 watersheds also contain important POG habitat, but the T77 conservation strategy alone represents far less C savings than IRAs, with only about 15% of the total C stock in T77s, mostly within the T77 POGs. The lower C stock value is likely an artifact of the selection process for the T77, which was weighted toward salmon conservation regardless of the presence of POGs, so long as watersheds were intact (no roads) and productive in terms of salmon. Nevertheless, the T77 watersheds have biodiversity and other values that extend well beyond the C-centric focus of our study [11].

4.4. Stock Change Due to Logging

The USDA Forest Service has repeatedly stated that emissions from logging on the TNF are insignificant compared to total US GHGs and thus logging emissions can be summarily dismissed since they are offset by both natural forest regeneration and storage in HWP pools [10,24]. However, offsetting emissions by forest regrowth involves a time lag of at least a century for an equivalent stock of C to be re-sequestered [30]. While forest regeneration on productive Tongass sites proceeds quickly (within a decade), and is from natural seed sources (nearby standing trees), young forests are expected to remain on short logging rotations with harvests planned every 55–70 years on productive sites under the TLMP transition plan. On average, after 100 years, storage in wood products from the PNW, for example, accounts for ~13% of the original C stock with an additional ~29% in landfills [29]. Thus, wood products represent little more than delayed emissions [30]. Additionally, the extensive road network, including log-landings and haul-out sites, means an unknown amount of the C stock may never be replaced so long as those areas remain treeless.

Our estimates of logging emissions from the TNF are conservative given that they involve the conversion of roundwood in cubic meters to CO_2 emissions. Accounting for out-of- boundary emissions in wood processing and log transport is beyond the scope of our study; however, these additional emissions can be substantial given that up to 50% of roundwood logs can be exported over large distances (e.g., to China and Japan) [10].

5. Conclusions

As one of the world's last relatively intact temperate rainforests, the TNF provides ecosystem services that are of global significance and warrant expanded conservation. The TNF represents ~12% of the entire Pacific Northwest Coastal Forest bioregion, an expansive rainforest region spanning several globally distinctive ecoregions and climatic subzones from the Coast Redwoods to the northern Kodiak archipelago in Alaska, which collectively make up 34% of all the world's temperate rainforests, the largest such concentration [3]. Some 2.1 M ha of the TNF remains as POG, also among the largest such amounts for temperate rainforests [2,3]. The TNF, contains 16% of the nation's IRAs, which, along with the Chugach National Forest to the north, represent the most relatively intact national forest in the national forest system. Its abundant salmon runs (all six *Oncorhynchus* species) and wildlife populations, some of which are imperiled in the lower 48 states, achieve their highest densities in intact watersheds such as the Tongass 77 [11].

Our study builds on the knowledge base of the Tongass' disproportionate values by documenting that some 20% of the entire national forest C stock is remarkably held by this single national forest alone, providing if nothing else a C reservoir of national significance.

Most of the C stock is in POGs, roughly distributed between roaded areas and IRAs. By contrast, only ~5% of the C stock is within young growth and mostly roaded areas.

The maritime climate and intact forests of the TNF have climate refugia properties compared to more extreme climatic zones in the interior of Alaska and temperate rainforests further south [41–43], thereby offering a relatively stable C reservoir. However, due to declining late-season snow cover that prevents late-winter root freezing, yellow-cedar is experiencing a range contraction, and is a climate-sensitive focal species [44]. Importantly, many fish and wildlife species that benefit from IRAs and POGs are the staple foods of Native Alaskans, representing an important bio-cultural connection made possible by the relative intactness of the Tongass rainforest system.

Despite its global recognition, including its near incomparable position among old-growth temperate rainforests, the TNF is a dynamic system where island biogeographic effects have contributed to isolation factors with potentially high species turnover rates [45]. Notably, the cumulative addition of novel anthropogenic fragmentation from expansive roads and clearcuts may result in more consequential isolation of vulnerable species over time, especially on Prince of Wales Island where logging and roads are greatest. For instance, the Alexander Archipelago wolf (*Canis lupus ligoni*) has been repeatedly proposed for listing under the USA Endangered Species Act with the US Fish and Wildlife Service recently determining that listing may be warranted (https://www.fws.gov/alaska/stories/service-completes-initial-review-petition-list-alexander-archipelago-wolf-species-status#:~:text=The%20U.S.%20Fish%20and%20Wildlife,you%20can%20access%20the%20document; accessed on 14 February 2022). Concerns over the status of wolf populations on Prince of Wales Island are mainly due to declining deer populations and hunting pressures [46]. However, the relative intactness of IRAs, POGs, and the T77 offer the best prospects for maintaining viable wildlife populations that are otherwise under combined pressures of climate change and anthropogenic habitat fragmentation.

Our results, coupled with broad scientific and public interest in the TNF as “America’s rainforest,” provide a foundation for a multi-pronged conservation strategy that includes: (1) protecting all remaining old growth, IRAs, and T77 priority areas from logging as strategic carbon reserves [38]; (2) supporting the transition to logging young-growth forests that by some accounts can already accommodate a full transition without further POG logging [47]; and (3) increasing ecological-based restoration of high road density areas (e.g., road decommissioning). A small portion (7978 ha) of young-growth forest is within IRAs where logging was likely conducted by helicopter. Those areas should be candidates for proforestation [37] to restore carbon stocks over time. Thus, a climate-smart strategy centered on sequestration and accumulation of C is generally essential to addressing the climate crisis [37] and would offer co-benefits, including a host of ecosystem services derived from C dense forests [48] as well as potential climate refugia [41–43].

The TNF is uniquely positioned for large-landscape conservation that protects remaining primary rainforest given that the transition out of old growth logging is taking place before most, if not all, of the primary forests are gone, unlike most nations that only transition when primary forests are liquidated and replaced by industrial forest lands [49]. As the national champion of forest C stocks, federally mandated protection of TNF POGs, IRAs, and T77 areas would offer global leadership on the establishment of land-based targets under the Paris Climate Agreement, while following through on the Glasgow leaders’ declaration to end global forest losses by 2030 (which included President Biden) [50].

Notably, Article 5.1 of the Paris Agreement states [19], “Parties should take action to conserve and enhance, as appropriate, sinks and reservoirs of greenhouse gases.” Additionally, the Summary for Policy Makers (SPM) of the Working Group II contribution to the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report [51] noted that “safeguarding biodiversity and ecosystems is fundamental to climate resilient development, in light of the threats climate change poses to them and their roles in adaptation and mitigation (very high confidence).” Our results support the inclusion of the Tongass National Forest in a forest carbon reserve system centered on IRAs, POGs, the T77, and a portion of young growth to conserve and enhance the substantial carbon values and resilience potential of this forest.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land11050717/s1, Figure S1: Approach to quantifying harvested wood product pools (HWP) storage and emissions; Figure S2: Spatial distribution of total carbon (metric tons ha^{-1}) in woody plant biomass and soil in at-risk scenarios for IRAs (inventoried roadless areas): (A) all IRAs, (B) Scenario 1, (C) Scenario 2, and (D) Scenario 3. Figure S3: Spatial distribution of T77 watersheds and total carbon (metric tons ha^{-1}) in woody plant biomass and soil pools combined. Figure S4: Committed 100-year emissions from both Tongass and Chugach National Forest timber harvests (1910–2013). Comparison of our study with prior research. Table S1: Carbon datasets used in this study. Table S2: Historic (1909–2021) and projected (2022–2100) harvest levels (thousand cubic meters per year, 1×10^3 m^3 yr^{-1}), committed 100-year emissions (thousand metric tons carbon dioxide equivalents per year, 1×10^3 tCO$_2$ yr^{-1}), annual realized emissions (1×10^3 tCO$_2$ yr^{-1}), and cumulative realized emissions (1×10^3 tCO$_2$ yr^{-1}) on the Tongass National Forest. All emissions estimates are based on a 100-year HWP disposition period. Supplemental references provided [52].

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Human ignitions on private lands drive USFS cross-boundary wildfire transmission and community impacts in the western US

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Wildfires in the western United States (US) are increasingly expensive, destructive, and deadly. Reducing wildfire losses is particularly challenging when fires frequently start on one land tenure and damage natural or developed assets on other ownerships. Managing wildfire risk in multijurisdictional landscapes has recently become a centerpiece of wildfire strategic planning, legislation, and risk research. However, important empirical knowledge gaps remain regarding cross-boundary fire activity in the western US. Here, we use lands administered by the US Forest Service as a study system to assess the causes, ignition locations, structure loss, and social and biophysical factors associated with cross-boundary fire activity over the past three decades. Results show that cross-boundary fires were primarily caused by humans on private lands. Cross-boundary ignitions, area burned, and structure losses were concentrated in California. Public lands managed by the US Forest Service were not the primary source of fires that destroyed the most structures. Cross-boundary fire activity peaked in moderately populated landscapes with dense road and jurisdictional boundary networks. Fire transmission is increasing, and evidence suggests it will continue to do so in the future. Effective cross-boundary fire risk management will require cross-scale risk co-governance. Focusing on minimizing damages to high-value assets may be more effective than excluding fire from multijurisdictional landscapes.

Global fire dynamics are shifting dramatically in the twenty-first century. Changing fire regimes are intersecting with the consequences of historical fire and forest management practices[1–3], as well as increasing expansion of the wildland urban interface (WUI)[4]. Rising temperatures, increased drought, longer fire seasons, and earlier snowmelt have all been associated with more burning in recent decades[5–7]. In addition, the accumulation of wildland fuels resulting from fire suppression and other land management practices is further increasing fire activity. Prior to Anglo-European colonization in the western United States, fire burned with a wide range of extents, frequencies, and severities, limited by the availability of fuel, favorable fire weather, and ignition sources[8]. As European colonization intensified, historical fire regimes were significantly altered by factors including the cessation of indigenous burning practices and the widespread adoption of aggressive fire suppression[9–11]. Meanwhile, human development in and around wildlands expanded by 41% between 1990 and 2010, making the WUI the fastest growing land use type in the US[4]. Increased development has resulted in both more risk and more loss. Millions of homes in the WUI are threatened by wildfires each year[12], and the annual number of structures lost to wildfire increased by 300% between 1990 and 2014[13].

As the WUI expands, there is often increased socio-ecological conflict, whereby anthropogenic pressures have negative impacts on natural resources; and natural disturbances, such as fire, have negative consequences for human communities[14,15]. The dramatic expansion of the WUI has exacerbated the wildfire problem by resulting in more human-caused ignitions[16], which are now the dominant cause of fire in the US[17] and the primary source of fire risk to communities[12]. Each year in the western United States (US) federal agencies undertake

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increasingly costly (~ \$5 billion year^{-1}) efforts to suppress wildfires and reduce social, economic, and ecological wildfire damages[18]. However, increased fire suppression has not translated into decreased damages. Wildfires are getting bigger, more destructive, and more deadly[19–21]. In California alone, the wildfires of 2018 burned 7,400 km^2 and resulted in the deaths of 103 people, the loss of 22,000 structures, and estimated economic damages totaling \$148.5 billion[20,22].

The tension between ecological processes (e.g., fire) and social processes (e.g., WUI development) in mixed ownership landscapes is brought into stark relief when fire ignites on one land tenure and spreads to other ownerships, especially when it results in severe damages to communities on private lands and/or highly valued natural resources on publicly managed wildlands. These cross-boundary (CB) wildfires present particularly acute management challenges because the responsibilities for preventing ignitions, stopping fire spread, and reducing the vulnerability of at-risk, high-value assets are often dispersed among disparate public and private actors with different objectives, values, capacity, and risk tolerances[23–25]. Some CB risk mitigation strategies exist, such as fire protection exchanges, which transfer suppression responsibility from one agency (e.g., state) to another (e.g., U.S. Forest Service), and CB fuel treatment agreements, which allow managers to influence components of wildfire risk beyond their jurisdictional boundaries[2,26]. Improving CB wildfire risk management has been identified as a top national priority[27], but effective, landscape-scale solutions are not readily apparent.

A common narrative used to describe CB fire is as follows: a wildfire ignites on remote public lands (e.g., US Forest Service), spreads to a community, showers homes with embers, and results in structure loss and fatalities[23,25,28]. In this framing, public land management agencies bear the primary responsibility for managing and mitigating CB fire risk, with effort focused on prevention, hazardous fuel reduction, and suppression—largely reinforcing the dominant management paradigm of fire exclusion[29,30]. An alternative risk management framing of this challenge has emerged, starting with the axiom that CB fire transmission is inevitable in fire-prone mixed ownership landscapes and that private landowners and homeowners are the actors best positioned to reduce fire risk to homes and other high-value assets regardless of where the fire starts[31]. In the absence of a broad-scale empirical assessment of CB fire transmission, it is difficult to determine which of these narratives more accurately reflects the nature of the problem, and whether CB fire risk management is best framed in terms of reducing fire transmission from public lands or decreasing the exposure and vulnerability of high-value developed assets on private lands.

Despite advances in simulated wildfire hazard assessments and legislation and policy promoting CB wildfire risk engagement, important knowledge gaps remain regarding the causes, ignition locations, structure loss, and social and biophysical factors associated with recent CB fire activity. One possibility is that all else being equal, CB fire activity simply increases proportionally with the number and extent of jurisdictional boundaries available for fires to cross. Alternatively, CB burning may be primarily controlled by the degree to which a landscape's temperature, precipitation, and fuels promote ignition and fire spread[32,33]. If biophysical drivers were dominant, we would expect that CB area burned would essentially mirror area burned by fire that did not cross jurisdictional boundaries, and we might anticipate that more CB fire would occur in areas where fire intensities often exceed the capacity of firefighters to prevent fire spread. A third possibility is that social factors such as population density and road networks may override climatic and fire behavior factors, as has been observed in a number of fire-prone regions[16,34,35]. These uncertainties make it difficult to prioritize specific mitigation actions and identify the actors best positioned to manage different aspects of fire transmission risk. Understanding why there is more CB fire activity in some places and less in others could help target mitigations based on causal factors, but the social and biophysical factors associated with CB fire transmission have not been systematically explored across the western US.

In this paper we present an empirical assessment of recent CB fire activity in the western US. We use the United States Department of Agriculture Forest Service (USFS) National Forest System and surrounding ownerships as our focal domain, and define CB fires as those fires that burned both USFS lands and other land tenures. The USFS is the largest fire management organization in the US and administers approximately 75% of federal wildfire appropriations[18]. We began by leveraging comprehensive fire occurrence, area burned, and structure loss datasets to undertake a spatially explicit, retrospective analysis of fire transmission across USFS jurisdictional boundaries. Next, we analyzed these spatial data using a machine learning statistical modeling approach to evaluate the strength and shape of relationships between CB fire activity and suite of biophysical and social factors. Specifically, we asked: (1) How much CB fire has occurred, and how have fire transmission rates changed in the last three decades? (2) Where, and on what ownerships, is CB activity most common? (3) Do the most destructive wildfires originate primarily on public lands managed by the USFS and spread to communities? (4) What are the social and biophysical factors most strongly related to variability in CB area burned and CB ignition densities on USFS and private lands, the two dominant sources and recipients of CB in our study domain?

Results

A total of 6.9 million ha burned in CB fires between 1992 and 2019, approximately half on USFS lands (3.5 million ha) and half on other ownerships (3.4 million ha). CB area burned varied by five orders of magnitude (8 ha—351,625 ha) among the 74 national forests surveyed. Fire transmission was concentrated in a relatively small group of national forests located primarily in California (Figs. 1 and 2). We observed substantial variation in the relative amounts of area burned by fires ignited off USFS lands that spread to national forests ("inbound") and area burned by fires that ignited on USFS lands and spread to other ownerships ("outbound"). CB area burned exhibited substantial inter-annual variability along with clear evidence of a general increase over the last three decades (Fig. 3). Inbound area burned on USFS lands increased at a higher rate (1,905 ha year^{-1}) than outbound area burned on lands the USFS has suppression responsibility according to protection exchanges (678 ha year^{-1}) and lands not protected by the USFS (732 ha year^{-1}).

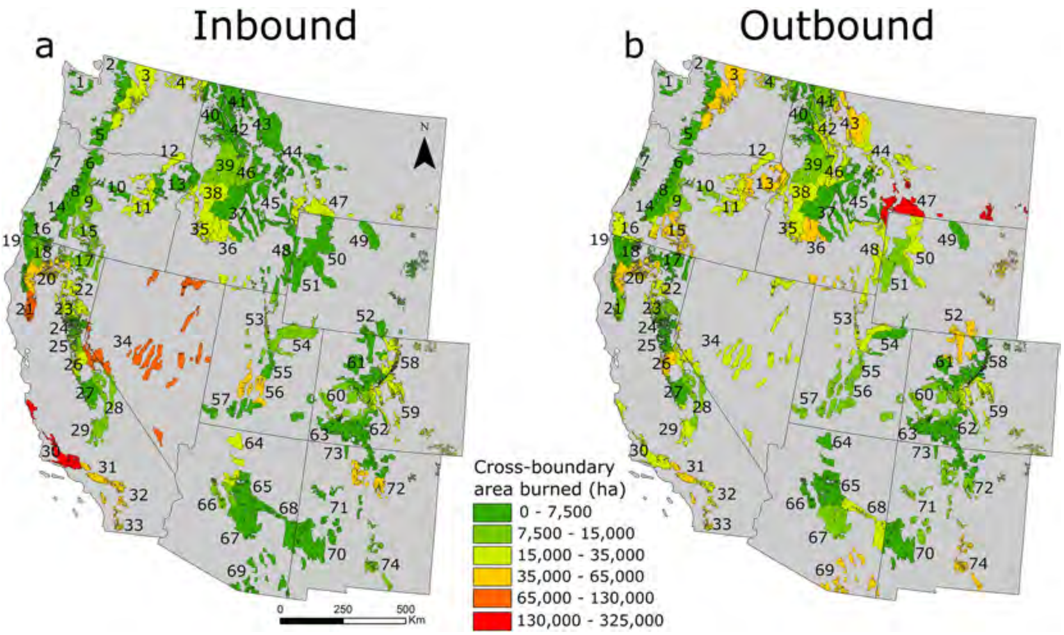
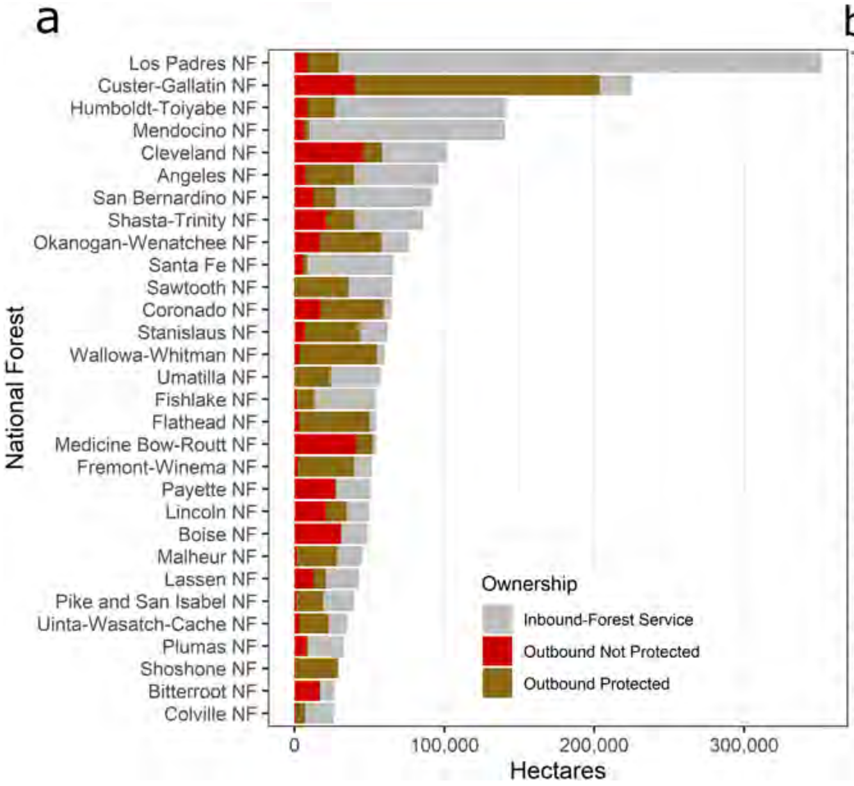


Figure 1. Area burned by CB fires that impacted USFS lands. Polygons represent USFS national forests. (**a**) USFS area burned by fires ignited on non-USFS lands (inbound). (**b**) Area burned outside of national forests by fires ignited on USFS lands (outbound). 1. Olympic, 2. Mt. Baker-Snoqualmie, 3. Okanogan-Wenatchee, 4. Colville, 5. Gifford Pinchot, 6. Mt. Hood, 7. Siuslaw, 8. Willamette, 9. Deschutes, 10. Ochoco, 11. Malheur, 12. Umatilla, 13. Wallowa-Whitman, 14. Umpqua, 15. Fremont-Winema, 16. Rogue River-Siskiyou, 17. Modoc, 18. Klamath, 19. Six Rivers, 20. Shasta-Trinity, 21. Mendocino, 22. Lassen, 23. Plumas, 24. Tahoe, 25. Eldorado, 26. Stanislaus, 27. Sierra, 28. Inyo, 29. Sequoia, 30. Los Padres, 31. Angeles, 32. San Bernardino, 33. Cleveland, 34. Humboldt-Toiyabe, 35. Boise, 36. Sawtooth, 37. Salmon-Challis, 38. Payette, 39. Nez Perce-Clearwater, 40. Idaho Panhandle, 41. Kootenai, 42. Lolo, 43. Flathead, 44. Helena-Lewis and Clark, 45. Beaverhead-Deerlodge, 46. Bitterroot, 47. Custer-Gallatin, 48. Caribou-Targhee, 48. Bighorn, 50. Shoshone, 51. Bridger-Teton, 52. Medicine Bow-Routt, 53. Uinta-Wasatch-Cache, 54. Ashley, 55. Manti-La Sal, 56. Fishlake, 57. Dixie, 58. Arapaho-Roosevelt, 59. Pike-San Isabel, 60. Grand Mesa Uncompahgre-Gunnison, 61. White River, 62. Rio Grande, 63. San Juan, 64. Kaibab, 65. Coconino, 66. Prescott, 67. Tonto, 68. Apache-Sitgreaves, 69. Coronado, 71. Cibola, 72. Santa Fe, 73. Carson, 74. Lincoln.

Approximately 11% of all fires on national forest lands burned across USFS boundaries. Most CB ignitions were human-caused (e.g., debris burning, equipment use, escaped campfires) and originated on private lands (Table 1). CB ignitions were most abundant in parts of southern California where USFS lands abut dense population centers, and relatively rare in sparsely populated landscapes such as Wyoming and Nevada, and cool, wet environments such as northwest Washington (Fig. 4). We quantified a CB ignition zone based on the distance most (90%) CB ignitions occurred from a USFS boundary. The CB ignition zone extended 2.6 km within USFS lands and 4 km outside of USFS lands (Fig. 5).

A systematic inventory of fire-induced structure loss from ICS-209 and ancillary spatial datasets resulted in a list of 91 fires that destroyed more than 50 buildings between 2000 and 2018 (Fig. 6). Fires starting on USFS lands represent (24%) of destructive fires, and these fires were responsible for 14.7% (5077) of the total structures destroyed (34,493). Only two destructive fires ignited on USFS lands were caused by lightning, the remainder were started by humans, including energy infrastructure. The majority (63) of destructive fires occurred in California, most of which were human-caused on private lands.

Boosted regression tree statistical modeling, a machine learning algorithm, demonstrated strong associations between CB fire activity and multiple social and biophysical factors (Table 2, Fig. 7). Models were fit for four response variables: (1) private CB ignitions, (2) USFS CB ignitions, (3) area burned by outbound CB fire, and (4) area burned by inbound CB fire. The performance of CB ignition models was very good (USFS deviance explained = 75%, cross-validated = 72%; private deviance explained = 84%, cross-validated = 75%). For the private ignitions model, population was the most important variable. Predicted ignitions displayed a hump-shaped response peaking at around 150,000 people within the CB ignition zone. Private ignitions increased sharply with jurisdictional boundary density and plateaued at moderate values. We observed a strong positive association between private ignitions and road density, and a weak positive association with average temperature. For the USFS ignitions model, road density was the most important variable and demonstrated a strong positive association with ignitions. Predicted USFS ignitions peaked in hot, dry locations with moderate population levels. There was evidence of residual spatial autocorrelation in both ignition models that was resolved when a residual autocovariate was added.



b

National Forest	Non-transmitted fire load (ha)	CB/NT
Los Padres NF	274,221	1.28
Custer-Gallatin NF	247,561	0.91
Humboldt-Toiyabe NF	175,773	0.80
Mendocino NF	94,330	1.49
Cleveland NF	96,464	1.06
Angeles NF	138,164	0.69
San Bernardino NF	113,615	0.81
Shasta-Trinity NF	297,783	0.29
Okanogan-Wenatchee NF	516,185	0.15
Santa Fe NF	60,860	1.08
Sawtooth NF	119,949	0.54
Coronado NF	384,060	0.17
Stanislaus NF	97,997	0.63
Wallowa-Whitman NF	301,594	0.20
Umatilla NF	102,581	0.56
Fishlake NF	68,873	0.79
Flathead NF	236,848	0.23
Medicine Bow-Routt NF	92,404	0.59
Fremont-Winema NF	87,903	0.59
Payette NF	583,667	0.09
Lincoln NF	97,974	0.51
Boise NF	560,580	0.09
Malheur NF	115,188	0.39
Lassen NF	55,272	0.78
Pike and San Isabel NF	82,998	0.48
Uinta-Wasatch-Cache NF	82,916	0.43
Plumas NF	105,557	0.31
Shoshone NF	105,069	0.28
Bitterroot NF	269,828	0.10
Colville NF	45,057	0.58

Figure 2. (**a**) National forests ranked according to area burned by CB fire between 1992 and 2019. Some forests are net receivers of inbound fire (e.g., Los Padres), while others are net transmitters (e.g., Custer-Gallatin). (**b**) Total non-transmitted fire load and the ratio of CB area burned (inbound and outbound) to the area burned by non-transmitted fire (CB/NT). CB fire is a major contributor to area burned in and around some national forests (e.g., Mendicino) and not others (e.g., Payette).

At the national forest scale, CB area burned model performance was comparatively worse (outbound deviance explained = 44%, cross-validated = 42%; inbound deviance explained = 32%, cross-validated = 30%), but we did observe important correlations. For the outbound model, the most important variable was area burned by non-transmitted (NT) fire, which was positively associated with outbound area burned up to intermediate values (~ 300,000 ha). A similar, but weaker relationship was observed between outbound area burned and inholdings. Fire intensity, represented by conditional flame length, was negatively associated with outbound area burned up to six meters, beyond which the response leveled off. Similarly, outbound CB area burned peaked at around 7 °C. CB area burned was relatively low at average annual temperatures greater than 15 °C. For the inbound area burned model, conditional flame length was the most important variable; CB area burned increased sharply as flame lengths increased from six to eight meters. Inbound area burned increased substantially between 12 and 18 °C average annual temperature. Population exhibited a strong positive association with inbound area burned up to approximately 300,000 people. The relationship between inbound area burned and inholdings was similar to the outbound model. Evidence of residual spatial autocorrelation in the inbound model was addressed with the addition a residual autocovariate. The outbound model did not exhibit residual spatial autocorrelation.

Discussion

Our study provides the first region-wide empirical assessment of CB fire transmission patterns in the western US. By leveraging multiple fire databases, we were able to identify ownership at ignition for CB fires that burned both USFS lands and other ownerships. The magnitude and directionality of CB fire transmission varied substantially across our study area, but overall, CB fires were more likely to originate on private lands than USFS lands. CB ignitions, area burned, and structure loss were all concentrated in parts of California, where approximately two-thirds of CB fire activity occurred on USFS lands from fires originating on other ownerships. Our findings do not support the assertion that a majority of the most destructive fires spread from USFS-managed wildlands to communities. Broad-scale statistical modeling of CB ignitions and area burned provided evidence that human development patterns are strongly associated with CB fire activity. The population of the CB ignition zone surrounding national forests in our study area increased by 39% between 1990 and 2010, and our results indicate that CB fire risk will likely continue to increase as human development expands into sparsely populated landscapes[4]. Our findings highlight the need for increased cross-scale multiparty risk governance and CB pre-fire planning to minimize the social and economic damages of CB fire while maintaining ecologically beneficial burning[37,38].

Our analysis provides an important empirical compliment to simulation studies based on large numbers of hypothetical fire events. Consistent with our results, modeling studies report that CB fire risk to communities is

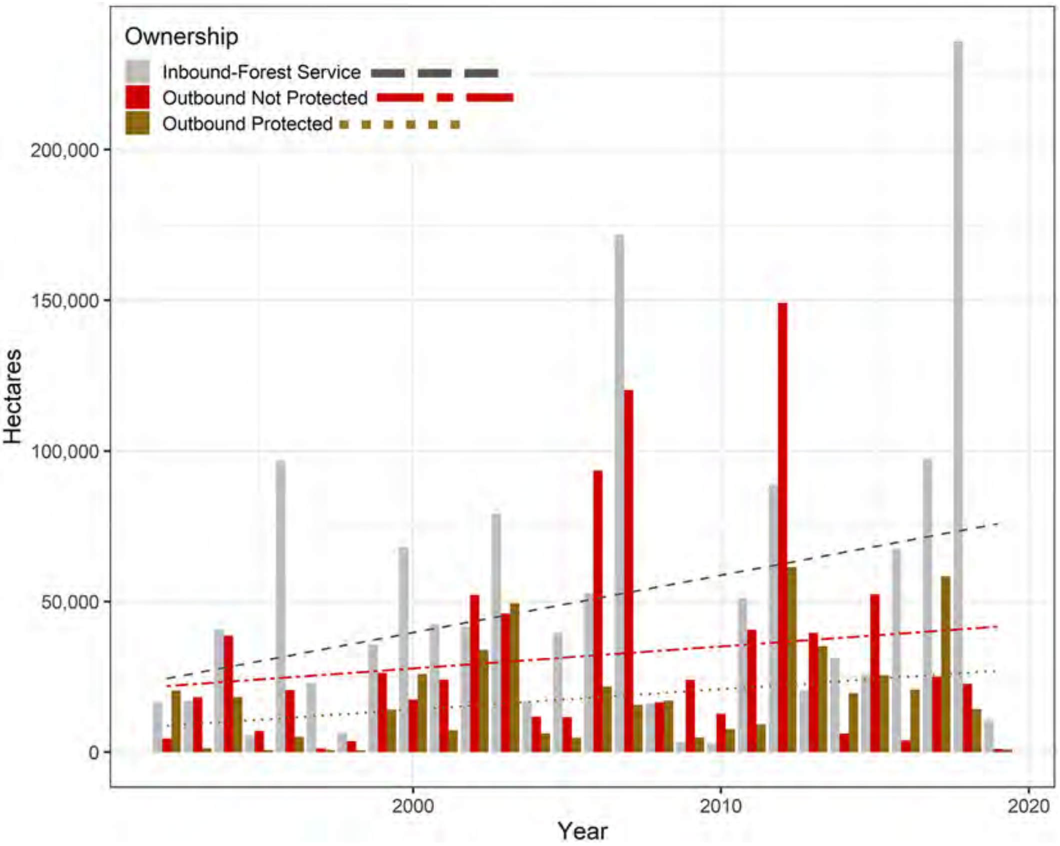


Figure 3. Area burned by CB fires derived from FIRESTAT data and binned by ownership category. Blue dots represent decadal averages of inbound and outbound acres combined. CB fire activity increased substantially during our study period. Area burned on USFS lands by fires originating on other ownerships ("inbound", gray) has increased more rapidly than area burned on non-USFS lands. Ownership categories are described in more detail in the Methods.

	Lightning-caused		Human-caused		Total	
Ignition location	**# fires**	**% of total**	**# fires**	**% of total**	**# fires**	**% of total**
Private	3036	14	10,235	46	13,271	60
USFS	2059	9	4052	18	6111	28
Other	997	5	1647	7	2644	12
Total	6092	28	15,934	72	22,026	100

Table 1. We identified a total of 22,026 CB fires that impacted USFS lands. The majority (88%) originated on either USFS or private lands, and the remainder started on other ownerships (e.g., state, city, other federal). Most CB fires were caused by humans (e.g., debris burning, equipment use, escaped campfires) on private lands.

highest in parts of California[23,39,40], and that community/private land tenures, rather than public lands, contribute the most fire risk to structures in the western US[24,41]. In contrast, our results differ in some important ways from simulation modeling studies. For instance, Palaiologou et al. 2019 reported high rates of simulated USFS to private fire transmission around the perimeters of the Gila, Apache-Sitgreaves, Tonto, Prescott, Coconino, and Kaibab national forests in the southwestern US[24]. Our analysis does not provide empirical evidence of substantial USFS to private fire transmission in these areas. A similar study reported that over 500 structures were exposed (but not necessarily lost) to fires spreading from these southwestern national forests *each year*[23]. However, our structure loss analysis only identified two fires that resulted in > 50 structures lost that involved these national forests between 2000 and 2018 (Yarnell Hill, 2013; Rodeo-Chediski, 2002). In their most recent comparison of empirical versus simulated wildfire impacts in the West, Ager et al. (2021)[39] found good alignment in annual area burned estimates, while building exposure was substantially overestimated in simulations[37]. Of course, asking what did happen and what might happen are different endeavors. The relevant empirical record for the former is necessarily limited to occurrences within the past few decades, while wildfire simulation systems provide realizations of tens of thousands of hypothetical contemporary fire-seasons, including some far more extreme

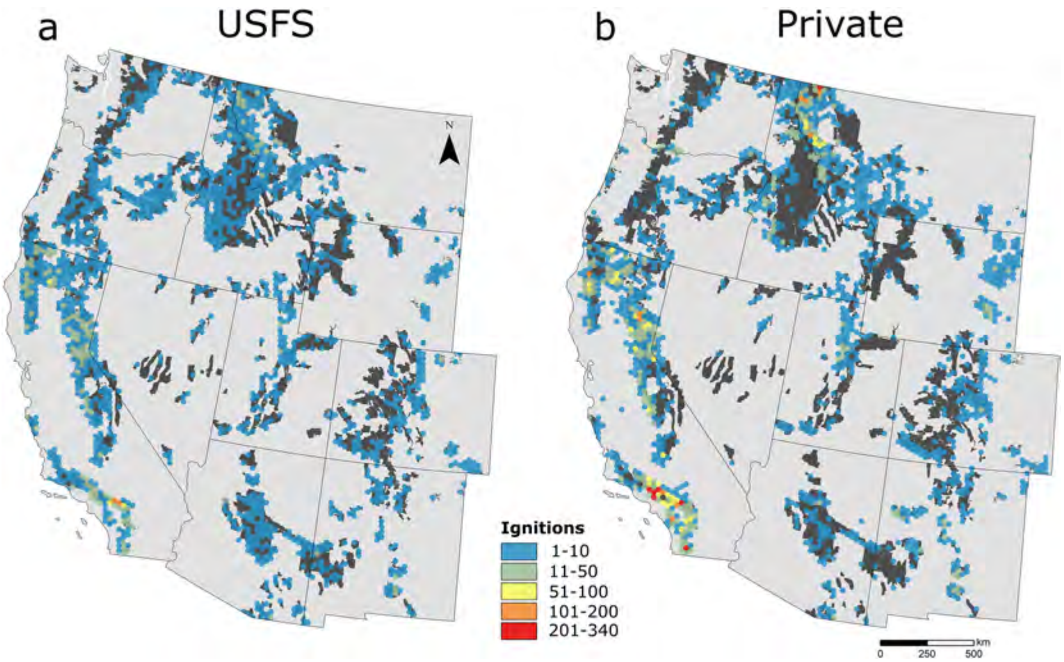


Figure 4. CB ignition densities derived from FPA FOD and FIRESTAT databases for fires originating on (**a**) USFS and (**b**) private lands between 1992 and 2017. Private ignition data are restricted to fires that impacted USFS lands; fires that originated on private land and spread to other state or federal jurisdictions are not included.

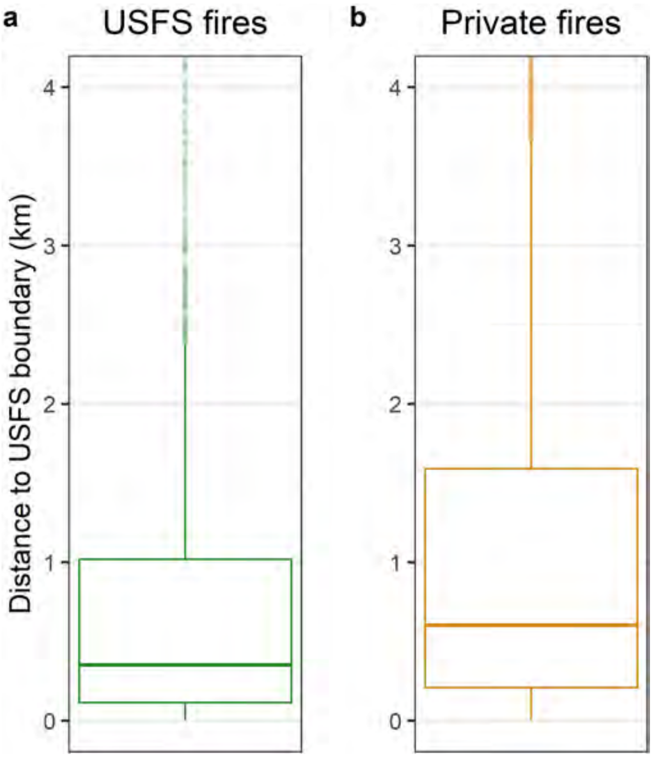


Figure 5. Distance from CB ignitions to USFS national forest borders for fires ignited on (**a**) USFS and (**b**) private lands between 1992 and 2017. To improve figure interpretability, the maximum distance shown here is constrained by the 90th percentile (2.62 km) of distance between a USFS ignition and national forest boundary. Private ignition data are restricted to fires that impacted USFS lands; fires that originated on private land and spread to other state or federal jurisdictions are not included.

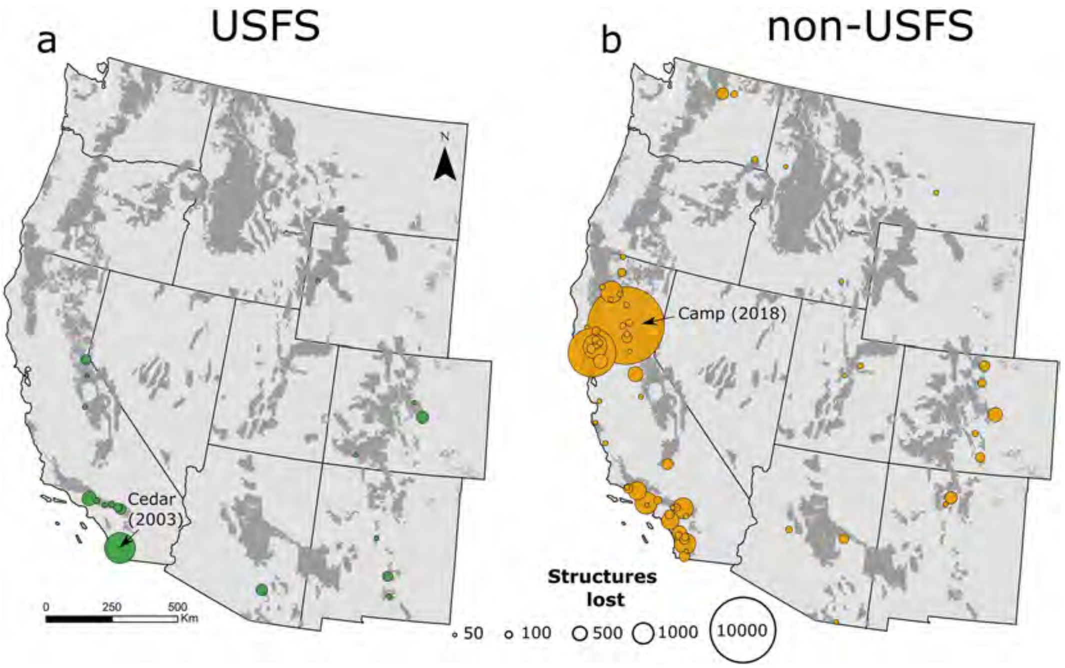


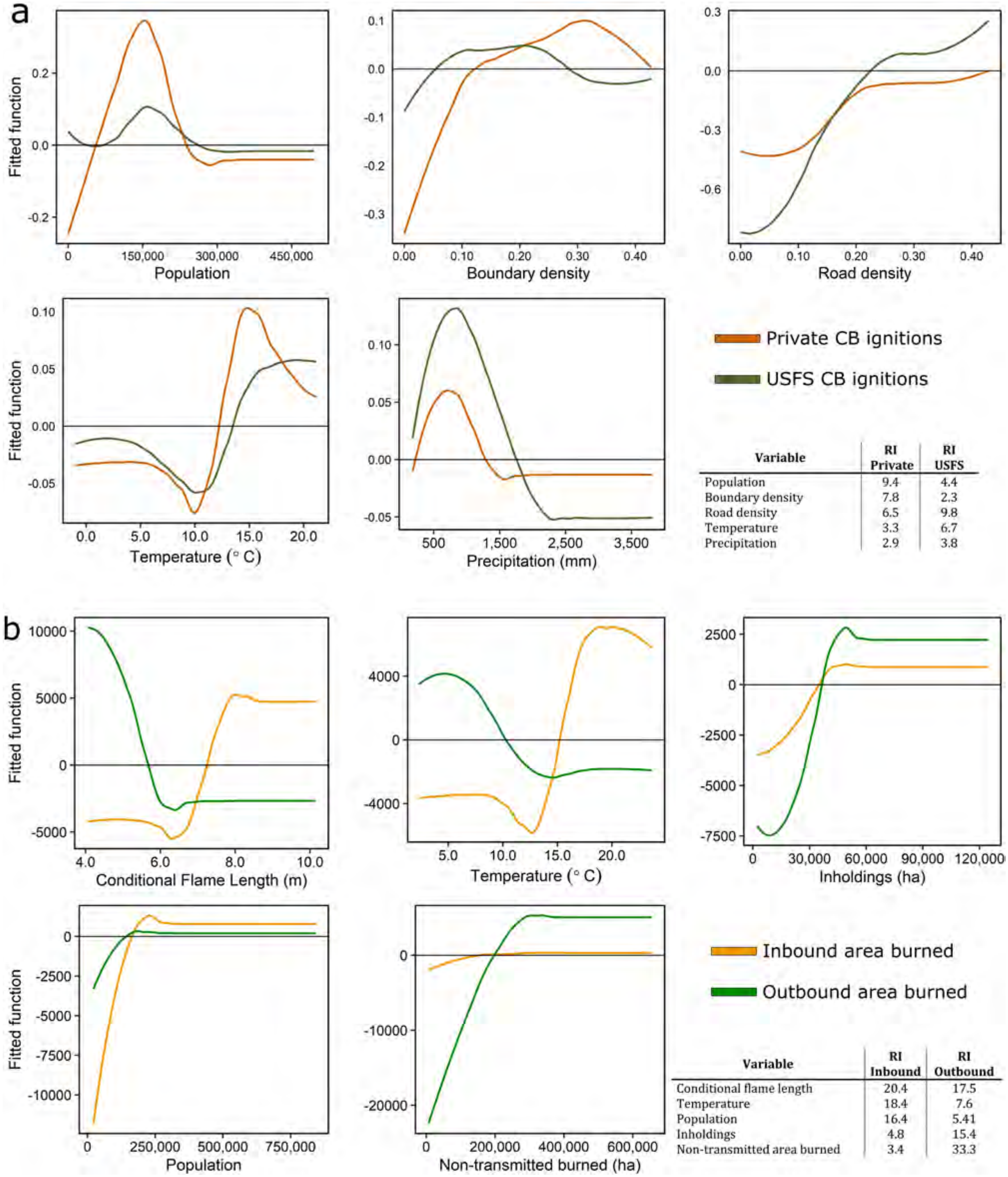
Figure 6. Location of destructive wildfires (> 50 structures lost) between 2000 and 2018 that originated on (**a**) USFS lands, and (**b**) non-USFS lands. Fire locations are symbolized by magnitude of structure loss. Relatively few destructive fires originated on USFS lands. The most destructive USFS and non-USFS fires during this time are the Cedar fire and the Camp fire, respectively.

Variable	Description	Source
Population[a]	Population within each sample area, averaged from 1990, 2000, and 2010 datasets	Radeloff et al.[4]
Road density	Data were rasterized; “road” cells were summed and divided by the area of the sample	https://www.here.com/
Boundary density[a]	Data were rasterized; “boundary” cells were summed and divided by the area of the sample	https://wfdss.usgs.gov/
Conditional flame length	Most likely flame length (m) at a given location if a fire occurs, based on wildfire simulations. Averaged across each sample area	Scott et al.[34]
Precipitation	Average annual precipitation (mm, 1981–2010) averaged across each sample area	PRISM
Temperature	Average daily mean temperature (°C, 1981–2010) averaged across each sample area	PRISM
Inholdings[b]	Area of non-USFS lands within national forest boundaries (ha) derived from jurisdictional spatial data	https://wfdss.usgs.gov/
Non-transmitted area burned[b]	Area burned (ha) by fires that did not spread beyond national forest borders to other ownerships	FIRESTAT

Table 2. Predictor variables for boosted regression tree (BRT) analyses. [a]For CB area burned models, these variables were only sampled in the 4-km external buffers around national forests. [b]Variables only included in CB area burned models.

than observed. Moreover, the nuances of fire protection efforts specific to the WUI and associated communities are not well captured in simulation systems, but likely help lessen actual exposure[39]. Clearly both empirical and simulated data are important for assessing CB fire risk. When combined, empirical and simulation analyses can contribute to holistic representations of where socio-ecological CB fire linkages have emerged in the past, and where they may be likely to develop or be reinforced in the future.

CB fire risk transmission is strongly mediated by human development patterns as a function of human-caused ignitions, road and boundary networks, and the distribution of high-value assets potentially exposed to CB fire[23–25,41]. In our analysis, CB ignitions peaked at intermediate population values, and CB area burned was low in very sparsely populated landscapes. These findings are consistent with observations that fire occurrence increases with population up to a threshold beyond which fire activity declines—a phenomenon attributed to frequent human-caused ignitions in moderately populated areas and reduced fire activity associated with highly fragmented fuels and abundant fire suppression resources in densely populated areas[16,34]. Likewise, CB ignitions increased with jurisdictional boundary density up to a certain point, but declined where boundaries were densest, which again may be attributable to the decreased potential for fire spread in discontinuous fuels and greater suppression effort around extensive human development. National forests with abundant inholdings experienced more CB fire than those with few inholdings, indicating that smaller land tenures like inholdings are not only more likely to receive incoming fire[24], they also appear to be sources of fire transmission to national forest lands.



Variable	RI Private	RI USFS
Population	9.4	4.4
Boundary density	7.8	2.3
Road density	6.5	9.8
Temperature	3.3	6.7
Precipitation	2.9	3.8

Variable	RI Inbound	RI Outbound
Conditional flame length	20.4	17.5
Temperature	18.4	7.6
Population	16.4	5.41
Inholdings	4.8	15.4
Non-transmitted area burned	3.4	33.3

Figure 7. Partial dependence plots and relative influence of variables used to model (**a**) CB ignitions and (**b**) CB area burned. Note that the scales vary on the *y* axes, which represent each variable's effect on (**a**) ignition counts and (**b**) CB area burned after accounting for the influence of other predictor variables. Predictions were center-scaled by subtracting the mean from each value. Partial dependence plots are shown in descending order of importance (left to right) determined by averaging variable relative importance (RI) values between models. Uninfluential variables (RI < 2.5) are not shown.

CB ignitions and area burned increased with road density, which we attribute to increased human-caused ignitions along road corridors that provide easy access to flammable vegetation in and around national forests[42]. The USFS has increasingly resorted to restricting access to entire national forests and even entire national forest regions to reduce the likelihood of human-caused ignitions during periods of high fire danger[43]. Decommissioning or limiting public access to roads may be another approach to limiting human-caused ignitions, but successful implementation would require input from fire managers who frequently utilize roads for access, fuel breaks, and pre-fire operational planning[44], as well as buy-in from the public who use roads for recreation access and other purposes.

Biophysical gradients were strongly associated with CB fire activity after accounting for social factors. CB ignitions were more common in hotter and drier climates, with some indication that CB fire occurrence was limited by fuel availability in the least productive, hot, dry locations[45]. Non-transmitted fire activity was a strong predictor for outbound area burned, but only weakly associated with inbound area burned, indicating that national forest fire load may not be an appropriate metric for prioritizing CB fire risk mitigations designed to protect valued natural resources on public lands. We were surprised to find that outbound and inbound area burned were associated with substantially different biophysical contexts. Outbound fire activity increased at simulated low fire intensities (i.e., light, flashy fuels) in hot, dry environments, while inbound fire increased at simulated high fire intensities (i.e., tall brush and timber fuels) in cooler, moister contexts. Both of these fire behavior environments present challenges to fire managers (e.g., high rates of spread; intense, long duration burning), but it is not clear why they would differentially influence fire transmission[46]. It is likely that our broadscale analysis of CB area burned was partly confounded by variability at spatial scales smaller than those measured[47]. Presently, comprehensive USFS CB fire activity data are not available at smaller spatial scales, and additional research is needed to determine the influence of a more comprehensive suite of biophysical factors on CB area burned at finer resolutions.

An empirical understanding of the geography of CB fire activity can provide a common operating picture for multiparty risk management oriented around which actors can most efficiently reduce aspects of risk[48]. One of the wildfire risk reduction strategies commonly proposed to prevent fires from spreading from federally-managed wildlands to communities is the reduction of hazardous fuels[49,50]. In some contexts, strategically placed fuel treatments can reduce fire severity and local fire spread[51,52]. However, fuel treatments are not ecologically appropriate in many fire-prone ecosystems and their effectiveness at landscape scales is limited[2,31]. Wildfires rarely interact with treatments before fuels recover to hazardous levels[53–55], and treatments are generally not designed to be effective during the extreme weather and fire behavior conditions associated with the small number of large, destructive fires that escape initial containment[31]. Federal agencies can also influence management on state and private lands through recently established collaborative authorities and strategic frameworks (e.g., Wyden Act, National Cohesive Strategy, Good Neighbor Authority, Shared Stewardship), but federal land managers are poorly positioned to incentivize community fire adaptation relative to state and local actors[56,57].

“The USFS manages over 67 million hectares interspersed among other land tenures across the western US, necessitating the agency’s engagement in CB wildfire risk management. However, the USFS could benefit from a critical evaluation of where it can meaningfully direct its resources to mitigate risks within the context of its mission, span of control, and authority. Rather than direct a majority of resources to the structure loss problem, which can be fundamentally decoupled from the land management problem[31,58], the USFS could instead emphasize forest health, resilience, and the natural amenity values that sustain communities and livelihoods. Given that (1) most CB ignitions are caused by humans on private lands, (2) high structure loss fires ignited on USFS lands are relatively rare, and (3) fire-induced structure loss is increasing despite substantial suppression and fuel reduction expenditures[31,59], CB fire risk to communities in particular may be best defined in terms of minimizing potential damages to developed high value assets like homes, and best oriented towards private lands, homeowners, and communities[31,58]. Prevention, hazardous fuel treatments, and suppression will remain important components of CB fire risk management strategies in many landscapes. However, based on the near ubiquity of fire transmission in fire-prone landscapes, escalating suppression expenditures, WUI expansion, and positive feedbacks between human development and CB fire risk, eliminating CB fire transmission is probably not operationally feasible and may not be ecologically desirable or socially effective31. There are a multitude of high-value assets on federally managed wildlands, such as water supplies, critical habitat, recreation infrastructure, and other natural and cultural resources, which may be better protected or enhanced through the reintroduction of fire rather than continued emphasis on control[2]”.

Land managers and communities may be best served by adapting to increasing CB wildfire in the western US, rather than attempting to minimize fire transmission[2,38]. Based on the empirical evidence presented here, reducing exposure and increasing the resilience of fire-adapted communities with the assumption that wildfire is inevitable seems like a more realistic approach than attempting to exclude fire based on the mistaken assumption that more fire suppression expenditures will result in less fire activity[30,31]. Community wildfire protection plans (CWPPs) are one of the key mechanisms designed to accomplish the National Cohesive Strategy’s goal of human populations and infrastructure that can withstand wildfire without loss of life and property[27,60]. Nearly all CWPPs focus on fuels reduction and the creation of fire breaks designed to prevent wildfire from spreading from wildlands to communities, instead of efforts to reduce the ignitability of homes and other values at risk when fires do spread to populated areas. In contrast to these CWPP implementations, our findings and others’ suggest that private landowners and communities are best positioned to develop and maintain communities that can withstand wildfire by minimizing the likelihood of home ignition, preventing human-caused fires from occurring in the WUI, and limiting development in high risk areas through land use planning and zoning regulations [31,58,61,62].

While communities and private land owners appear to occupy the nexus of CB fire risk management, the social and ecological linkages created by CB fire necessitate engagement from all stakeholders at multiple scales[25]. Effective CB fire risk management strategies will likely require different strategies tailored to specifi multijurisdictional contexts and based on localized systemic analyses, including, but not limited to, fuel treatments on public lands, exposure reduction on private lands, and the prevention and suppression of human-caused ignitions in high-risk locations on all ownerships. This shift in risk management emphasis may call for a reexamination of the most appropriate role for the USFS in some areas, perhaps to a mode of leveraging wildfire risk science to better frame problems and convening dialogues around co-management of wildfire risk.

Recent advances in wildfire risk science used in conjunction with empirical assessments of CB fire activity can help align risk management with the wildfire reality in multijurisdictional landscapes. When combined with local experiential knowledge, spatially explicit decision support tools like quantitative risk assessments[63], suppression difficulty maps[64], and potential control location atlases provide stakeholders with a common operating picture that can be used as the basis for co-managing risk[30,65]. Mapping the components of fire risk allows all landowners to simultaneously assess their exposure to wildfire and their contribution to the exposure of adjoining jurisdictions[66,67]. Transparency in pre-fire planning and risk governance can help build consensus around which actors are responsible for managing specific components of CB fire risk. Additionally, a shared CB fire risk knowledge base can be leveraged across state, county, and local scales to develop land use planning and zoning regulations designed to prevent development in areas where wildfire risk is unacceptably high[30,68].

That much of the research on CB fire has focused on community exposure[23,25,69] stems from the inherent imbalance between the values at risk in communities and the values at risk in publicly managed wildlands. Often it is considered more important to protect homes than it is to protect wildland ecosystems[31]. Rebuilding communities after wildfire is a challenging, complex process that can take years[70]. Meanwhile, post-fire ecological recovery can take decades[71], or never occur at all if pre-fire vegetation can't reestablish due to repeat burning, unfavorable climate, or a lack of surviving seed sources[72,73]. Our analysis was not designed to evaluate the ecological impacts of CB fire activity, and future empirical work on CB wildfire risk may therefore wish to consider the impacts of CB fire on a broader set of ecosystem processes and functions.

Future work could also add clarity on the prevention and response dimensions of CB fire risk. For instance, are closures and restrictions on non-USFS lands viable and would they measurably affect patterns of human-caused ignitions? Recognizing that fire response on mixed ownership landscapes entails a patchwork of entities, factors not explored here relate to the authorities, objectives, capacities, and capabilities of various response organizations (see Artley 2009)[26]. It may be the case that the USFS can effectively manage risk of outbound transmission due to factors like more robust planning and information systems and dedicated fire staff. Mapping a topography of the response system, how these and other factors vary, and how response to federal versus non-federal ignitions vary could be illuminating in this regard.

Wildfire and its controls are non-stationary, and the utility of past trends for forecasting future CB fire activity is probably limited[74]. In some ways, simulation modeling studies share this limitation because these models are parameterized with historical fuels, weather, and ignitions data[40]. While not taking historical patterns as givens, we anticipate fire transmission will continue to increase given directional trends in climate, the number of human-caused large fires, and human development near national forest boundaries[7,17]. Structure loss is also increasing[59], but this trend may not be inevitable if the focus of wildfire governance can be shifted away from fire exclusion and towards reducing the likelihood of losses when fires invariably occur[31,58].

Conclusion

Our empirical assessment of CB fire activity can support the development of strategies designed to foster fire-adapted communities, successful wildfire response, and ecologically resilient landscapes. Adapting to increasing CB wildfire in the western US will require viewing socio-ecological risk linkages between CB fire sources and recipients as management assets rather than liabilities. We believe that a shared understanding of CB fire dynamics, based on empirical data, can strengthen the social component of these linkages and promote effective governance. The current wildfire management system is highly fragmented[74], and increased social and ecological alignment between actors at multiple scales is necessary for effective wildfire risk governance[14,30]. Cross-boundary fire activity can contribute to multijurisdictional alignment when fire transmission incentivizes actors to collaboratively manage components of risk that manifest outside their respective ownerships[15]. A broader acknowledgement that CB is inevitable in some fire-prone landscapes will ideally shift the focus away from excluding fire in multijurisdictional settings towards improved cross-jurisdictional pre-fire planning and reducing the vulnerability of high-value assets in and around wildlands[30,31]. Federal agencies like the USFS can provide capacity, analytics, and funding, but given that private lands are where most high-value assets are located and where most CB fires originate, communities and private landowners may be best positioned to reduce losses from CB wildfire.

Methods

Study area.

We analyzed CB fire transmission to and from 74 national forests in 11 western US states. Lands managed by the USFS not designated as national forests were excluded (e.g., Lake Tahoe Basin Management Unit). National forest lands in the western US are part of a diverse mosaic of land tenures consisting of private, state, and tribal and other federal ownerships. National forest lands in our study area cover 57 million ha and contain a wide variety of forest and rangeland ecosystems spanning broad climatic and fire regime gradients.

Data sources.

Cross-boundary wildfires. We identified CB fires using data from the Fire Statistics System (FIRESTAT). The FIRESTAT database contains a record for every fire with which the USFS was involved. FIRESTAT area burned data are classified into three coarse ownership categories: USFS lands, non-USFS lands not protected by the USFS, and non-USFS lands for which the USFS has protection responsibility pursuant to interagency protection exchange agreements. FIRESTAT records have spatial location information for the reported points of origin for most fires, but those data vary in format and precision (i.e., ranging from only Public Land Survey System subsection attributions to GPS-based latitude and longitudes). It also includes NFS unit (i.e., forest) codes and names that have changed over time. We therefore leveraged standardization and quality control procedures used to produce the national Fire Program Analysis Fire-Occurrence Database (FPA FOD), which is a compilation of wildfire records from local, state, and federal fire reporting systems, including FIRESTAT (Short 2017)[75]. At the time of our analysis, data were only available for fires that occurred between 1992 and 2017. FPA FOD procedures and data were used to attribute spatial ignition and nominal NFS unit data to CB fires. We restricted our FIRESTAT analysis to fires that occurred between 1992 and 2019 to align with the start year of the FPA FOD timespan, which is 1992 due to concerns about completeness and quality of spatial data prior to that year[76].

Incident Status Summaries. Incident Command System Incident Status Summary Forms (ICS-209) report daily fire and suppression resource characteristics for significant wildfires. We used ICS-209 reports to identify the most destructive incidents between 2000 and 2018 using a threshold of 50 or more structures lost. We assigned a total structure loss count to each wildfire as well as the jurisdiction of the point of origin to evaluate whether or not the fire originated on USFS lands. A small number of destructive fires originated from multiple ignition sources located in different jurisdictions. When needed, we consulted local fire managers to properly attribute ownership for these event (see supplementary material). Where possible, we augmented ICS-209 destroyed structure counts with spatial building loss data. See Caggiano et al. (2020) for details[56].

Statistical modeling data. We modeled CB fire activity in relation to predictor variables representing climate, fire intensity, human development, and jurisdictional boundary patterns. Average annual temperature and annual precipitation (1981–2010) were acquired from PRISM[77]. We used conditional flame length data derived from simulation modeling to represent average potential fire behavior[36]. Road density data was calculated based on HERE roads shapefile data (https://www.here.com). Jurisdictional boundary density data was calculated based on the Wildland Fire Decision Support System boundary shapefile data (WFDSS, https://wfdss.usgs.gov). We rasterized the road and boundary datasets and divided the number of "presence" cells (i.e., road, or jurisdictional boundary) by the total number of cells in each sample unit to generate density values. We calculated the abundance of inholdings using WFDSS jurisdictional boundary spatial data, and we derived area burned by non-transmitted fire from FIRESTAT data. To quantify population, we averaged 1990, 2000, and 2010 population estimates from wildland urban interface data developed by Radeloff et al.[4].

Analysis. *Quantifying fire transmission.* CB fires were identified as fires that burned both USFS lands and other ownerships based on FIRESTAT data. We aggregated FIRESTAT area burned data by the three ownership categories described above (USFS, non-USFS, non-USFS protected) to quantify the magnitude of CB fire transmission for each of the national forests in our study area and for our study area as a whole. Additionally, we summarized area burned by ownership for each year between 1992 and 2019 to evaluate temporal trends in CB fire transmission.

Mapping fire transmission. We assessed the geographic distribution of fire transmission by mapping national forests in our study area in terms of inbound and outbound area burned. Additionally, we mapped CB ignitions that originated on either USFS or private lands. These two ownership categories were the dominant sources and recipients of CB fire in our study domain. To attribute CB ignition ownership as precisely as possible, we linked CB fires identified from FIRESTAT to FPA FOD spatial fire origin data based on a shared, unique identifier. FPA FOD ignition location data were used to extract more detailed ownership information from the Protected Areas Database of the United States[78] and 2019 Census Block Groups data (Wildland Decisions Support System, https://wfdss.usgs.gov). We assessed the geographic distribution of CB fire ignitions by summarizing the density of ignitions by ownership within a 20-km resolution hexagonal tessellated grid. Lastly, we leveraged the combined FPA FOD-FIRESTAT CB ignition spatial data to determine the distance between both private CB ignitions and USFS CB ignitions and the closest national forest boundary. We used the 90th percentiles of these two datasets to delineate a "cross-boundary ignition zone," which we then utilized as the spatial extent for sampling predictor variables used in the statistical analyses described below.

Attributing ownership to destructive fires. We used FPA FOD data, state fire agency documentation, and news articles to attribute ownership to destructive fires. Where possible, we also assigned a cause to each destructive fire (e.g., lightning, arson). In some cases, it was very difficult to determine a specific ownership category for fires that did not ignite on federal lands (e.g., private, state, county, or city lands). This did not pose a significant problem because our primary objective was to differentiate between fires ignited on or off USFS lands. Attributing ownership to fire complexes (multiple fires managed as one incident) also presented a challenge because complexes were sometimes composed of fires that were ignited on different jurisdictions. Two complexes we are aware of (Okanogan Complex, BTU Lightning Complex) consisted of fires that originated on both USFS and non-federal lands. In both cases, we classified these fires as "non-USFS" based on available data and conversations with local fire managers. The USFS ignitions in these complexes either constituted a small minority of all ignitions (BTU Lightning Complex) or did not substantially impact communities (Okanogan Complex). Removing these fires, or changing their ownership classification, would not substantially alter our results or our interpretation.

Statistical modeling. We analyzed CB ignitions and CB area burned in relation to a suite of social and biophysical predictor variables representing climate, fire intensity, human development, and jurisdictional boundary patterns (Table 2). We fit models for the following four response variables: (1) private CB ignitions, (2) USFS CB ignitions, (3) area burned by outbound CB fire, and (4) area burned by inbound CB fire. CB ignitions were modeled at the scale of the 20-km resolution hexagonal grid used for mapping ignitions. Private and USFS CB ignition counts derived from the FPA FOD database were summed within every grid cell intersecting a national forest boundary. We normalized ignition counts by hexagon area where grid cells were clipped by the extent of our study area. We modeled CB fire activity at the national forest scale using inbound and outbound (protected and non-protected combined) area burned data from FIRESTAT. CB area burned predictor variables were sampled within the CB ignition zone identified using FPA FOD spatial data and described above.

We used boosted regression trees (BRT) to assess the relative importance of predictor variables and relationships between predictor variables and our four CB fire response variables. Models were fit for the appropriate family for each data distribution (ignition counts: Poisson, area burned: Gaussian), and parameterized to ensure at least 1000 trees were produced during the fitting process (learning rate = 0.001, tree complexity = 5, bag fraction = 0.5). We assessed model performance based on modeled and tenfold cross-validated percentages of deviance explained, which indicates the goodness of fit between modeled values and observed values[79]. We evaluated the importance of predictor variables using relative influence values and we used partial dependence plots to interpret the effects of predictor variables on the response after accounting for the average effects of all other variables in the model[80]. We tested for residual spatial autocorrelation using Moran's I, and models with evidence of residual spatial autocorrelation were fit with a residual spatial autocovariate[79]. We assessed collinearity between predictors using a correlation matrix (see supplementary material). We considered variables to be highly correlated beyond a threshold of $r > |0.7|$, the point at which collinearity begins to meaningfully distort BRT model outputs[81]. In several cases we observed strong correlations between predictor values sampled inside and outside of national forest boundaries. To avoid possible model distortion and to simplify model interpretation, we averaged interior and exterior precipitation, temperature, and conditional flame length values prior to modeling. We conducted all analyses in R (ver. 4.0.3, R Core Team 2019). BRT modeling was performed using gbm[82] and dismo[83] R packages.

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Author contributions

W.M.D. performed the analysis and led the writing of the paper. M.P.T. and C.J.D. conceived of the study, contributed to the analysis, and co-wrote the paper. K.C.S. provided fire occurrence data and M.D.C. provided structure loss data, both co-wrote the paper.

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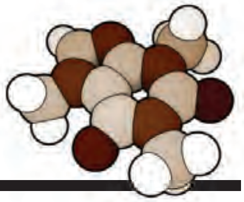

ENVIRONMENTAL SCIENCE

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]

POLICY

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.

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.

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.

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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. ■

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Science

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LETTER • OPEN ACCESS

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LETTER

Fire, water, and biodiversity in the Sierra Nevada: a possible triple win

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Abstract

Reducing the risk of large, severe wildfires while also increasing the security of mountain water supplies and enhancing biodiversity are urgent priorities in western US forests. After a century of fire suppression, Yosemite and Sequoia-Kings Canyon National Parks located in California's Sierra Nevada initiated programs to manage wildfires and these areas present a rare opportunity to study the effects of restored fire regimes. Forest cover decreased during the managed wildfire period and meadow and shrubland cover increased, especially in Yosemite's Illilouette Creek basin that experienced a 20% reduction in forest area. These areas now support greater pyrodiversity and consequently greater landscape and species diversity. Soil moisture increased and drought-induced tree mortality decreased, especially in Illilouette where wildfires have been allowed to burn more freely resulting in a 30% increase in summer soil moisture. Modeling suggests that the ecohydrological co-benefits of restoring fire regimes are robust to the projected climatic warming. Support will be needed from the highest levels of government and the public to maintain existing programs and expand them to other forested areas.

Introduction

Fire has been an integral ecosystem process in western U.S. forests for millennia. Lightning was the primary ignition source, and later, American Indians added ignitions by burning for cultural purposes. The invasion of Euro-Americans in the mid-1800s disrupted natural fire occurrence by both reducing the influence of Indigenous burning practices and introducing widespread livestock grazing, which limited fuel continuity and fire spread (Taylor *et al* 2016, Pyne 2019). Active fire suppression, which began in the early 20th century, further disrupted natural fire occurrence and ultimately led to a widely adopted policy of full fire suppression across all U.S. federally managed lands (Stephens *et al* 2016). This suppression policy was highly effective at eliminating fire for decades but recent wildfire activity has increased and this has been accompanied with severe land management problems (Calkin *et al* 2015).

In 1962, the Secretary of the Interior asked a committee to investigate wildlife management problems in the U.S. national parks. This committee, named after its chair, Dr Starker Leopold, took the broader ecological view

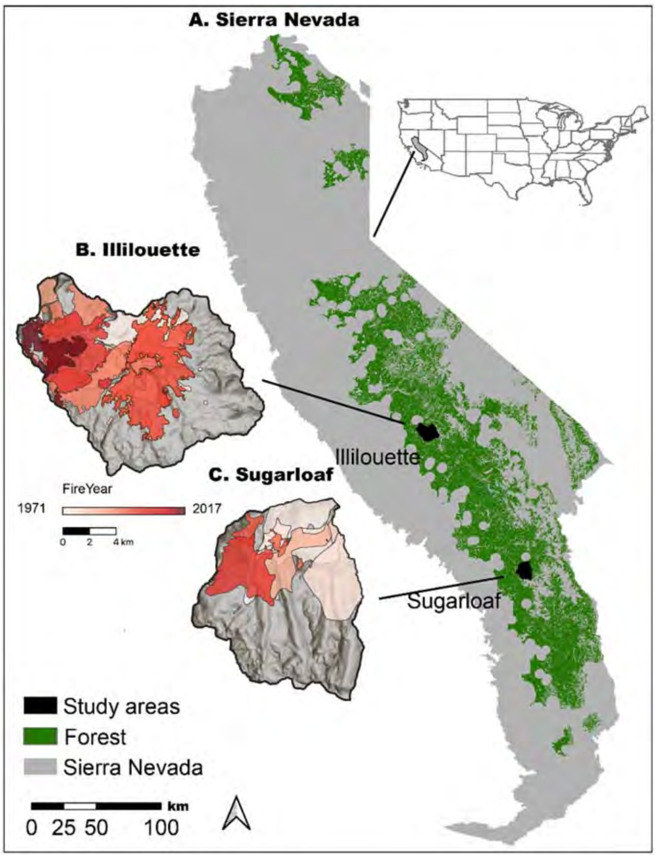

Figure 1. Sierra Nevada forests with managed wildfire potential, locations of study areas, and perimeters of wildfires that burned in Illilouette and Sugarloaf creek basins during the wildfire management program (~1972-present). Fire perimeters were obtained from a database generated by the state of California (FRAP 2020) and are shaded based on wildfire year (darker red = more recent). Forested areas with actual or potential managed wildfire use (green areas in A) are classified as those outside of the wildland urban intermix (WUI; Radeloff *et al* 2017) threat zone and where the contiguous land area is at least as large as our smaller study basin (Sugarloaf; ~13,000 ha). Forested areas are defined according to LANDFIRE biophysical settings data (Rollins 2009). WUI threat zone definition follows the strategic fire management zone alternative A of the Sierra National Forest land management plan (USDA 2019).

that parks should be managed as ecosystems (Leopold *et al* 1963). As a result, the U.S. National Park Service changed its policy in 1968 to recognize fire as an ecological process. Fires would be allowed to burn if they could be contained within fire management units and accomplished approved management objectives (figure 1).

Sequoia and Kings Canyon National Parks established a natural fire management zone in 1968 immediately after this policy change (Kilgore and Briggs 1972), and thus began the first tentative experiments with managing naturally ignited fires deep in park wilderness. This was followed in 1972 with a similar zone designation in Yosemite National Park (van Wagtendonk 1978). These three national parks have the longest periods of allowing lightning fires to burn in the USA. The objective of these programs was to restore the ecological role of fire under prescribed conditions (figure 2). Among land management agencies, these national parks have been world leaders in the increasingly difficult effort to allow lightning-ignited fires to burn. Concerns over smoke, at-risk species, the threat posed by fires to nonfederal lands, and the uncertainty of potential impacts should fires grow beyond expected boundaries have hindered full implementation of managed wildfire programs (Miller *et al* 2012). Even with these constraints, the parks and a few U.S. Forest Service wilderness areas remain committed to allowing wildland fires to play their ecological role. The U.S. Forest Service is currently moving ahead with plans to expand natural fire programs in California (Meyer 2015).

In this paper we summarize what has been learned from 50 years of managed fire programs in Sierra Nevada national parks. Very few areas with such a legacy of fire-use exist making these areas critical natural laboratories which have accordingly received increasing attention from scientists. As managers, policy makers, and the public work to create long-term solutions to conserve U.S. forests, these areas could prove invaluable in future program and policy design.

Figure 2. Repeat photographs taken from field plots in Illilouette Creek basin. The left two images (A), (B) were taken 1 and 9 years following low severity fire. The right two images (C), (D) were taken 1 and 9 years following moderate severity fire. Fire severity class for these plots was based on Landsat-derived Relative differenced Normalize Burn Ratio, using thresholds presented in Miller and Thode (2007). A small patch of fire-killed trees is also evident in Image D, just beyond the red oval, which contains numerous snags and saplings that regenerated following the 2001 Hoover Fire. Red ovals identify the same point in the photographs.

Fire severity and vegetation

Fire severity in the basins was assessed using the Relative differenced Normalized Difference Vegetation Index (RdNDVI) for fires prior to 1984 and Relative differenced Normalized Burn Ratio (RdNBR) for fires post 1984. RdNDVI and RdNBR were derived based on Parks *et al* (2018) Google Earth Engine algorithm. Both RdNDVI and RdNBR distributions for each fire was thresholded (Miller and Thode 2007), where values between 0 and 315 were classified as low severity, 316 and 640 as moderate severity, and values above 641 were classified as high severity. These thresholds were calibrated by Collins *et al* (2009), based on fires that occurred in Yosemite National Park. Despite 80–100 years of fire exclusion policies from ~1880 to 1970, the frequency of contemporary fire activity in both basins is similar to the pre fire exclusion period using dated fire scars (~1700–1880 C.E.; Collins and Stephens 2007). The long fire-free period (~1880–1970) coincided with substantial tree recruitment relative to the historical and contemporary natural fire periods (Collins and Stephens 2007) and allowed for considerable surface fuel accumulation (Parsons and Debenedetti 1979). Given these changes one might assume that fire severity, as measured using remotely sensed imagery (e.g., Miller and Thode 2007), would be elevated when fire was reintroduced. This was not the case in either basin. In Illilouette, the first widespread fire under the managed wildfire program, the 1974 Starr King Fire, burned nearly 1600 ha (van Wagtendonk 1978) and only 9% was at high severity (Collins *et al* 2009). Since then, only 14% of the total burned area in Illilouette was classified as high severity, and in Sugarloaf, high severity accounted for 16% of total burned area. For comparison, 27% of the area outside of the Illilouette and Sugarloaf basins in the Sierra Nevada burned at high severity from 1984 to 2018 (figure 3).

The return of fire to these basins has allowed investigation into the processes driving natural fire-vegetation dynamics. The fact that neither timber harvesting or road building occurred in either basin strengthens inferences from these investigations. Within individual fires, the dominant vegetation type (i.e., *Pinus*-dominated forest, *Abies*-dominated forest, montane chaparral) and weather were most strongly connected to fire severity (Collins *et al* 2007). At the landscape level, time-since-last-fire, previous fire severity (for reburns), and dominant vegetation type influenced fire severity (Collins and Stephens 2010, van Wagtendonk *et al* 2012).

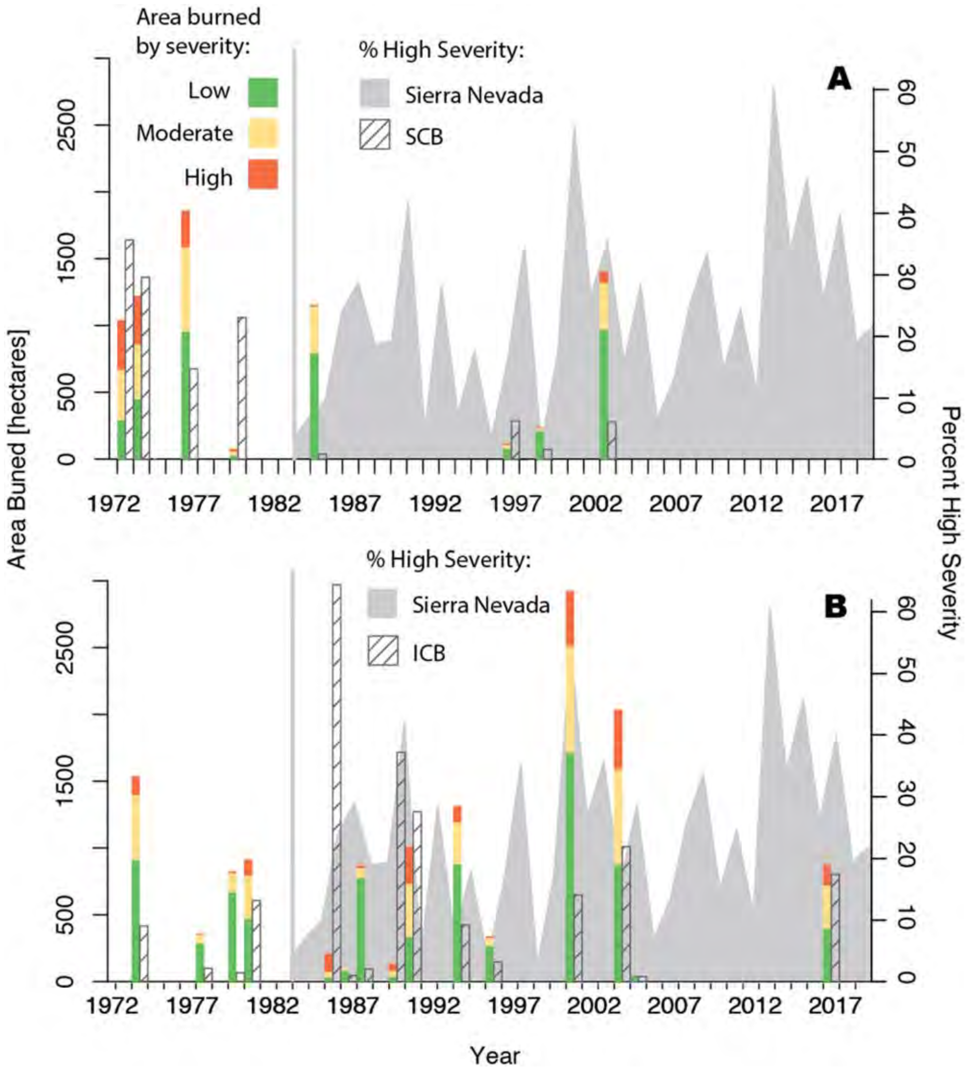

Figure 3. Proportion of fire area burned at low, moderate, and high severity as classified by LANDSAT-derived RdNDVI (prior to 1984) and RdNBR (post 1984) severity indices for fires burned in Sugarloaf Creek Basin-SCB (A) and Illilouette Creek Basin-ICB (B). Fire severity class thresholds were based on those in Collins *et al* (2009) and Miller and Thode (2007) for RdNDVI and RdNBR, respectively. Proportion of the yearly fire area burned at high severity is shown as vertical bars with diagonal line in both panels, which corresponds with the right vertical axis. For comparison, the proportion of yearly fire area burning at high severity in the entire Sierra Nevada bioregion (Rakhmatulina *et al* 2021a) is shown in light gray, also corresponding with the right vertical axis.

Time-since-last-fire also exerted a strong control on whether fires re-burned over previous fire areas (Collins *et al* 2009).

Assessments of landscape-scale vegetation change using aerial photography during the managed fire period revealed different outcomes for Illilouette (1970–2012; Boisramé *et al* 2017a) and Sugarloaf (1973–2014; Stevens *et al* 2020). In Illilouette, the proportion of the basin comprised of conifer forest decreased from 82% to 62%, being replaced by shrublands and meadows. In Sugarloaf, forest cover changed very little: from 83% to 82%. Accordingly, contemporary vegetation cover classes (forest, shrub, sparse and dense meadow) are more balanced, with greater landscape heterogeneity in Illilouette compared to Sugarloaf (Stevens *et al* 2020). Plot-level forest structure data collected in the early 1970s provided further evidence that forest stand structure in Sugarloaf did not change markedly as a result of the managed fire program (Stevens *et al* 2020). However, across both basins, conifer-dominated areas that burned in managed fires (including reburns) had highly variable structure and composition, ranging from open *Pinus jeffreyi* dominated forests, dominated by large trees (tree density: 104 ha^{-1}; basal area 19.5 m^{2}ha^{-1}) to dense, closed-canopy structures dominated by *Abies concolor and A. magnifica* (tree density: 446 ha^{-1}; basal area 53 m^{2}ha^{-1}) (Collins *et al* 2016). The two primary drivers of this variability were the local biophysical environment and recent fire severity. Despite this high variability, surface fuel loads and tree densities in both basins are markedly lower than in comparable portions of the Sierra Nevada where fire has been successfully excluded in the modern era (Collins *et al* 2016).

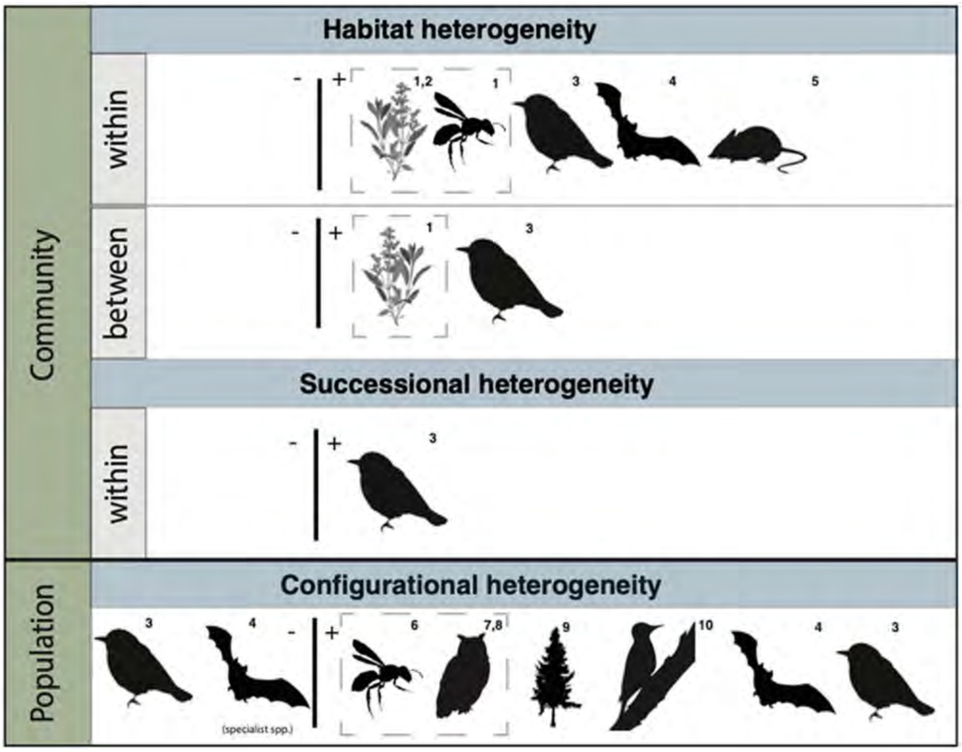

Figure 4. Studies finding evidence for (+) or against (−) the proposed mechanisms by which pyrodiversity begets biodiversity. Pyrodiversity may promote biodiversity by increasing variation in landscape composition (habitat and successional heterogeneity) and/or by increasing variation in the spatial arrangement of fire elements (configurational heterogeneity). The dashed grey boxes indicate studies were primarily conducted or at least partially in the Illilouette and Sugarloaf basins. Other studies examine the effect of mixed severity fires in the Sierra Nevada forests, the restoration of which is the intention of managed wildfire programs. 1 Flowering plants and bees- Ponisio *et al* 2016; 2 Understory plants - Wilkin *et al* 2021 (in press); 3 Birds - Tingley *et al* 2016; 4 Bats - Steel *et al* 2019; 5 Small mammals - Roberts *et al* 2015; 6 Bees- Ponisio 2020; 7,8 Birds (spotted owls) - Hobart *et al* 2021 and Kramer *et al* 2021; 9 Trees- Blomdahl *et al* 2019. 3,4 found evidence both for and against a specific mechanism depending on species.

The divergent effects of the managed fire program on vegetation in the two basins has several possible explanations. Illilouette has higher precipitation and vegetation productivity than Sugarloaf (Stevens *et al* 2020); therefore, it is possible that the increase in fuel during the fire exclusion period was greater in Illilouette, resulting in more frequent fires with larger high severity proportions that created larger patches of non-forest vegetation. Another possible reason for the difference is many fires have been suppressed in the last 15 years in Sugarloaf (Stevens *et al* 2020). The increase in vegetation heterogeneity in Illilouette is clearly related to the greater incidence of small high severity patches in this basin and the stability of fire severity classes over the decades (figure 3).

Biodiversity

Wilderness areas managed for wildfire in the Sierra Nevada support greater pyrodiversity (variability in fire severity, season, size, frequency) and consequently greater landscape heterogeneity (van Wagtendonk and Lutz 2007, Boisramé *et al* 2017a, Steel *et al* 2021) than comparable fire-suppressed areas. Ecological theory predicts that diversity, including pyrodiversity, begets biodiversity (Martin and Sapsis 1992). Multiple mechanisms by which pyrodiversity promotes biodiversity have been proposed at community and population scales (Kelly *et al* 2017, Jones and Tingley 2021, figure 4). Studies in Illilouette and Sugarloaf have shown that pyrodiversity created by managed wildfire is associated with higher biodiversity (bees and understory plants: Ponisio *et al* 2016, Ponisio 2020, Wilkin *et al* 2021 in press) and is compatible with at least some mature forest specialists (California spotted owl, *Strix occidentalis occidentalis*: Hobart *et al* 2021, Kramer *et al* 2021). Because few population- or community-level studies on the effect of fire management have been conducted primarily in Illilouette and Sugarloaf, we also considered studies conducted in similar Sierra Nevada landscapes. Corroborating Illilouette and Sugarloaf studies, pyrodiversity in other comparable regions is positively related to mammal, bird, bat, and tree biodiversity (Roberts *et al* 2015, Tingley *et al* 2016, Blomdahl *et al* 2019, Steel *et al* 2019) (figure 4). These lines of evidence suggest use of managed wildfire and restoration of pyrodiverse landscapes is broadly supportive of biodiversity in Sierra Nevada and similar ecosystems.

We also found support for a variety of mechanisms underlying the positive effect of pyrodiversity in and around the Illilouette and Sugarloaf basins. Within bird, bee, plant, and bat communities, habitat heterogeneity underlies enhanced biodiversity (figure 4). Specifically, pyrodiversity leads to local variation in fire history generating spatial niche diversity and allowing a greater number of species to coexist (Kelly *et al* 2017). Among communities, studies on flowering plants and birds found that the fire severity heterogeneity enhances beta-diversity (figure 4) because species are associated with different fire histories. These results highlight the potential for managed wildfire areas and their expansion to improve regional biodiversity, which is adversely affected by the homogenizing effects of both fire suppression and large high severity fires.

The successional heterogeneity mechanism has not been explicitly addressed for many taxa in the Sierra Nevada and is often conflated with habitat heterogeneity because different fire severities are often characterized as supporting species from different successional stages (e.g., higher severity fires support 'early successional' species) (Ponisio *et al* 2016). However, Tingley *et al* (2016) found that both habitat and successional heterogeneity enhanced bird coexistence in the Sierra Nevada. It is likely, therefore, that a combination of spatial and temporal heterogeneity of fire histories promotes biodiversity, as originally proposed by Martin and Sapsis (1992).

At the population scale, fire-generated heterogeneity promoted persistence in specific species of birds and bats that use areas with different fire histories for specific food resources/prey species, shelter, and/or avoid predation (Tingley *et al* 2016, Steel *et al* 2019, figure 4). For example, Black-backed woodpeckers (*Picoides arcticus*) benefited from configurational heterogeneity (number, size, and arrangement of habitat patches) along high severity patch edges perhaps reflecting the trade-offs of predation risk, nest site availability, and food resources within high severity patches (Stillman *et al* 2019, 2021). Similarly, fire refugia can support survival during and immediately following fire for California spotted owls (*Strix occidentalis occidentalis*) and some tree species (Blomdahl *et al* 2019, Hobart *et al* 2021, Kramer *et al* 2021). We would expect to find similar positive responses to configurational heterogeneity for other species that have resource/shelter needs associated with patches of different fire severities or unburned forest, but negative responses for some habitat specialists. In Illilouette, Ponisio (2020) found that the combination of local pyrodiversity enabled populations of species with the ability to switch floral interaction partners to persist through a severe drought. Fire-supported heterogeneity may therefore enhance community resistance to climate change in other species that, similar to bees, benefit from the different resources afforded by patches with disparate fire histories.

Together, the ample evidence across taxa (birds, mammals, insects and plants) and ecological scales (population, within and between communities) that pyrodiversity benefits biodiversity through a variety of mechanisms. This suggests that the expansion of the managed wildfire model to analogous areas in the Sierra Nevada mixed conifer forest would benefit biodiversity regionally and perhaps help ecological communities adapt to growing threats associated with global change.

Hydrology and climate change

The conversion of dense, fire-excluded forest to a mosaic of grasslands, wet meadows, shrublands, and forest stands of varying age and density changed the partitioning of the water balance in Illilouette (Boisramé, *et al* 2017b, figure 5). A statistical model trained on field moisture measurements suggested that the observed conversion of forest areas to meadows in the central area of the Illilouette basin between 1969 and 2012 led to increases in summer soil moisture by as much as 30 percentage points (Boisramé *et al* 2018). These estimates are supported by *in situ* soil moisture monitoring in Illilouette and Sugarloaf, which consistently shows soil water content under meadow and shrub canopies to be 10 to 30 percentage points greater than under neighboring forest canopies (Boisramé *et al* 2018, Stevens *et al* 2020).

Identifying the processes responsible for these relations between vegetation and water storage remains challenging. Simulation in Illilouette with ecohydrological models suggests that forest reduction was associated with reduced snowpack sublimation and summer transpiration so that 2012 vapor fluxes from the basin declined by approximately 40 mm year^{-1} relative to 1969, similar to the increase in streamflow (Boisramé *et al* 2019). Observations made with time-lapse cameras in Illilouette and Sugarloaf show that snowpack is thinnest and melts earliest beneath forest canopies compared to shrub and meadow areas (Boisramé *et al* 2019, Stevens *et al* 2020). Increased subsurface water storage and reduced transpiration demands probably contributed to very low tree mortality in Illilouette during the extreme drought years of 2014–2015 (Boisramé *et al* 2017b). Flow observations at the Happy Isles stream gauge on the Merced River and model predictions suggest that these water balance changes produced modest increases in annual streamflow, with approximately 50 mm year^{-1} additional flow from Illilouette after 40 years of managed wildfire (Boisramé *et al* 2019). Reassuringly, neither the modeling nor gauge observations show evidence of increased peak flows (floods), which are often identified as a potential hydrological risk of increasing fire frequency. In contrast to Illilouette, the less pronounced

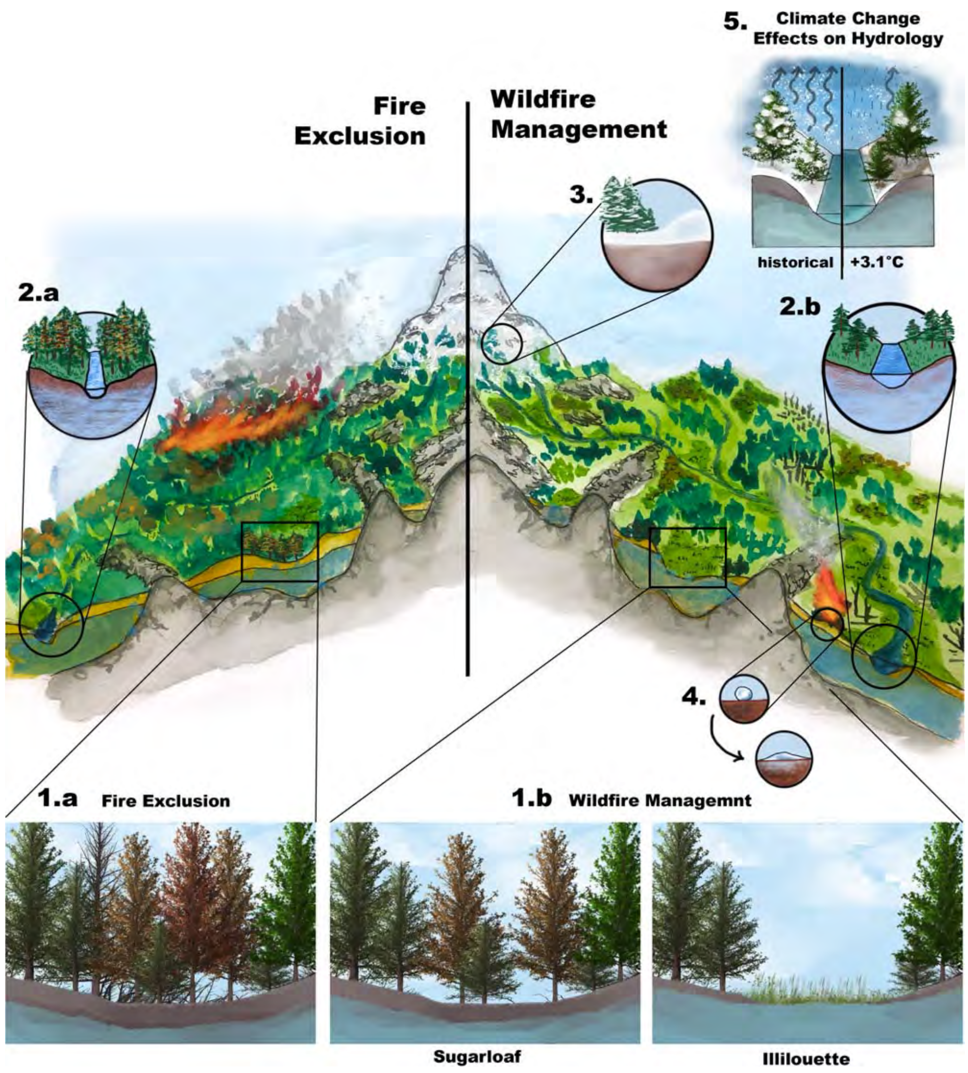

Figure 5. The left panel depicts a fire suppressed landscape, and the right panel shows a landscape experiencing frequent fires under a wildfire management strategy. The right panel is more representative of a landscape change that occurred in Illilouette basin, which experienced greater vegetation transitions from forest to shrublands and grasslands, resulting in an overall wetter landscape than Sugarloaf basin (1.b). As seen in Illilouette, wildfires increased basin streamflow (2), which is partially attributed to greater snow water equivalent in open areas compared to under canopies (3). No large-scale post-fire erosion is observed in Illilouette, likely due to frequent freeze-thaw cycles which reduce post-fire soil hydrophobicity (4). As climate is predicted to warm by 3.1 °C without significant change in precipitation totals, snowpack will be reduced, which is predicted to decrease basin evaporation through sublimation reduction, causing a marginal net increase in streamflow relative to historically observed conditions (5).

vegetation changes in Sugarloaf during the managed fire program do not appear to have resulted in noticeable hydrological changes (Stevens *et al* 2020).

Climatic warming is expected to impact the hydrology of the Sierra Nevada by increasing the fraction of precipitation falling as rain and moving peak streamflow earlier in the year (Rakhmatulina *et al* 2021a). Climate change is also likely to alter the characteristics of managed wildfires in Illilouette and Sugarloaf, although forecasting these changes is challenging (Gonzalez *et al* 2018). Observations over the past 50 years in Illilouette show no trends in fire severity or burned area in spite of climatic warming during that period (figure 3), presumably because both of these characteristics have been moderated by fuel consumption and associated disruptions in fuel continuity across the landscape (Collins *et al* 2009). Lightning ignitions, however, may become more frequent in Illilouette given warmer and drier weather. Increasing fire frequency from climate change accelerates the pace of hydrological changes without altering the long-term hydrological state (Rakhmatulina *et al* 2021a). These results suggest that the hydrological co-benefits of restoring fire regimes are robust to the projected climatic warming in the Sierra Nevada.

Considerable uncertainties remain, however, regarding the feedbacks between fire, vegetation, and the water cycle as climate changes. For instance, it is not clear how important the expansion of wet meadow areas might be in creating natural 'fire breaks' that constrain the extent of future fire. Even the modest increases in soil moisture that occurred in the basin to date could influence fires, with recent studies showing that fuel moisture can be significantly increased by wet soils, reducing ignition probabilities (Rakhmatulina *et al* 2021b). Similarly, several hydrological implications of the managed wildfire program, including the impacts on water quality, require more research. Examination of LIDAR imagery from before and after the 2017 Empire Fire in Illilouette, however, shows little evidence of large-scale erosion (Boisramé unpublished data 2020). The fact that freeze-thaw cycling in Sierra Nevada soils can rapidly erode post-fire hydrophobicity (Rakhmatulina and Thompson 2020) could contribute to rapid recovery of soil's ability to absorb and store water in these basins after fire.

Conclusion

Reducing the risk of large, severe wildfires while also increasing the security of mountain water supplies and enhancing biodiversity are urgent priorities. Here we found evidence for this synergism in Illilouette but not fully in Sugarloaf. While differences in the productivity of these forested areas could have contributed to this disparity, the shortage of managed wildfires in Sugarloaf is likely the biggest factor. The number of fires larger than 40 ha from 1973 to 2016 was much higher in Illilouette ($n = 21$) than Sugarloaf ($n = 10$). This disparity is particularly evident in recent decades, with Illilouette experiencing 12 fires larger than 40 ha since 1985 and Sugarloaf only experiencing 4 (Stevens *et al* 2020). The amount of recent fire activity in Sugarloaf may represent a deficit compared to the historical fire return interval (Collins and Stephens 2007). This recent fire deficit is illustrated by the fact that wildfires have burned only 1 ha in Sugarloaf between 2004 and 2017 with 59% of active ignitions suppressed, compared with 7,289 ha burned in Illilouette and only 23% of ignitions suppressed in the basin between 1969 and 2003 (Stevens *et al* 2020).

The challenges of maintaining a managed wildfire program are daunting, even in remote areas. Ignitions during droughts have been suppressed for fear of adverse fire effects or lack of public and political support in allowing fires to burn. Climate change is expected to create more alternating periods of drought and high precipitation (Abatzoglou and Williams 2016), which will probably be the environment that fire managers will have to adapt to. Political challenges were evident to Yosemite National Park managers when the 2017 Empire Fire was allowed to burn in Illilouette at the same time as the 2017 Wine Country fires were burning large areas of Napa, Sonoma, and Mendocino counties and destroying tens of thousands of structures. National park managers are to be commended for creating these managed wildfire programs and working to maintain them into the future.

Current revisions to the Land and Resource Management Plans for U.S. National Forests in the southern Sierra Nevada emphasize managed wildfire over 69% to 84% of National Forest land (Rakhmatulina *et al* 2021a). Areas that have similar characteristics to Illilouette and Sugarloaf in terms of forest type and remoteness are extensive in the Sierra Nevada (figure 1), demonstrating the potential to increase the area managed by wildfire. National Forest lands often have different land use histories than National Parks, including extensive historical logging which can change forest and fuel structures and create additional challenges to restoration by fire alone (Collins *et al* 2017, Jeronimo *et al* 2019), but the successes of the managed fire programs in the parks discussed here do provide a useful template for scaling up the landscape application of managed wildfire to other lands. If managers decide to implement managed fire programs they should be robust to climate change (fires continue to be self-limiting and fire severity classes remain stable) but may be more volatile as the time required to produce a fire mosaic is expected to be much shorter from the impacts of climate change (Rakhmatulina *et al* 2021a). Continued support at the highest levels of government, as well as from the public, would be needed to maintain existing managed wildfire programs and expand them to others forested areas. Were fire to be removed from managed fire areas, woody cover and water use would again increase, diminishing the positive impacts of these programs (continued fire use would produce relatively low levels of smoke for many months which could negatively impact some people). Perpetual support for these programs and for the scientific investigations that can interpret their effects is key if we want to avoid increasingly destructive high severity wildfires that damage ecosystems and human communities.

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Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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LETTER

Have product substitution carbon benefits been overestimated? A sensitivity analysis of key assumptions

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Abstract

Substitution of wood for more fossil carbon intensive building materials has been projected to result in major climate mitigation benefits often exceeding those of the forests themselves. A reexamination of the fundamental assumptions underlying these projections indicates long-term mitigation benefits related to product substitution may have been overestimated 2- to 100-fold. This suggests that while product substitution has limited climate mitigation benefits, to be effective the value and duration of the fossil carbon displacement, the longevity of buildings, and the nature of the forest supplying building materials must be considered.

Introduction

Forest ecosystems represent important stores of global terrestrial carbon and are the focus of possible climate mitigation strategies [1–3]. Along with that stored in forest ecosystems, carbon can be stored in wood products in-use and after disposal [4, 5]. Another way forests could mitigate climate change is through product substitution, a process whereby products from the forest substitute for others (i.e. concrete and steel) which, if used, would result in more fossil carbon release to the atmosphere [6–16]. While wood-based building materials generally embody less fossil-derived energy in their manufacture than steel and concrete, resulting in a net displacement of fossil carbon, its effectiveness as a climate mitigation strategy depends on the amount of carbon displaced and its duration. Current estimates of climate mitigation benefits of product substitution are generally based on three critical, often unstated assumptions: (1) the carbon displacement value remains constant [8–16], (2) the displacement is permanent and therefore of infinite duration [12–16] which implies no losses via cross-sector leakage, and (3) there is no relationship between building longevity and substitution longevity [10]. Below, each of these assumptions is reviewed.

Although most analyses of product substitution benefits implicitly assume a constant displacement value over time [8–16], it is subject to change. Schlamadinger and Marland [12] hypothesized energy substitution displacement values increase over time because of increased efficiencies. For product substitution, I hypothesize it will likely move in the opposite direction for three reasons. First, changing manufacturing methods impact embodied energy: for example, as long as it is available, the addition of fly ash could lead to a 22%–38% reduction in embodied energy required for concrete reducing the displacement value [17]. At the same time, increased processing of wood to create materials suitable for taller buildings (e.g. cross laminated timbers) would likely lead to a lower displacement value given laminated beams have 63%–83% more embodied energy than sawn softwoods [9, 17]. Second, the increases in energy efficiency hypothesized by [12] related to rising energy costs and recycling [9, 18, 19] and as noted by [8, 16] would also result in a decrease in product substitution displacement because the key relationship involves the difference in emissions and not the ratio as in energy substitution [20] (see supplemental information is available online at stacks.iop.org/ERL/14/065008/mmedia for detailed analysis of the displacement formula). Finally, changing the mix of fossil fuels used to generate energy can also substantially change the amount of carbon released per unit energy consumed and if natural gas continues to increase relative to coal, as has been observed [21], then the displacement value would likely decline in the future. The same is true if non-fossil energy sources such as solar, wind, or hydropower are increasingly used as projected [22].

One possible mechanism leading to permanent displacement is that fossil carbon not used by the building sector is also not used in any other sector in the future. However, this seems unlikely given carbon leakage [20, 23–25]. While the rate of product substitution-related leakage is difficult to estimate (in part because the form and location of the fossil carbon is not specifically known), it is unlikely to be zero given fossil carbon-based fuels are expected to be depleted in the next 107–235 years [26, 27] (see supplemental information). Even if these depletion time estimates are off by centuries, the duration of the displacement is not infinite and the claim that 'saved fossil emissions are forever' [12] is untenable. I hypothesize that without a mechanism to prevent its use, that fossil carbon displaced by product substitution will gradually be released by other sectors and will not be excluded from depletion as implied by [10, 12].

The key assumption of no relationship between product longevity and product substitution longevity has been asserted [10], but not fully explained. If there always is a preference for non-wood building materials, then avoiding their use avoids fossil carbon emissions, hence the displacement would continue to accumulate [20]. However, if wood is preferred then the use of wood does not necessarily increase cumulative displacement [20]. Despite differences in regional preferences for wood [28], most if not all assessments of product substitution tacitly assume wood is not preferred and that preferences never change. As a consequence, the product substitution store never saturates and implying there is no negative feedback in the net cumulative displacement. In all other forest-related carbon pools, a negative feedback exists between pool size and output (i.e. they are donor controlled systems): the larger the pool size, the larger the output flow. This causes these pools to saturate in time as long as the input remains constant. It is striking that this behavior is true for wood products, but not for product substitution (see supplemental information). In [12] product and energy substitution are treated the same. However, I believe they are quite different. In the case of energy, once energy is used it does not have a lifespan or store per se. However, in the case of wood products when the product lifespan is exceeded it has to be replaced with either wood-based or some other materials. If it is the former, the fossil carbon displacement continues, but does not necessarily increase [20] (see supplemental information). If it is the latter, the fossil carbon that was displaced is released to the atmosphere [20]. I therefore hypothesize that when wood is or becomes the preferred building material the product substitution pool has a negative feedback directly related to building longevity.

The objective of this study is a sensitivity analysis of these three assumptions and their impact on projected climate mitigation benefits. In addition to examining each assumption separately, I examined how they might work together to determine whether product substitution carbon benefits eventually become as large relative to the forest ecosystem and harvested materials as previous analyzes suggest [10–15]. To perform this analysis I used a relatively simple landscape model assuming an idealized, regulated system and focused on conditions in which product substitution benefits would be highest (i.e. clear-cut harvest, high manufacturing efficiency, and maximum use of products in buildings). The cases examined are therefore illustrative of the kinds of behavior the assumptions create, but not an exhaustive analysis of all forest ecosystems, management or manufacturing systems. Nor does the analysis try to identify the most likely values of displacement factors, carbon leakage, or product lifespans: e.g. [29, 30].

Methods

Each of the three assumptions was examined individually and then jointly for three contrasting initial conditions using a simple landscape model[1] that tracks the stores for the live, dead, and soil carbon pools in the forest ecosystem, the products in use and disposal, and the virtual carbon stores associated with product substitution. Each of these pools was modeled as a simple input–output, donor controlled sub-model following first order dynamics in which the output was regulated by a rate-constant describing the fraction lost per year. For product substitution, the fossil carbon displaced was the input, and losses were associated with use of fossil carbon by other sectors (hereafter called leakage losses) and those associated with the replacement of wooden buildings (hereafter called replacement losses). All simulations were conducted for a 300 year period as in [8] using a 50 year harvest cycle.

Displacement decline

In this set of simulations I assumed no losses associated with leakage or building replacement. The initial displacement value of 2.1 Mg C per 1 Mg C wood use [20] was reduced by 25%, 50% and 100% over either a 25, 50, or 100 year period. The 100% decline represents the possibility that fossil carbon will be completely replaced as a source of energy in the location of manufacture. As a control, the displacement value was assumed to not decline.

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[1] A more complete description of the model and parameters are available as supplemental information online.

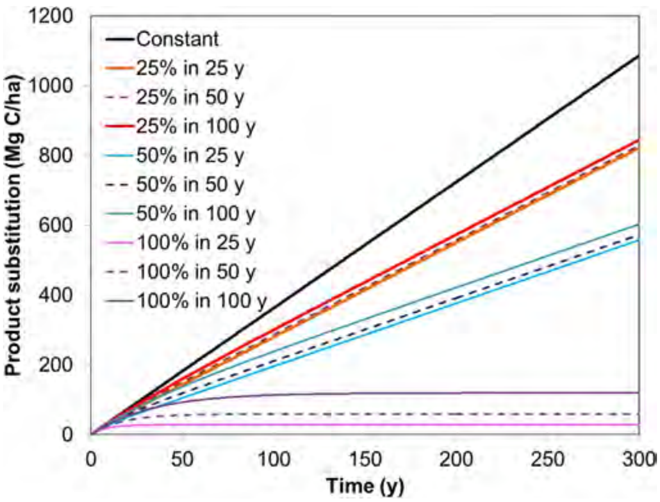

Figure 1. Accumulation of product substitution carbon when displacement is reduced 25%–100% over a 25–100 year period for a 50 year clear-cut harvest interval. For these simulations losses via leakage and replacement were zero[3].

Leakage losses

In this set of simulations I assumed the displacement value remained 2.1 Mg C per 1 Mg C wood use and there were no losses associated with building replacement. To examine the sensitivity of substitution benefits to cross-sector leakage, I simulated five possible scenarios: (1) no leakage, (2) 12%, (3) 6%, (4) 3%, (5) 1.5%, (6) 0.75, and (7) 0.375% yr^{-1}. In these scenarios leakage via other sectors was assumed to be continuous and not a one-time phenomenon. While expressed as a constant percentage lost per year, these values imply depletion times ranging between 25 and 800 years, which are 71%–340% of the currently estimated range of 35–235 years [26, 27].

Replacement losses

In this set of simulations I assumed the displacement value remained 2.1 Mg C per 1 Mg C wood use and there were no losses associated with cross-sector leakage. I varied the average building life-span to be 25, 50, 100, and 200 years, which bracket current estimates[2]. To provide a comparison to past studies, I reduced replacement losses to zero since this parameterization mimics the consequences of assuming no relationship between building longevity and product substitution longevity (see supplemental information).

Overall effect

To assess the overall effect of product substitution assumptions I examined a clear-cut system for three possible initial conditions: (1) an old-field planted to a production forest, (2) a production forest that originated from an old-growth forest landscape that began conversion 100 years ago, and (3) an old-growth forest converted to a production forest. In each case I assumed that 65% of the live carbon would be harvested, that 75% of that harvest would be converted into buildings. To explore the sensitivity of the assumptions on their overall impact I used the displacement and leakage loss parameter values that gave the minimum, median, and maximum effect based on the earlier simulations. In the case of replacement losses, I assumed an average building lifespan of either 50 years, 100 years, or an infinite number of years. The various combinations resulted in 47 simulations per initial condition. The model parameterization was based on a productive forest in the Pacific Northwest, a major source of wood building materials and US carbon stores [31].

Results

Displacement decline

There was a direct relationship to the total product substitution virtual store and the degree displacement declined, although the faster the decline in the displacement, the lower the final value (figure 1). For example, a 25% decline in 25, 50, and 100 years led to a final reduction in the product substitution virtual store of 24.3%, 23.6%, and 22.3%, respectively. This suggests that while the timing of the decline had an effect, the major response was to the level. The product substitution virtual store saturated only for the cases in which displacement went to zero and even if this took 100 years, product substitution stores estimates at 300 years were reduced by ≈89%.

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[2] Estimates of housing longevity are highly variable with exponential rate-constants ranging from 0.0069/y to 0.03/y [12–16]. In some cases building longevity has been modeled as a step function, with rapid losses after 80 years [10–11]. These estimates give an average lifespan or turnover time of 33–144 years. I explored a range of 25 to 200 years to bracket this uncertainty. Note that the average lifespan is not the same as the maximum lifespan of buildings: for an average lifespan of 50 years, the maximum lifespan would be over 230 years.

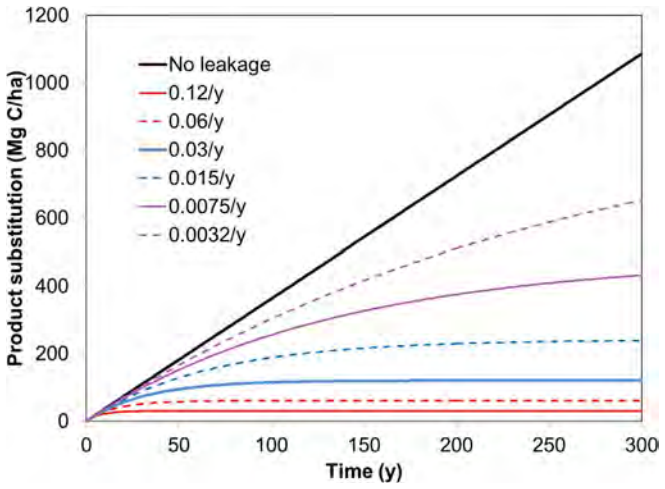

Figure 2. Accumulation of product substitution carbon when the time for displacement to be lost via leakage varies from 25 to 800 years for a 50 year clear-cut harvest interval. Displacement was assumed constant and replacement losses zero[3].

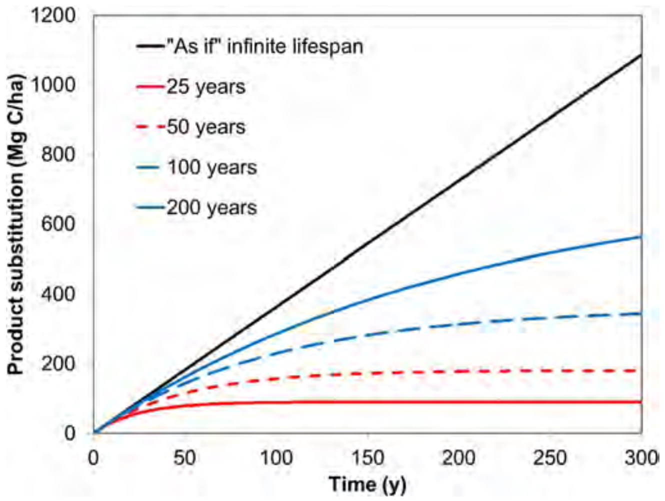

Figure 3. Accumulation of product substitution carbon when the average longevity of building varies for a 50 year clear-cut harvest interval. For these simulations displacement was constant and there were no leakage losses[3].

Leakage losses

Regardless of the time required for cross-sector leakage to occur, this process substantially limited the product substitution virtual store relative to the case without leakage (figure 2). With a leakage as low as 0.375% yr^{-1} (≈one-third the current estimate of the minimum depletion rate [27]) the store at 300 years was ≈40% lower than when there was no leakage. If the leakage rate-constant was 12% yr^{-1}, then ≈97% less would be stored relative to the no leakage scenario. Moreover, if the current range of depletion times (i.e. 35–235 years) is correct, then cross-sector leakage would reduce the estimates by 78%–96%. This indicates that leakage via other sectors may substantially undermine any attempt to displace fossil carbon using product substitution.

Replacement losses

For an average building longevity of 50 years the product substitution store at 300 years was ≈17% of that of the case in which product substitution behaved as if it had infinite lifespan (figure 3). Even when average building lifespan was 200 years, this store at 300 years was ≈52% that of when product substitutions behaved as if they had an infinite lifespan. This indicates that assuming no relationship between product substitution lifespan and building lifespan overestimates benefits.

Overall effect

Product substitution, estimated using past assumptions regarding displacement decline, leakage, and relationship to building longevity, increased for each initial condition; increasing the most when old-growth forests were harvested (figure 4). When alternative assumptions about product substitution were used, the shape of the product substitution accumulation curve varied: generally increasing for the old-field conversion to an asymptote, decreasing or increasing

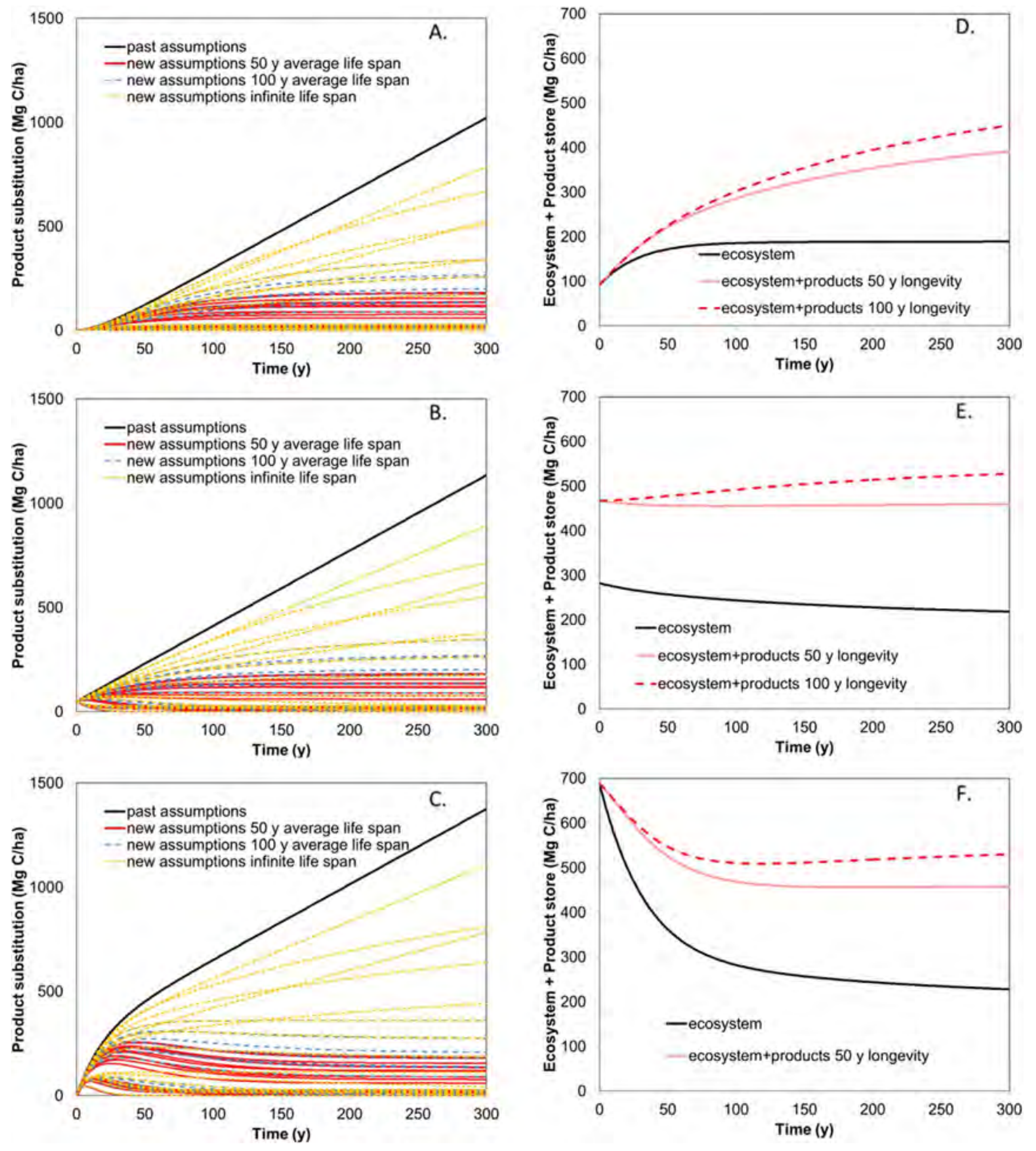

Figure 4. Accumulation of ecosystem, products in-use and disposed, and product substitution carbon stores for a 50 year clear-cut harvest interval in the Pacific Northwest for three possible scenarios: a plantation forest established on an agricultural field (A), (D); a production forest system that is continued (B), (E); an old-growth forest replaced by a forest plantation (C), (F). For past assumptions there was no decline in displacement value, there was no leakage, and buildings were assumed to have an infinite lifespan[3,4].

to an asymptote for the plantation system depending on replacement assumptions, and for most combinations reaching a peak at 10–40 years for the old-growth forest converted to a plantation scenario. This analysis indicates that to increase the overall amount of carbon stored in the system, that conversions of old-growth forests in the Pacific Northwest to plantations should be avoided, whereas creation of plantations on old-fields should be encouraged. Moreover, existing plantation systems are unlikely to increase their carbon stores unless building longevity is substantially increased (figure 4(e)).

Regardless of the initial conditions, product substitution was lower when alternative assumptions regarding displacement decline, leakage, and relationship to building lifespan were used, ranging from virtually zero to 80% of the past assumptions at year 300 depending on the parameter values assumed (tables S-2 to S-4). At the very least this suggests product substitution estimates are extremely uncertain. However, 85% of the 141 combinations examined were <50% than currently estimated. Those few exceeding 50% involved the assumption that substitution replacement losses were zero (i.e. an infinite lifespan) and had either an unrealistically low rate of

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[3] See figures S-7 to S-10 for detailed view of the first 50 years.

[4] See supplemental text and figure for similar results for a productive Southeastern US forest.

leakage (i.e. less than one-third that indicated by the maximum depletion time) or a minimal decline in displacement. Moreover, although past assumptions would indicate product substitution forms a large share of carbon stores at year 300 (74%–80% depending on the initial conditions), 90% of the alternative combinations examined indicated it was less than 50%. The combinations in which product substitution stores comprise the majority share of stores assumed an infinite lifespan and either minimal displacement decline or extremely low cross-sector leakage rates (tables S-2 to S-4).

Discussion

Past analyses suggest product substitution benefits at the landscape level continue to increase at a constant rate into the future [6–16]. Moreover, they imply that while a carbon debt can be created in some situations (e.g. harvest of primary forests), that this debt is eventually paid back via product substitution [10, 12, 32]. While I examined only a few illustrative cases, in the case of product substitution, these debts would not be paid back if the displacement declines or there are losses via cross-sector leakage or related to product replacement. That is because negative feedbacks associated with losses can prevent product substitution from accumulating forever. These negative feedbacks could exist regardless of the forest ecosystem, the harvest system, and the efficiency of processing harvests into products as well as the proportion allocated to buildings. Thus, while I did not examine the effect on a wide range of ecosystems, or alternative harvest systems, or systems in which buildings are minor faction of harvested carbon, these underlying relationships would not be altered for these new situations[4].

The assumption that the product substitution benefit has no losses (e.g. [10]) results in at least two sets of untenable predictions: (1) if fossil fuel carbon is stored each time a wooden building is constructed, then theoretically it would be possible for fossil fuel carbon to be stored long after this carbon has been depleted by other sectors; hence this assumption may violate the conservation of mass; (2) this assumption also views the following as the same: (a) harvest that completely replaces wood building losses, (b) harvest that does not replace wood building losses, (c) harvest that exceeds wood building losses leading to more wood buildings, and (d) wood buildings that are not replaced. These cases clearly differ [20] (see supplemental information). This assumption also introduces a logical inconsistency: products appear to have different lifespans depending on whether their direct carbon (finite) or substitution carbon (infinite) effects are being considered (figure S-4).

Although displacement decline over time influences the accumulation of product substitution benefits, its effect is smaller than leakage or replacement losses. In contrast, leakage loss has as dramatic effect as longevity even if it occurs at a very slow rate implying the effect of product substitution is to delay eventual fossil carbon release, but not to stop it altogether. This may be important because it buys time, but this is not the same as the displaced fossil carbon never being released as suggested by [10, 12].

Collectively the past assumptions commonly used to assess the mitigation benefits of product substitution lead to a carbon pool that does not saturate causing the product substitution pool to eventually exceed the carbon stores in the forest ecosystem and in the associated wood products. Moreover, because there are no losses from the products substitution pool, its highest rate of increase occurs for the harvest interval providing the highest yield, typically a very young age relative to the forest ecosystem carbon maximum [32]. With no relationship to building longevity, there is no relationship to the size of the wood products pool despite the fact that more wooden buildings would imply more success in displacing fossil carbon. Finally, this set of assumptions makes product substitution benefits relatively insensitive to the initial conditions of the forest ecosystem because product substitution benefits always increase over time.

The alternative set of assumptions explored here suggests that the highest overall climate mitigation may not necessarily be achieved by maximizing the harvest yield using short rotation forestry [33]. Moreover, if product substitution is the primary climate mitigation strategy, wood building materials need to keep their carbon advantage by maintaining or increasing their displacement value. This suggests that while wood can be used in buildings taller than the general current practice, this may have less mitigation value than anticipated if these materials embody more fossil energy than current wood-based materials. Given the strong potential relationship between building and product substitution longevity, increasing the life-span of buildings or reusing building materials could potentially help meet future demand and increase mitigation benefits. Without a policy to assure that fossil carbon displaced by one sector is not used by another sector, product substitution benefits could be quite limited. While it is unlikely any policy could completely eliminate cross-sector leakage, designating long-term reserves might delay releases until their climate impacts are reduced to acceptable levels.

Conclusions

Despite its general and limited nature, this sensitivity analysis found that product substitution benefits have likely been overestimated for many scenarios and are generally smaller than those related to the forest ecosystem and their derived products. This new analysis suggests that if product substitution is to be used as part of a climate mitigation strategy, then more attention will have to be paid to maintaining the amount of carbon displaced, reducing the rate of carbon cross-sector leakage, and increasing the longevity of buildings. This new analysis also suggests that the best strategy for forest-related climate mitigation for an important timber region, the Pacific Northwest, is largely determined by the initial conditions of the management system. Afforestation leads to an increase in carbon stores in the ecosystem, wood products, and substitution benefits for many decades. On existing production forests, substitution benefits could be maintained by continuing the current system or increased by harvesting more (but only as long as ecosystem carbon stores do not decline) and/or increasing the longevity of buildings. Conversion of older, high carbon stores forests to short rotation plantations would over the long-term likely lead to more carbon being added to the atmosphere despite some of the harvested carbon being stored and production substitution occurring [33].

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Carbon Balance and Management

RESEARCH Open Access

Attribution of net carbon change by disturbance type across forest lands of the conterminous United States

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Abstract

Background: Locating terrestrial sources and sinks of carbon (C) will be critical to developing strategies that contribute to the climate change mitigation goals of the Paris Agreement. Here we present spatially resolved estimates of net C change across United States (US) forest lands between 2006 and 2010 and attribute them to natural and anthropogenic processes.

Results: Forests in the conterminous US sequestered −460 ± 48 Tg C year^{-1}, while C losses from disturbance averaged 191 ± 10 Tg C year^{-1}. Combining estimates of net C losses and gains results in net carbon change of −269 ± 49 Tg C year^{-1}. New forests gained −8 ± 1 Tg C year^{-1}, while deforestation resulted in losses of 6 ± 1 Tg C year^{-1}. Forest land remaining forest land lost 185 ± 10 Tg C year^{-1} to various disturbances; these losses were compensated by net carbon gains of −452 ± 48 Tg C year^{-1}. C loss in the southern US was highest (105 ± 6 Tg C year^{-1}) with the highest fractional contributions from harvest (92%) and wind (5%). C loss in the western US (44 ± 3 Tg C year^{-1}) was due predominantly to harvest (66%), fire (15%), and insect damage (13%). The northern US had the lowest C loss (41 ± 2 Tg C year^{-1}) with the most significant proportional contributions from harvest (86%), insect damage (9%), and conversion (3%). Taken together, these disturbances reduced the estimated potential C sink of US forests by 42%.

Conclusion: The framework presented here allows for the integration of ground and space observations to more fully inform US forest C policy and monitoring efforts.

Keywords: Forests, Disturbance, Harvest, Insects, Fire, Drought, Greenhouse gas, Land use, Climate change, FIA, UNFCCC

Background

The 2015 Paris Climate Change Agreement, with consensus from 192 signatories, calls for achieving a balance between anthropogenic emissions by sources and removals by sinks in the second half of this century [1]. Forests are currently responsible for the capture and storage of an estimated 25% of global anthropogenic emissions [2]. If Paris goals are to be achieved, further enhancement of forest-based carbon (C) removals to mitigate emissions in other sectors will be a critical component of any collective global strategy [3], especially as no alternative sink technologies have yet been proven at scale. Thus, spatially identifying terrestrial sources and sinks of carbon, and understanding them well enough to predict how they will respond to management decisions or future climate change, will pose major science and policy challenges in the years to come.

Remote sensing products can provide regular and consistent observations of Earth's surface to help identify the condition of forest ecosystems and changes within them at a range of spatial and temporal scales [4]. Over the past

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several years, the remote sensing research community has used these products to monitor tropical deforestation, forest C stocks and associated C emissions, largely in support of REDD+ initiatives in developing countries [5–12]. In many developed countries, periodic national forest inventories form the basis of annual greenhouse gas (GHG) reporting to the United Nations Framework Convention on Climate Change (UNFCCC). The sample-based design of these inventories may offer little in the way of detailed and spatially-explicit information on the distribution of forest biomass [13], timing and location of timber harvesting in managed forests, or the cause and timing of other types of forest disturbances. If the ultimate aim of the Paris Agreement is to introduce practices that lead to reduced emissions and enhanced removals of C from the world's managed forests, including in temperate and boreal biomes, then a lack of disaggregated, spatially-explicit information could pose challenges over the coming years related to knowledge of where changes are occurring and where interventions are likely to be most effective.

Several C budget models have been developed to simulate ecosystem response to climate drivers and other disturbances, and these models represent an established approach to estimating C fluxes at national to regional scales. For example, Canada's National Forest Carbon Monitoring Accounting and Reporting System (NFC-MARS) uses the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3), and is used also as a decision support tool for forest managers to quantify forest C dynamics at a landscape scale. Different models emphasize different aspects of ecosystem dynamics, with some accounting for competition between plant functional types, nutrient limitation, and natural disturbances. Time series of anthropogenic land-cover changes are usually prescribed based on spatially explicit data. The models can reflect spatial and temporal variability in C density and response to environmental conditions, but their modeled C stocks may differ markedly from observations [14].

Such models are not used explicitly in the GHG inventory for the US to report forest C fluxes. Instead, the current US inventory system uses the C stock-difference accounting approach [15] enabled by the annual national forest inventory conducted by the United States Department of Agriculture (USDA) Forest Service Forest Inventory and Analysis (FIA) program. The difference in C stocks in five C pools is estimated via sequential re-measurements of permanent ground inventory plots. When forest stocks decline, it is assumed that C emissions have occurred from the land to the atmosphere if not reconciled with a transfer to another land use category. Conversely, when forest C stocks increase it is assumed that C has been sequestered from the atmosphere by terrestrial vegetation. In this way, estimated net C change in the US forest sector is the integrated result of both anthropogenic and natural processes—harvest, land use change, fire, drought, insect infestation, wind damage—all of which influence the magnitude of forest C stocks in each pool. Results are most statistically robust when compiled at large spatial scales (e.g., state or regional), such that quantification of finer-scale spatial patterns is less precise. Though changes are well constrained via sequential re-measurements on inventory plots, the US [16, 17] has only recently begun using methods to disaggregate the effects of various disturbance types on forest stocks and fluxes (although this separation is not a requirement of IPCC Good Practice Guidance, [18]).

The objective of this study was to synthesize information from remote sensing observations of forest carbon stocks and disturbance with information collected by various US agencies into a framework that (1) more explicitly attributes C losses to major disturbance types (land use change, harvesting, forest fires, insect damage, wind damage and drought); and (2) disaggregates net C change into relevant IPCC reporting categories of non-forest land converted to forest land, forest land converted to non-forest land, and forest land remaining forest land. This framework allows for the integration of ground and space observations to more fully inform US forest C policy and monitoring efforts.

Methods

We built a spatially-explicit empirical model that combines information from many data sources to infer disturbance and resulting C dynamics within each hectare of forest land in the 48 conterminous states of the US, totaling an area of more than 2.1 million km^2. For the purposes of regional comparison and analyses, we divided the US into three broad regions (North, South, West) based on similar histories of forestland use ([19], Fig. 1) and into nine smaller subregions based on those used in the US FIA program. Forest types were defined as hardwood or softwood, following the National Land Cover Data (NLCD) classification (deciduous forest class: hardwoods; evergreen forest class: softwoods). The time period of analysis is 1 January 2006 to 31 December 2010.

Data inputs

Forest area map (2005)

Forest extent in the base year 2005 was determined from the NLCD and the global tree cover and tree cover change products of Hansen et al. [8]. Specifically, an area was determined to be forested if categorized as

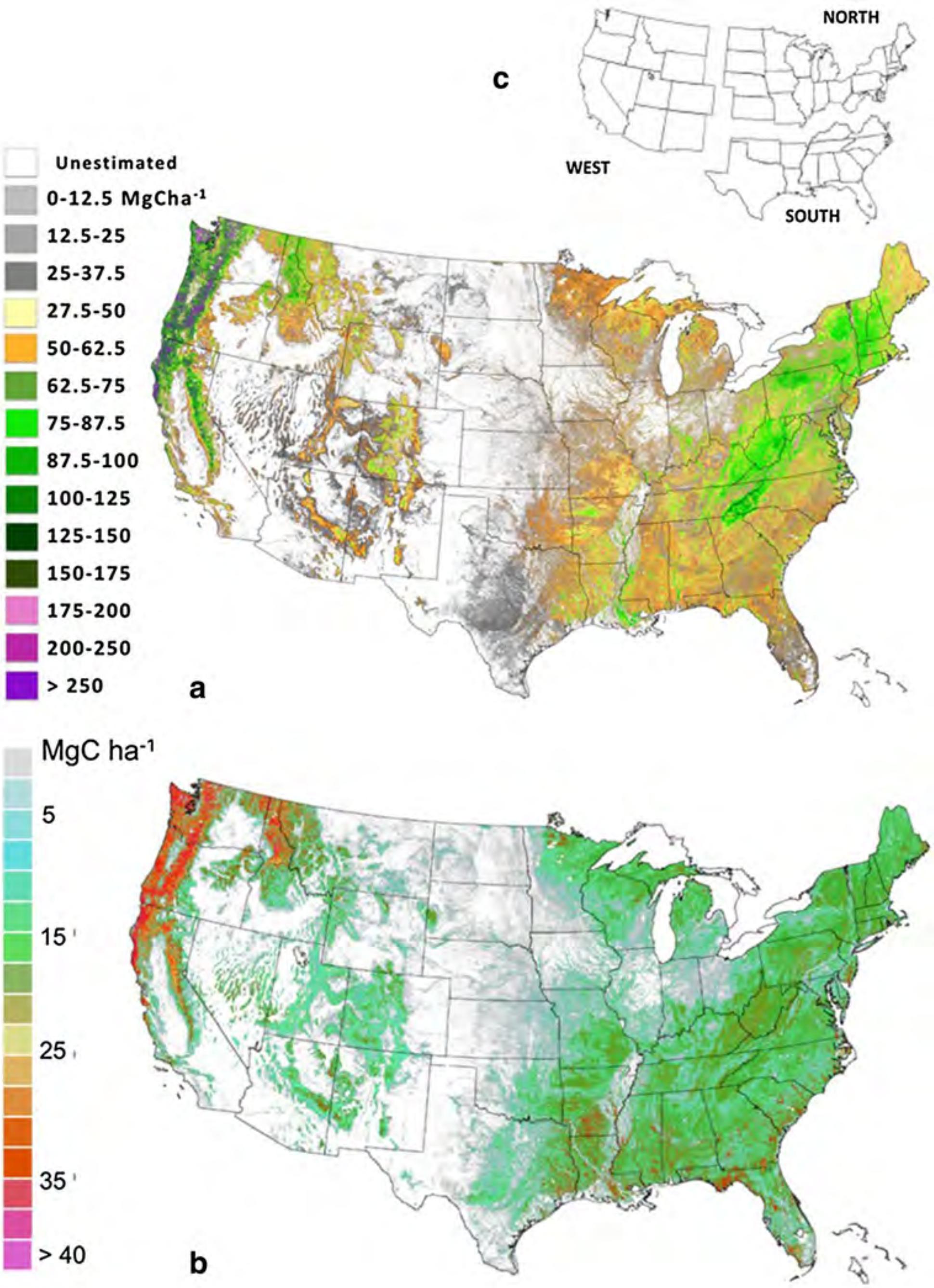

Fig. 1 **a** Map of aboveground live woody biomass carbon density (Mg C ha^{-1}) and **b** uncertainty across forest lands of the conterminous US at 1-ha resolution for circa the year 2005. **c** The regional analysis was performed by dividing the US into three sub-regions as recommended by Heath and Birdsey [19]. The above and belowground carbon density maps and the uncertainty maps can be downloaded from NASA's distributed Data Active Archive Center (http://dx.doi.org/10.3334/ORNLDAAC/1313)

hardwood or softwood in the NLCD 2006 dataset[1] and, according to the Hansen et al. [8] dataset, it (a) met the tree cover threshold of 25% in the year 2000 and was not lost between 2001 and 2005 or (b) did not meet the tree cover threshold of 25% in 2000 but was identified as having gained tree cover (i.e., afforestation/reforestation) between 2000 and 2012. The NLCD has been shown to significantly underestimate tree cover [20] and thus the forest area estimates used in this analysis—defined by both NLCD and Hansen et al. [8]—are likely to be conservative. However, these two data products currently represent the best available spatially explicit data for forest extent in the conterminous US (CONUS).

Forest biomass density maps (circa 2005)

We developed maps of C stocks (50% of biomass) in aboveground live biomass in US forest land as part of NASA's C Monitoring System (CMS) program based on a combination of remote sensing observations and FIA data (Fig. 1). The overall methodology used in mapping the aboveground live forest biomass C density is described in Saatchi et al. [5]. After filtering for cloud effects, slopes, and signal-to-noise ratio, more than 700,000 samples of lidar (light detecting and ranging) data acquired between 2003 and 2008 from the Geoscience Laser Altimeter System (GLAS), onboard the Ice, Cloud and land Elevation Satellite (ICESat) were used as samples of the vertical structure of US forest land. We used the Lorey's height [21] measured in 65,000 single-condition FIA plots (i.e., plots with a single domain mapped on each plot) to calibrate the lidar-derived height metric and used the relationship between Lorey's height and aboveground C density for 28 forest types to convert the lidar data into estimates of aboveground live C density. All FIA plots with a probability of disturbance causing reduced canopy cover (<50%) were removed from the height-biomass model development to reduce any potential discrepancy between ground and lidar height metrics. Lidar-derived biomass samples were then extrapolated over the landscape using a combination of optical and radar satellite imagery that captures the variations of forest structure and cover to create wall-to-wall maps of forest aboveground live biomass C density. We used nine remote sensing imagery layers as spatial predictor variables. Optical and thermal data from Landsat imagery (bands 3, 4, 5 and 7) were aggregated to 100 m spatial resolution from 30 m native resolution along with the leaf area index derived from Landsat imagery [22]. In addition, we used the advanced land observing satellite (ALOS) phased area L-band synthetic aperture radar (PALSAR) imagery at two polarizations (HH and HV backscatter) along with topographical data of surface elevation and slope from Shuttle Radar Topography Mission (SRTM) resampled to 100 m resolution from 20 and 30 m native resolutions, respectively. ALOS PALSAR plays an important role in quantifying variation in forest biomass. In particular, the HV polarization provides the largest contribution among the data layers to predicted biomass because it has a strong direct sensitivity to biomass up to 100–150 Mgha^{-1} (depending on forest type), is less impacted by soil moisture and other environmental variables, and may contribute significantly in extrapolating larger biomass forests through texture and spatial correlation. Similarly, SRTM data include information on topography and also forest height. We used the national elevation data (NED) to represent the ground surface elevation and used the difference between SRTM and NED as an indicator of forest height. This variable also contributed significantly to explaining the spatial variation of biomass over forests with biomass values >150 Mgha^{-1}.

The aboveground C density samples derived from GLAS data were combined with satellite imagery using the maximum entropy estimation (MaxEnt) algorithm to estimate aboveground biomass density for each 1-ha pixel. MaxEnt is a probability-based algorithm that estimates the posterior likelihood distribution of a variable by maximizing the entropy of said probability distribution while maintaining the constraints provided by the training samples [23]. We selected a random subset consisting of 70% of the samples (~500,000 samples) for model input and used the remaining 30% for model evaluation and validation. The product from the MaxEnt estimator includes both the mean aboveground carbon (AGC) density for each 1-ha pixel and the estimation of the error derived from a Bayesian probability estimator for each pixel. Spatial uncertainty analysis and uncertainty propagation were used to evaluate the overall uncertainty of AGC at the pixel level. This process included the quantification of error at each step of the process and the use of the Gaussian error propagation approach:

$$\text{Error} = \sqrt{\varepsilon^{\mathbf{2}}_{\mathbf{measurement}} + \varepsilon^{\mathbf{2}}_{\mathbf{allometry}} + \varepsilon^{\mathbf{2}}_{\mathbf{sampling}} + \varepsilon^{\mathbf{2}}_{\mathbf{prediction}}}$$

where each of the terms are the relative errors at that pixel and represent the measurement errors of lidar for capturing the forest height, the error associated with the lidar aboveground C allometry model for each forest type, the error associated with sampling the 1-ha pixel

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[1] Within each 1 ha pixel, the wet woodland class was included as forest but was not used to determine whether the pixel was hard- or softwood. Hard- or softwood was determined based on the plurality of NLCD hard- or softwood 30 m pixels within the hectare, ignoring the sub-fraction of wet woodlands and selecting softwood when hard- and softwood fractions were equal.

with GLAS footprint size (~0.25 ha), and the MaxEnt prediction error. In evaluating the errors at the state and county level, we also included the spatial correlation of the prediction error from the MaxEnt approach [24].

In the FIA, belowground forest biomass is quantified using a root-shoot ratio [25]. Knowledge of root biomass dynamics is fundamental to improving our understanding of carbon allocation and storage in terrestrial ecosystems [26]. We used the relationship between belowground carbon (BGC) and AGC from the FIA data to develop a BGC spatial distribution at the same scale as AGC [5, 27]. In estimating the uncertainty in BGC, we followed the same approach as AGC with the addition of including the errors associated with the model used in relating AGC to BGC.

FIA stock change data (2006–2010)

To estimate average net changes in the stock of live AGC and BGC between 2006 and 2010 in forests disaggregated by disturbance type, we queried the FIA database (http://apps.fs.fed.us/fiadb-downloads/datamart.html) to extract more than 141,000 records associated with remeasured permanent plots, where each extracted record represents a "condition" (i.e., domain(s) mapped on each plot according to attributes such as land use, forest type, stand size, ownership, tree density, stand origin, and/or disturbance history) of a measured plot at two points in time, typically 5 years apart. Disturbed plots were stratified into a lookup table by geographic region (North, South, or West), forest type (hardwood or softwood), disturbance type (fire, insect, wind, conversion, or harvest), and disturbance intensity (Table 1). A similar lookup table was developed for undisturbed plots stratified by geographic region, forest type, and base C stock in the year 2005 (Table 2).

Disturbance maps (2006–2010)

Sources of disturbance data used in this analysis are summarized in Table 3 and include spatially-explicit data on locations of fire, insect damage, wind damage, land use change, drought, and timberlands. The timberlands map was used to attribute net carbon gains occurring within vs. outside timberland areas. Because harvested wood may come from intermediate treatments (treatments not intended to cause regeneration), partial harvest or clearcutting forests, deforestation, and non-forest land trees, the area of clearcuts as observed within timberland areas through remote sensing imagery cannot represent all these wood sources [28]. Therefore for estimating C losses from timber harvest, we used data collected in the US based on mill surveys rather than remote sensing observations.

Timber product output data (TPO 2007)

The volume of roundwood products, mill residues and logging residues reported in the TPO database (Table 3), separated by product class and detailed species group, were used to estimate C losses from wood harvest. The spatial resolution of the data was the "combined county", which represented the minimum reportable scale from the timber product output (TPO; FIA Fiscal Year 2013 Business Report, [29]) data while retaining necessary confidentiality.

Model assumptions

IPCC Tier 2 estimation

The terrestrial C cycle includes changes in C stocks due to both continuous processes (i.e., growth, decomposition) and discrete events (i.e., disturbances such as harvest, fire, insect outbreaks, land-use change). Continuous processes can affect C stocks in all areas every year, while discrete events (i.e., disturbances) cause emissions and redistribute C in specific areas in the year of the event. In accounting for net C change in this analysis, we use country-specific data (Tier 2) and apply the simplifying methodological assumption [15] that all post-disturbance emissions (after accounting for C storage in harvested wood products) occur as part of the disturbance event, i.e., in the year of disturbance, rather than modeling these emissions through time as in IPCC's Tier 3 approach. The application of lower tier methods also assumes that the average transfer rate into dead organic matter (dead wood and litter) is equal to the average transfer out of dead organic matter, so that the net stock change in these pools is zero [15]. This assumption means that dead organic matter (dead wood and litter) C stocks need not be quantified for land areas that remain forested. The rationale for this approach is that dead organic matter stocks, particularly dead wood, are highly variable and site-specific, depending on forest type and age, disturbance history and management. Because the FIA data used in this analysis do not include measurements of soil C or dead C pools and no robust relationships currently exist that relate these pools to a more easily measured pool (such as the derivation of belowground biomass from aboveground biomass using root:shoot ratios), we excluded the soil C and dead C pools from our analysis. As a result, our estimate of net C change using the stock-difference approach is equal to the net change in C stocks in the aboveground and belowground live biomass pools only, with a fraction of the aboveground live biomass assumed to be transferred to the wood products pool, where a portion is permanently sequestered in long-lived products and the remainder emitted to the atmosphere (see below).

Table 1 Look-up table of annual fractional change (average = μ; standard error = σ) in aboveground carbon (AGC) and belowground carbon (BGC) in disturbed forests based on FIA plot data

Region	Forest type	Disturbance	Initial C	N	AGC μ	AGC σ	BGC μ	BGC σ
North	Softwood	Fire	Low	2	−0.003	0.012	−0.001	0.013
North	Softwood	Fire	Medium	3	−0.052	0.031	−0.053	0.031
North	Softwood	Fire	High	5	−0.150	0.030	−0.157	0.030
North	Softwood	Weather	Low	63	−0.013	0.016	−0.014	0.016
North	Softwood	Weather	High	10	−0.163	0.013	−0.169	0.013
North	Softwood	Insect	Low	85	−0.003	0.007	−0.003	0.008
North	Softwood	Insect	Medium	82	−0.044	0.023	−0.046	0.023
North	Softwood	Insect	High	45	−0.126	0.035	−0.133	0.032
North	Softwood	Harvested	Low	521	−0.046	0.035	−0.048	0.036
North	Softwood	Harvested	High	246	−0.152	0.026	−0.158	0.025
North	Hardwood	Fire	Low	40	−0.003	0.009	−0.003	0.009
North	Hardwood	Fire	Medium	29	−0.045	0.024	−0.048	0.023
North	Hardwood	Fire	High	11	−0.131	0.034	−0.136	0.034
North	Hardwood	Weather	Low	412	−0.011	0.016	−0.011	0.016
North	Hardwood	Weather	High	34	−0.160	0.017	−0.164	0.016
North	Hardwood	Insect	Low	656	−0.002	0.008	−0.002	0.008
North	Hardwood	Insect	Medium	432	−0.045	0.020	−0.046	0.020
North	Hardwood	Insect	High	118	−0.132	0.029	−0.136	0.028
North	Hardwood	Harvested	Low	2177	−0.047	0.035	−0.047	0.035
North	Hardwood	Harvested	High	806	−0.154	0.023	−0.157	0.023
South	Softwood	Fire	Low	127	−0.002	0.007	−0.003	0.008
South	Softwood	Fire	Medium	174	−0.048	0.021	−0.052	0.022
South	Softwood	Fire	High	52	−0.124	0.027	−0.131	0.028
South	Softwood	Weather	Low	78	−0.016	0.016	−0.017	0.016
South	Softwood	Weather	High	16	−0.161	0.026	−0.168	0.023
South	Softwood	Insect	Low	46	−0.002	0.008	−0.004	0.008
South	Softwood	Insect	Medium	66	−0.054	0.022	−0.059	0.023
South	Softwood	Insect	High	60	−0.135	0.030	−0.142	0.029
South	Softwood	Harvested	Low	1787	−0.044	0.034	−0.048	0.036
South	Softwood	Harvested	High	586	−0.149	0.025	−0.157	0.024
South	Hardwood	Fire	low	112	−0.002	0.008	−0.003	0.008
South	Hardwood	Fire	Medium	86	−0.042	0.021	−0.045	0.022
South	Hardwood	Fire	High	37	−0.131	0.033	−0.139	0.030
South	Hardwood	Weather	Low	484	−0.014	0.016	−0.015	0.016
South	Hardwood	Weather	High	32	−0.162	0.019	−0.167	0.017
South	Hardwood	Insect	Low	145	0.000	0.013	−0.002	0.011
South	Hardwood	Insect	Medium	121	−0.047	0.022	−0.051	0.022
South	Hardwood	Insect	High	38	−0.133	0.031	−0.138	0.031
South	Hardwood	Harvested	Low	1235	−0.048	0.036	−0.051	0.036
South	Hardwood	Harvested	High	609	−0.146	0.029	−0.152	0.027
West	Softwood	Fire	Low	13	−0.007	0.008	−0.007	0.008
West	Softwood	Fire	Medium	8	−0.049	0.023	−0.050	0.026
West	Softwood	Fire	High	0	*−0.126*	*NA*	*−0.133*	*NA*
West	Softwood	Weather	Low	5	−0.003	0.008	−0.003	0.008
West	Softwood	Weather	High	0	*−0.162*	*NA*	*−0.168*	*NA*
West	Softwood	Insect	Low	12	0.001	0.007	0.001	0.007
West	Softwood	Insect	Medium	3	−0.041	0.016	−0.044	0.018
West	Softwood	Insect	High	0	*−0.131*	*NA*	*−0.138*	*NA*

Table 1 continued

Region	Forest type	Disturbance	Initial C	N	AGC μ	AGC σ	BGC μ	BGC σ
West	Softwood	Harvested	Low	28	−0.027	0.030	−0.028	0.031
West	Softwood	Harvested	High	0	*−0.150*	*NA*	*−0.157*	*NA*
West	Hardwood	Fire	Low	4	−0.002	0.008	−0.002	0.008
West	Hardwood	Fire	Medium	3	−0.057	0.021	−0.059	0.021
West	Hardwood	Fire	High	0	*−0.131*	*NA*	*−0.138*	*NA*
West	Hardwood	Weather	Low	0	*−0.013*	*NA*	*−0.013*	*NA*
West	Hardwood	Weather	High	0	*−0.161*	*NA*	*−0.165*	*NA*
West	Hardwood	Insect	Low	13	−0.003	0.008	−0.003	0.009
West	Hardwood	Insect	Medium	3	−0.041	0.025	−0.044	0.028
West	Hardwood	Insect	High	0	*−0.132*	*NA*	*−0.136*	*NA*
West	Hardwood	Harvested	Low	4	−0.039	0.031	−0.039	0.033
West	Hardwood	Harvested	High	0	*−0.151*	*NA*	*−0.155*	*NA*

Italics imputed from other regions

Disturbance attribution

Forest land was assumed to be disturbed if included in at least one of the disturbance maps (Table 3) during the 2006–2010 time period: (1) maximum burn severity score of at least two (low) over the 5 years of fire data; (2) insect damage of at least three trees per acre over the 5 year study period; (3) within a path of a tornado or a buffered region around the hurricane path where wind speeds typically exceeded 95 miles per hour (category 2 hurricane)[2] between 2006 and 2010; (4) converted to agriculture, barren land or settlement in the NLCD layer between 2006 and 2011 (considered as deforestation events); or (5) had an average drought intensity score of more than two in the NDMC Drought Monitor map between the years of measurement. For fire and insect disturbance, three levels of disturbance intensity were assigned based on burn severity score (from the MTBS dataset) or insect damage per acre (from the Aerial Detection Survey), respectively. Two levels of wind disturbance intensity were assigned and areas determined to have been converted to agriculture or settlement were assumed to experience one uniform intensity of disturbance. All other forest land was assumed to be undisturbed between 2006 and 2010. In areas where multiple types of disturbance were identified within a 1 ha forest land pixel, we assumed only one disturbance type was driving the C loss. Disturbance type priority was set based on the intensity of the disturbance and level of confidence in the data sets. In general, more intense disturbances and higher quality products took priority over less intense disturbances and those products assessed as having more uncertainty. The disturbance location and intensity products were assumed to be in the following quality order, from least to most inherent uncertainty: conversion, fire, wind, insect damage. For instance, a pixel identified as experiencing an intense fire disturbance and a low intensity insect disturbance was assigned the high intensity fire disturbance as the single disturbance driving loss. This assumption simplified the processing but added additional uncertainty to the estimates. The assigned disturbance type priority varied across multiple iterations of our uncertainty analysis. It was not possible to attribute harvest disturbance to specific pixels, therefore C losses from harvest were estimated at the county scale using TPO data.

Estimation of net carbon change

Net carbon change from fire, wind, insect damage, land use change, and drought

If a hectare of forest land in the US was categorized as disturbed between 2006 and 2010 based on the disturbance maps, then the intensity and type of disturbance was identified. The pixel was then linked to an annualized percent net change in C stock estimate, based on its identified category in the FIA-based lookup tables. These annualized percent change values were multiplied by the initial base C stock in 2005 in each pool (aboveground biomass, belowground biomass) and multiplied by 5 years to estimate total net change in C within the pixel between 2006 and 2010.

Net carbon change from harvest

Annual C losses associated with harvest activities were estimated using mill surveys compiled into the USDA

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[2] This wind speed threshold was selected based on the Saffir Simpson Hurricane Wind Scale, which indicates that trees start to be uprooted and fall at category 2 sustained wind speeds between 96 and 110 mph. The hurricane tracks were buffered to a symmetrical width of 100 km.

Table 2 Look-up table of annual fractional change (average = μ; standard error = σ) in aboveground carbon (AGC) and belowground carbon (BGC) in undisturbed forests, based on FIA plot data

Region	Forest type	Drought	Initial C	n	AGC μ	AGC σ	BGC μ	BGC σ
North	Softwood	No	<25	5167	0.064	0.135	0.080	0.199
North	Softwood	No	25–50	3459	0.023	0.034	0.023	0.034
North	Softwood	No	50–100	2085	0.016	0.024	0.016	0.024
North	Softwood	No	≥100	345	0.013	0.034	0.013	0.034
North	Softwood	Yes	<25	50	0.028	0.030	0.031	0.035
North	Softwood	Yes	25–50	50	0.008	0.034	0.008	0.035
North	Softwood	Yes	50–100	12	0.016	0.040	0.016	0.040
North	Softwood	Yes	≥100	2	0.013	0.017	0.013	0.016
North	Hardwood	No	<25	12,559	0.074	0.102	0.087	0.131
North	Hardwood	No	25–50	13,656	0.025	0.036	0.025	0.036
North	Hardwood	No	50–100	14,173	0.014	0.026	0.014	0.026
North	Hardwood	No	≥100	3265	0.010	0.030	0.010	0.030
North	Hardwood	Yes	<25	19	0.016	0.058	0.016	0.062
North	Hardwood	Yes	25–50	12	0.006	0.040	0.006	0.041
North	Hardwood	Yes	50–100	7	0.001	0.026	0.000	0.027
North	Hardwood	Yes	≥100	1	0.006	NA	0.005	NA
South	Softwood	No	<25	3648	0.314	0.355	0.452	0.621
South	Softwood	No	25–50	2940	0.082	0.069	0.085	0.072
South	Softwood	No	50–100	2345	0.039	0.049	0.039	0.050
South	Softwood	No	≥100	673	0.021	0.050	0.020	0.051
South	Softwood	Yes	<25	464	0.340	0.407	0.487	0.694
South	Softwood	Yes	25–50	348	0.081	0.071	0.084	0.074
South	Softwood	Yes	50–100	299	0.038	0.039	0.038	0.041
South	Softwood	Yes	≥100	110	0.020	0.038	0.020	0.039
South	Hardwood	No	<25	6585	0.133	0.191	0.176	0.291
South	Hardwood	No	25–50	6180	0.040	0.044	0.041	0.045
South	Hardwood	No	50–100	8244	0.021	0.032	0.021	0.032
South	Hardwood	No	≥100	2697	0.014	0.032	0.014	0.032
South	Hardwood	Yes	<25	630	0.140	0.184	0.185	0.272
South	Hardwood	Yes	25–50	498	0.042	0.062	0.044	0.064
South	Hardwood	Yes	50–100	756	0.021	0.029	0.021	0.030
South	Hardwood	Yes	≥100	275	0.011	0.029	0.011	0.029
West	Softwood	No	<25	56	0.061	0.102	0.079	0.123
West	Softwood	No	25–50	45	0.027	0.048	0.028	0.049
West	Softwood	No	50–100	61	0.022	0.026	0.022	0.027
West	Softwood	No	≥100	80	0.014	0.019	0.014	0.019
West	Softwood	Yes	<25	0	*0.310*	*NA*	*0.443*	*NA*
West	Softwood	Yes	25–50	0	*0.072*	*NA*	*0.075*	*NA*
West	Softwood	Yes	50–100	0	*0.037*	*NA*	*0.037*	*NA*
West	Softwood	Yes	≥100	0	*0.020*	*NA*	*0.020*	*NA*
West	Hardwood	No	<25	33	0.037	0.055	0.043	0.061
West	Hardwood	No	25–50	26	0.023	0.026	0.025	0.028
West	Hardwood	No	50–100	45	0.026	0.041	0.027	0.043
West	Hardwood	No	≥100	38	0.019	0.025	0.020	0.027
West	Hardwood	Yes	<25	0	*0.137*	*NA*	*0.180*	*NA*
West	Hardwood	Yes	25–50	0	*0.041*	*NA*	*0.043*	*NA*

Table 2 continued

Region	Forest type	Drought	Initial C	n	AGC μ	AGC σ	BGC μ	BGC σ
West	Hardwood	Yes	50–100	0	*0.021*	*NA*	*0.021*	*NA*
West	Hardwood	Yes	≥100	0	*0.011*	*NA*	*0.011*	*NA*

Italics imputed from other regions

Table 3 Fourteen independent datasets were integrated and used to produce net carbon change estimates by disturbance type

Product	Source	Spatial coverage	Temporal coverage	Url
Tree cover Tree cover change	[8]	Complete CONUS	Tree cover: single snapshot in 2000 Loss: annual 2001–2010 Gain: 2000–2012	http://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.1.html
Fire	Monitoring trends in burn severity	Complete CONUS	Annual 2006–2010	http://www.mtbs.gov/products.html
Wind	NOAA's storm prediction center—tornado tracks	Complete CONUS	Annual 2006–2010	http://www.spc.noaa.gov/gis/svrgis/
Wind	NOAA's storm prediction center—hurricane paths	Complete CONUS	Annual 2006–2010	http://nhc.noaa.gov/gis/
Insect	USFS aerial detection survey	Sub-set of CONUS	Annual 2006–2010	http://www.fs.fed.us/foresthealth/technology/adsm.shtml
Forest type	National land cover database—hardwood or softwood	Complete CONUS	Single snapshot in 2000	http://www.mrlc.gov/
Conversion	National land cover database	Complete CONUS	Snapshots in 2006 and 2011	http://www.mrlc.gov/
Drought	NDMC drought monitor	Complete CONUS	Weekly between 2006 and 2011	http://droughtmonitor.unl.edu/
Timberlands	Mark Nelson USFS for 2007 resources planning act	Complete CONUS	Snapshot in 2007	N/A
Biomass density Carbon stocks	Sassan Saatchi	Complete CONUS	Snapshot in 2005	http://dx.doi.org/10.3334/ORNLDAAC/1313)
Harvest	USFS timber products output	Combined county CONUS	Survey in 2007	http://www.fia.fs.fed.us/program-features/tpo/
FIA	USFS forest inventory and analysis program	Sites in CONUS	Between 1997 and 2013	http://www.fia.fs.fed.us/

TPO database for the year 2007. Due to the periodic nature of the TPO report for 2007 data, harvest emission estimates were assumed to be representative for all 5 years included in our analysis (2006–2010). Volumes of roundwood products, mill residue and logging residues were converted to biomass using oven-dry wood densities [30]. The fraction of C in primary wood products remaining in end uses or in landfills after 100 years per product class[3] was assumed to be permanently sequestered, and was estimated from values published in Smith et al. [31]. Fuelwood, posts/poles/pilings and miscellaneous product classes were assumed to be fully emitted. Emissions from mill residues were considered equal to the summed mill residues from fuel by-products, miscellaneous by-products and unused mill residues, plus emissions from fiber by-products. All fiber by-products were assumed to form pulp and to follow the emissions assumptions of pulp products. All logging residues were assumed to be emitted. Timberlands were delineated based on the boundaries of the US timberlands map (Table 3), and annual net C gains within timberlands were estimated following the look-up tables for growth in undisturbed forests as described below.

Net carbon change from forest growth/regrowth

Forest land in the US that did not experience deforestation through land use conversion or significant damage by wind, insect, fire, or drought over the analysis period, as well as new forest land (i.e., afforestation/reforestation), were linked to values of annual net change

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[3] The TPO and Smith et al. [31] product classes were mapped to one another as follows: Sawlog = softwood/hardwood lumber (depending on species); veneer = softwood plywood; pulp = paper; composite = oriented strandboard.

in C stock, based on the area's identified category in the lookup tables derived from FIA measurement data. These annualized percent change values were multiplied by the initial C stock in 2005 in each pool (aboveground biomass, belowground biomass) and multiplied by 5 years to estimate total net change in C within each 1-ha pixel between 2006 and 2010.

Total annual net carbon change

The FIA-based estimated net change in C represents the sum of net C losses (caused by disturbances) and net C gains (caused by forest growth) that occurred between FIA measurement dates at the site. Similarly, our estimate of net C change (ΔC_{net}) during the 5-year period at the combined county scale was calculated as:

$$\begin{aligned}\Delta C_{net} = {} & \Delta C_{undist} + \Delta C_{A/R} + \Delta C_{conversion} \\ & + \Delta C_{timberlands} + \Delta C_{insect} + \Delta C_{fire} \\ & + \Delta C_{wind} + \Delta C_{drought}\end{aligned}$$

where ΔC_{undist} is the net C change in forest land outside of timberlands that did not experience land use conversion or significant damage by wind, insects, fire or drought. $\Delta C_{A/R}$ is the net C change in new forest land. $\Delta C_{conversion}$, ΔC_{wind} ΔC_{insect}, and ΔC_{fire} represent the net C change in forestland that was converted or significantly disturbed by conversion, wind, insects, and fire, respectively. $\Delta C_{drought}$ is the net C reduction in sequestration in forest land experiencing drought from what was expected during non-drought periods. $\Delta C_{timberlands}$ is the net C change on timberlands (as delineated by the timberlands map), calculated as the sum of net C gains (as estimated from FIA lookup tables) and C losses (as estimated from the TPO data, accounting for the fraction of harvested C stored permanently in the long-lived product pool). By convention, C losses are represented as positive values and C gains as negative values. Consequently, various forms of disturbance result in a weaker (i.e., less negative) overall sink than would occur otherwise in the absence of disturbance.

Uncertainty analysis

We estimated statistical bounds for the estimates of net C change by conducting a Monte Carlo uncertainty analysis [32]. The four sources of uncertainty included in the simulation were associated with the forest biomass density maps, the stock-change lookup tables derived from FIA data, each of the disturbance maps, and the TPO data. The simulation was conducted at the combined county scale. Uncertainty in the biomass density maps was derived from a secondary simulation in which the input datasets were resampled to generate 100 replicate training datasets, or realizations, that had the same qualities of the original training dataset, but different random error. A new MaxEnt model was fit to each of these 100 replicated datasets and used to create 100 full resolution biomass maps. Uncertainty in the FIA-based ΔC values were calculated using the variance in the look-up tables:

$$uncertainty\% = \frac{\frac{\sigma}{\sqrt{n}} * 1.96}{\mu} * 100$$

Uncertainty in the area affected by disturbance was estimated to be 30%, with an estimated 5% bias in under reported area. We conducted the simulation using three separate rule sets for selecting a disturbance type for pixels identified as experiencing multiple disturbances during the 5-year study period. Uncertainty in the TPO data at the combined county scale was also assumed to be 30%.

We ran 10,000 Monte Carlo simulations with stochastic elements in place for the four uncertainty components. We assumed that 80% of the randomly generated error was random and 20% of the error was systematic within the simulation. To implement this assumption, we estimated the error associated with each component twice—once at the simulation iteration level and again for each individual combined county. The iteration level uncertainty was multiplied by 0.2 before it was added to the original combined county estimate, while the combined county level stochastic element was multiplied by 0.8 before it was added. In this way, we accounted for both random error as well as systematic error in our estimates.

This uncertainty analysis was intended to provide context to the estimates and assist in the process of identifying methods and data in need of refinement or replacement. The uncertainty analysis is not exhaustive, in the sense that additional sources of uncertainty exist that are not accounted for in the analysis presented here. These additional sources include but are not limited to (a) potential temporal mismatch between the biomass data providing initial carbon stocks in 2005 and the activity data beginning in 2006 and (b) uncertainty in the equations and factors used in the FIA to convert tree measurements to estimates of wood volume and carbon stocks. Given these additional sources of uncertainty, the uncertainty bounds presented here are almost certainly an underestimate of the actual uncertainty.

Results

Forest land in the conterminous US, as defined here totaling 221 million ha in 2005, sequestered -460 ± 48 Tg C $year^{-1}$ between 2006 and 2010, while average C losses from forest disturbances were 191 ± 10 Tg C $year^{-1}$. Combining estimates of net C gains and net C losses results in net C change of -269 ± 49 Tg C $year^{-1}$ (Fig. 2). These results are broadly

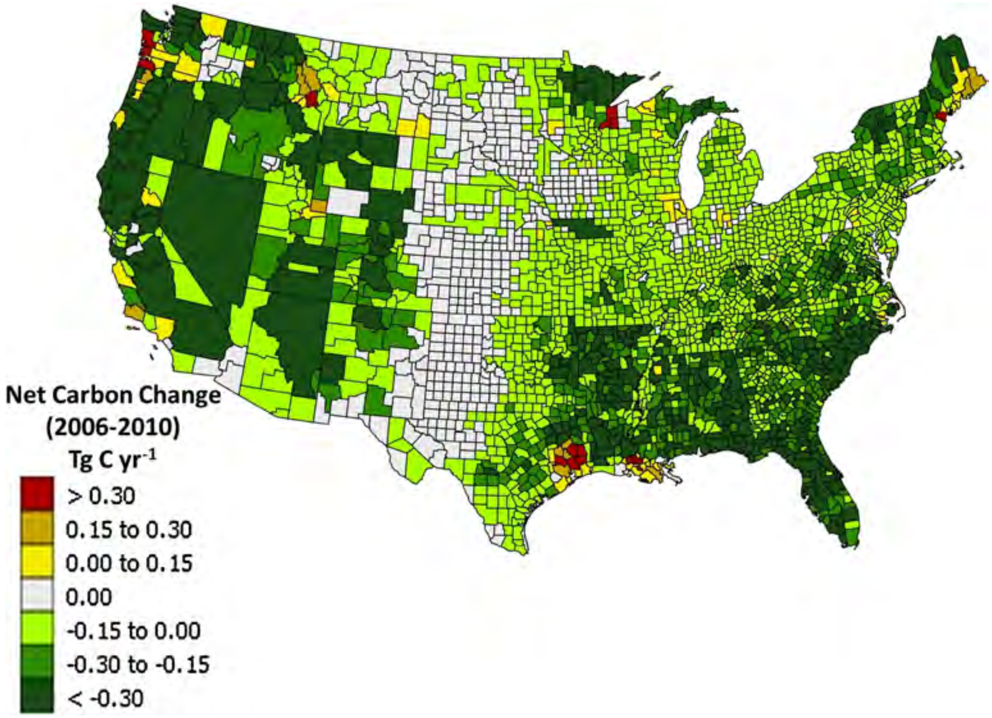

Fig. 2 Average annual net carbon change (Tg C year^{-1}) at the combined county scale across the CONUS. Most combined counties (91%) are net C sinks while areas with extensive forest disturbance can be net C sources to the atmosphere

consistent with estimates reported in the US. GHG inventory for forests in 2010 (-293 Tg C year^{-1}, [33]) but we estimate a larger net sink than reported in Zheng et al. [28] (-181 Tg C year^{-1}), although the spatial and temporal domains varied across these analyses, as did the C pools included.

New forests, averaging 0.4 million ha per year, sequestered -8 ± 1 Tg C year^{-1}, while deforestation, averaging 0.1 million ha per year, resulted in C losses of 6 ± 1 Tg C year^{-1}. Forest land remaining forest land lost 184 ± 10 Tg C year^{-1} to disturbance (13% from natural disturbance, 87% from harvest); these were compensated by net carbon gains of 452 ± 48 Tg C year^{-1}, 75% of which occurred within timberland areas (Table 4). C losses from natural and human induced disturbances reduced the potential net C sink in US forests by 42% compared to the potential sink estimated without disturbance effects included, an estimate that is similar to other studies [28, 34].

Regional variation in net C change across the nation was substantial. The South sequestered more C in growing forests (-271 ± 28 Tg C year^{-1}) than the North (-97 ± 10 Tg C year^{-1}) or the West (-92 ± 11 Tg C year^{-1}), while at the same time losing more C to the atmosphere from disturbances (105 ± 6 Tg C year^{-1}) than the other regions (41 ± 2 Tg C year^{-1} for the North and 44 ± 3 Tg C year^{-1} for the West). Forest C change in the South was substantial, in terms of both C losses and gains, because this region is home to a majority of the wood harvest occurring in the US (60% of all C loss from harvest occurred in the South), and is therefore also home to the largest area of regenerating forests that are sequestering C at high rates. At the state level, the highest C losses occurred in the forests of Georgia, Alabama, Washington, Mississippi, Louisiana, and Oregon, with each of these states losing more than 11 Tg C year^{-1} (Table 5). Georgia, Florida, Alabama, Mississippi, and North Carolina gained the most forest C in the time period, with each sequestering at least 24 Tg C year^{-1}. C gains exceeded C losses in all states. Forests in approximately 6% of combined counties were a net source of C to the atmosphere (Fig. 2).

We estimated net C losses from six separate disturbance processes: fire, insect infestation, wind, timber harvest, land use conversion, and drought (Fig. 3). C losses from harvest (162 ± 9.9 Tg C year^{-1}) were more than five times higher than losses from all other processes combined (30 ± 2.6 Tg C year^{-1}). Fire (7 ± 1.0 Tg C year^{-1}), wind (5 ± 0.7 Tg C year^{-1}), insect infestation (10 ± 1.3 Tg C year^{-1}), and deforestation (6 ± 0.7 Tg C year^{-1}) each contributed a similar magnitude of C losses across the CONUS, while drought

Table 4 Average annual net C change (Tg C year^{-1}) across US forests between 2006 and 2010, disaggregated into categories of non-forest land to forest land, forest land to non-forest land, and forest land remaining forest land

Category	Area (Mha year^{-1})	Net C gain (Tg C year^{-1})	Net C loss (Tg C year^{-1})
Non-forest land to forest land	0.4	−8 ± 1	
Forest land to non-forest land	0.1		6 ± 1
Forest land remaining forest land	221.1	−452 ± 47	185 ± 10
Insect damage	0.9		9 ± 1
Forest fire	0.6		7 ± 1
Wind damage	0.6		5 ± 1
Drought	0.8		1 ± 0
Timberlands	152.0	−342 ± 42	162 ± 10
Undisturbed forest	54.9	−109 ± 19	
Total	221.6	−460 ± 48	191 ± 10
Net C change			−269 ± 49

Results are further disaggregated by disturbance type within the forest land remaining forest land category

accounted for about 1 ± 0.2 Tg C year^{-1}. Individual disturbances had spatially distinct distributions (Fig. 4a). On average, drought affected areas had C sequestration rates 20% lower than drought-free areas.

C losses in the South were highest (105 ± 6 Tg C year^{-1}) with the highest fractional contributions from harvest (92%) and wind (5%), with a particularly high concentration of loss coming from the South Central region (including the states of Texas, Oklahoma, Mississippi, Louisiana, Kentucky, Tennessee, Alabama, and Arkansas; Fig. 4b). The West had the second highest C loss (44 ± 3 Tg C year^{-1}) with significant contributions from harvest (66%), fire (15%), and insects (13%). The North had the lowest C loss (41 ± 2 Tg C year^{-1}) with most significant proportional contributions coming from harvest (86%), insect damage (9%), and conversion (3%).

Our results can also be used to estimate net C impacts of localized disturbances at finer spatial scales. A tornado struck Lakewood, Wisconsin on 7 June 2007 and caused severe forest damage, resulting in net C loss of more than 0.3 Tg C across a 13,000 ha swath (Fig. 5a). The wild fire in southern California's Santa Barbara County, termed the "Zaca" fire, started on 4 July 2007 and caused extensive damage to more than 97,000 ha of forest in the Los Padres National Forest, resulting in net C loss of more than 4 Tg C (Fig. 4b).

The highest fractional contribution of C loss in all states was from harvest (Table 4), and 64% of these losses were from logging residues [both above- (19%) and below-ground (23%)] and mill residues (22%). Across all wood product classes, the production of pulpwood resulted in the highest forest C losses (26 Tg C year^{-1}), followed by saw logs (18 Tg C year^{-1}), although a high proportion of C in saw logs is in use or in landfills, both which are considered to be long-term C storage (Fig. 6).

Discussion

Comparison with other studies

We estimate that Hurricanes Gustav and Ike in 2008, the only two hurricanes above category 2 to make landfall during the study period, damaged forests in Texas and Louisiana and led to net C change of more than 22 ± 2 Tg C (or 4 ± 0.5 Tg C year^{-1} on average over the 5 year period). Other studies report average annual C loss in US forests due to hurricane damage in the 20th century of 14 Tg C year^{-1} [35]. Zhou et al. [36] estimate total C emissions from wood harvest in 35 eastern US states as 168 Tg C year^{-1} between 2002 and 2010, while our estimate for the same geographic extent is 132 ± 8 Tg C year^{-1} between 2006 and 2010. Other national scale estimates of emissions from wood harvest are lower, such as that of Williams et al. [37] (107 Tg year^{-1} in 2005) and Powell et al. [34] (74 Tg C year^{-1} between 1986 and 2004). Hicke and Zeppel [38] estimated that bark beetles and fire together resulted in gross emissions of 32 Tg C year^{-1} in the western US between 1997 and 2010. We estimate that insects and fire resulted in net C change of 17 ± 2 Tg C year^{-1} between 2006 and 2010. We conclude that, given the different spatial extents, time periods and C pools included, results from our analysis that cover all disturbance types are broadly consistent with these and other more specialized studies (see Williams et al. [39] for a comprehensive review).

Priorities for improved forest carbon change estimates

Results generated from this analysis are dependent on the algorithm that assigns each hectare of forest land to a category that is then associated with a C stock change value. By including spatial data sets of carbon stocks and disturbance from remote sensing observations, the

Table 5 State level estimates of forest area in 2005 (millions of ha), net C gains, net C losses, and net C change (Tg C year^{-1}) together with the percent of C loss attributable to harvest, drought, fire, wind, insect infestation, and land use conversion within the state

State	Forest area	C gain	C loss	Net C change	Fire (%)	Insect (%)	Wind (%)	Conversion (%)	Drought (%)	Harvest (%)
Alabama	8.5	−27.3	12.5	−14.9	0	1	0	1	0	97
Arizona	2.0	−2.4	0.4	−1.9	22	0	1	0	0	77
Arkansas	7.4	−22.6	8.6	−14.0	1	2	0	2	0	95
California	9.3	−16.8	9.4	−7.4	32	0	7	1	0	60
Colorado	5.1	−6.7	0.3	−6.3	8	0	0	1	0	92
Connecticut	0.9	−1.2	0.2	−1.0	0	0	1	31	0	68
Delaware	0.2	−0.2	0.1	−0.1	0	0	0	4	0	95
District of Columbia	<0.1	0.0	0.0	0.0	0	0	0	100	0	0
Florida	6.4	−28.5	6.3	−22.2	3	0	0	3	0	94
Georgia	9.4	−33.2	14.4	−18.8	1	1	0	2	0	96
Idaho	7.1	−10.2	4.9	−5.3	29	0	23	0	0	48
Illinois	2.3	−2.8	1.1	−1.7	0	0	0	3	0	97
Indiana	2.3	−2.8	1.7	−1.1	0	0	3	1	0	95
Iowa	1.2	−1.5	0.4	−1.1	0	1	0	3	0	96
Kansas	0.9	−1.1	0.2	−0.9	0	1	0	3	0	95
Kentucky	5.7	−11.5	3.3	−8.2	1	0	0	6	0	93
Louisiana	5.4	−18.0	11.1	−6.9	0	19	0	1	0	79
Maine	6.8	−7.7	6.7	−0.9	0	0	15	1	0	84
Maryland	1.2	−1.5	0.8	−0.8	0	0	6	7	0	86
Massachusetts	1.5	−1.9	0.6	−1.3	0	0	4	18	0	78
Michigan	8.5	−10.3	4.3	−6.0	0	0	1	1	11	87
Minnesota	7.7	−9.5	3.2	−6.3	1	0	3	1	0	96
Mississippi	7.0	−24.3	11.6	−12.7	0	2	0	2	0	96
Missouri	7.1	−8.7	2.7	−6.0	1	2	0	4	0	93
Montana	7.3	−8.6	5.0	−3.5	14	0	49	0	0	37
Nebraska	0.3	−0.4	0.1	−0.2	2	1	0	0	0	97
Nevada	0.7	−0.8	0.1	−0.7	15	0	0	0	0	84
New Hampshire	2.1	−2.6	0.8	−1.8	0	2	4	6	0	88
New Jersey	1.0	−1.3	0.5	−0.8	2	0	40	14	0	43
New Mexico	2.6	−3.2	0.3	−2.8	33	0	16	0	0	51
New York	8.3	−10.7	3.1	−7.6	0	0	5	4	0	91
North Carolina	7.6	−23.7	9.6	−14.1	0	0	0	1	2	95
North Dakota	0.2	−0.3	0.0	−0.3	0	1	0	2	0	96

Table 5 continued

State	Forest area	C gain	C loss	Net C change	Fire (%)	Insect (%)	Wind (%)	Conversion (%)	Drought (%)	Harvest (%)
Ohio	3.6	−4.4	1.2	−3.2	0	0	7	7	0	86
Oklahoma	3.6	−9.0	1.6	−7.3	2	2	0	3	0	94
Oregon	9.2	−20.6	11.1	−9.6	4	0	2	6	0	88
Pennsylvania	7.6	−9.8	4.0	−5.8	0	0	13	3	0	84
Rhode Island	0.2	−0.2	0.1	−0.2	0	0	3	11	0	85
South Carolina	4.8	−18.4	6.5	−11.9	1	1	0	2	0	97
South Dakota	0.5	−0.6	0.2	−0.3	2	0	0	0	0	98
Tennessee	6.2	−14.2	4.0	−10.1	0	1	0	3	0	95
Texas	7.9	−23.3	9.8	−13.6	1	23	0	2	0	74
Utah	2.2	−2.2	0.3	−1.8	24	0	38	0	0	38
Vermont	2.0	−2.5	0.6	−1.9	0	0	2	1	0	96
Virginia	6.7	−16.5	6.1	−10.4	1	0	0	2	0	97
Washington	7.9	−17.3	11.7	−5.6	3	0	8	19	0	70
West Virginia	5.3	−6.9	2.5	−4.4	0	0	1	6	0	93
Wisconsin	7.2	−8.4	6.3	−2.0	0	1	23	0	5	70
Wyoming	2.7	−3.3	0.8	−2.5	21	0	25	0	0	54
Total	221.5	−459.5	191.1	−268.4	4	3	5	3	1	85

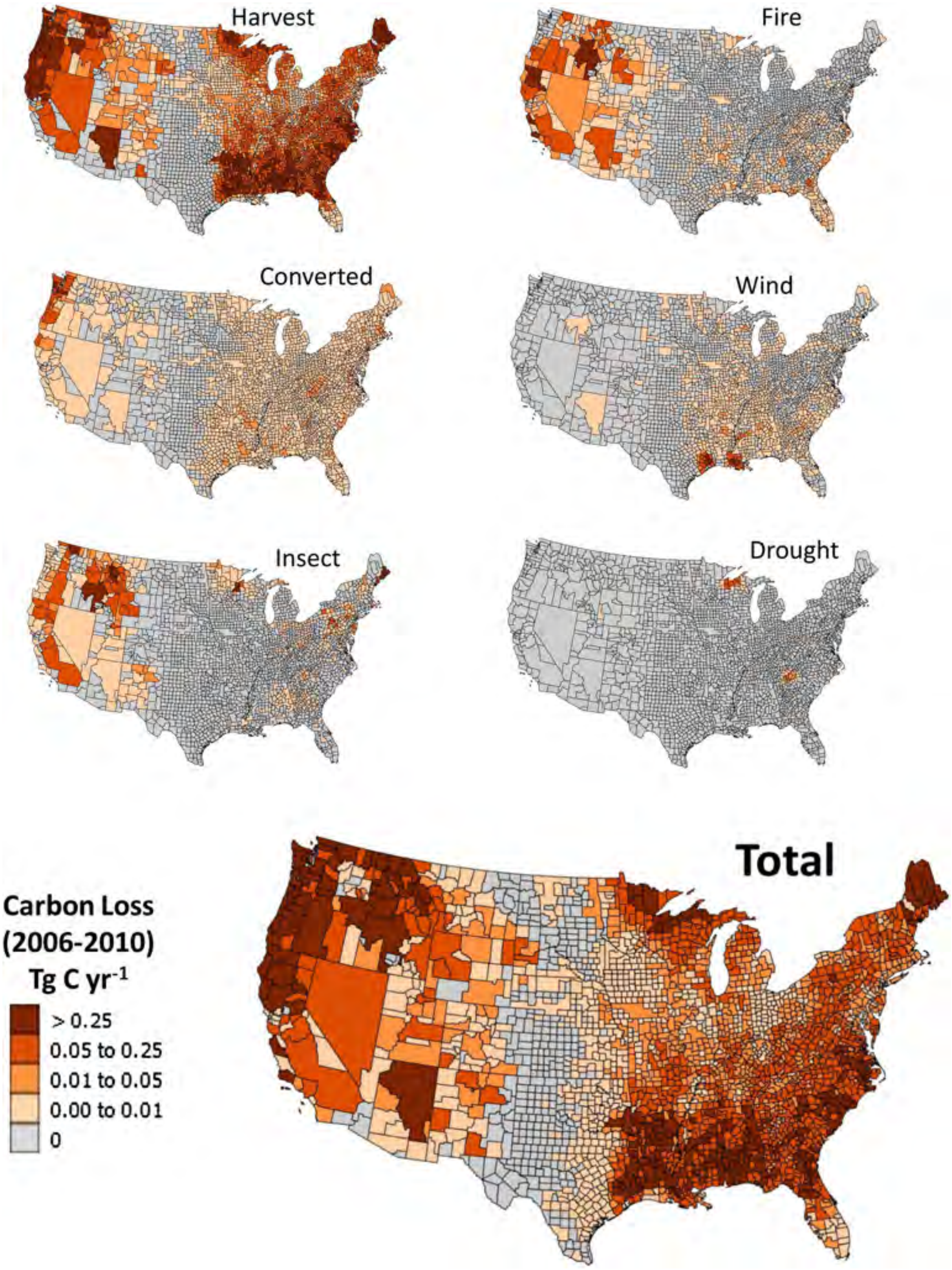

Fig. 3 Average annual net carbon loss (Tg C year^{-1}) attributed to the most likely disturbance type and estimated at the combined county scale for harvest, fire, land use conversion, wind, insect, and drought. Combining these six sources results in estimates of total annual net C loss from disturbance occurring between 2006 and 2010

methodology avoids making gross assumptions on the regional distribution of carbon stocks and disturbance, thus improving estimates of C loss. The strength of this approach is estimated in the uncertainty analysis. Our framework is therefore completely dependent on the underlying data sources and, as the data improve, so will the estimates. Although the US is among the world's leaders in technology and open data, where high quality geospatial datasets are publicly available and inventory programs are maintained by various federal and state agencies, opportunities for improvement remain.

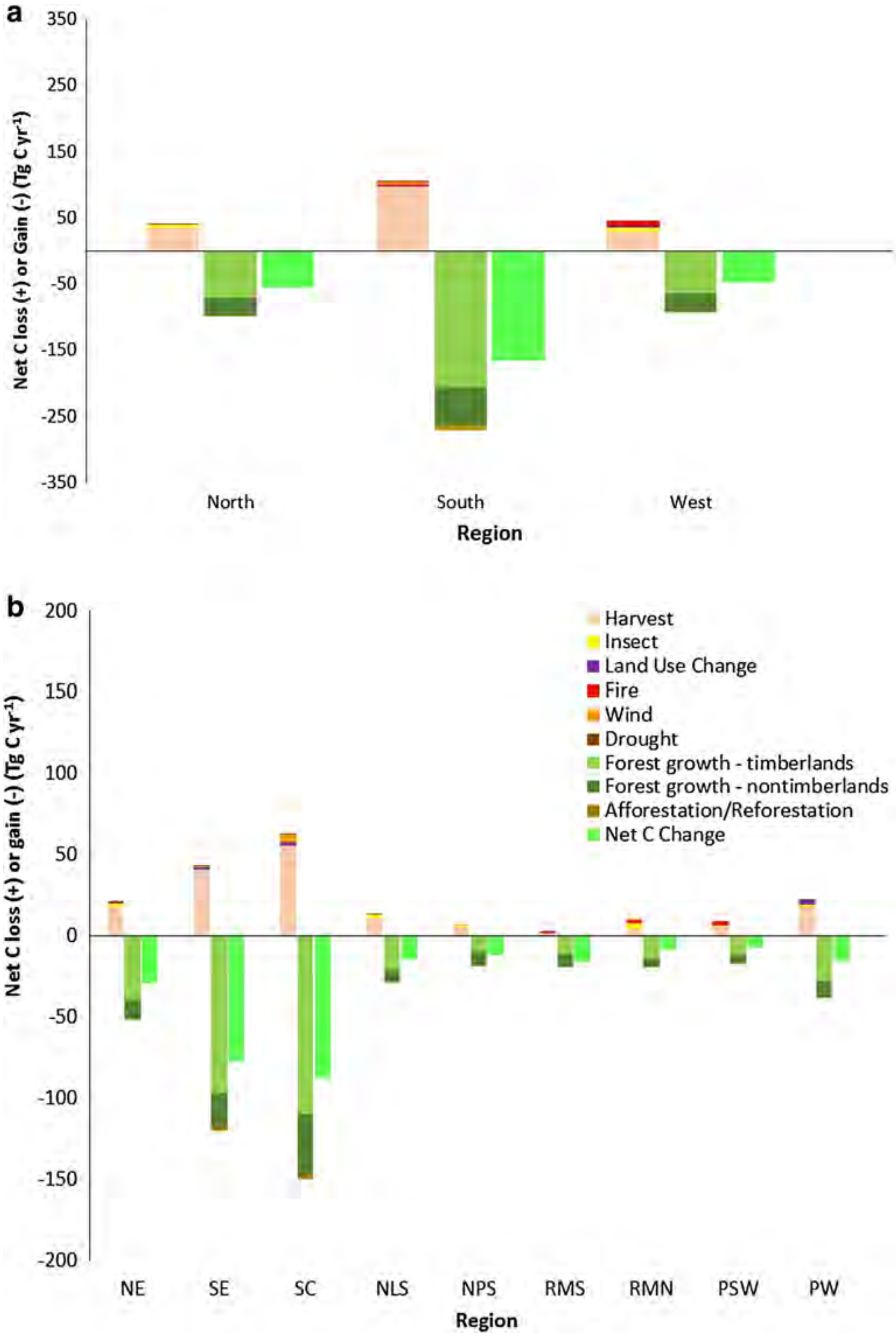

Fig. 4 Average annual net carbon change by disturbance type in **a** the North (79 million ha of forest), South (87 million ha), and West (56 million ha) regions and **b** by FIA region: northeast (NE; 41 million ha), southeast (SE; 35 million ha), southcentral (SC; 52 million ha), northern lake states (NLS; 23 million ha), northern plains states (NPS; 15 million ha), pacific west (PW; 17 million ha), rocky mountain northern (RMN; 14 million ha), rocky mountain southern (RMS; 15 million ha), and the pacific southwest (PSW; 9 million ha)

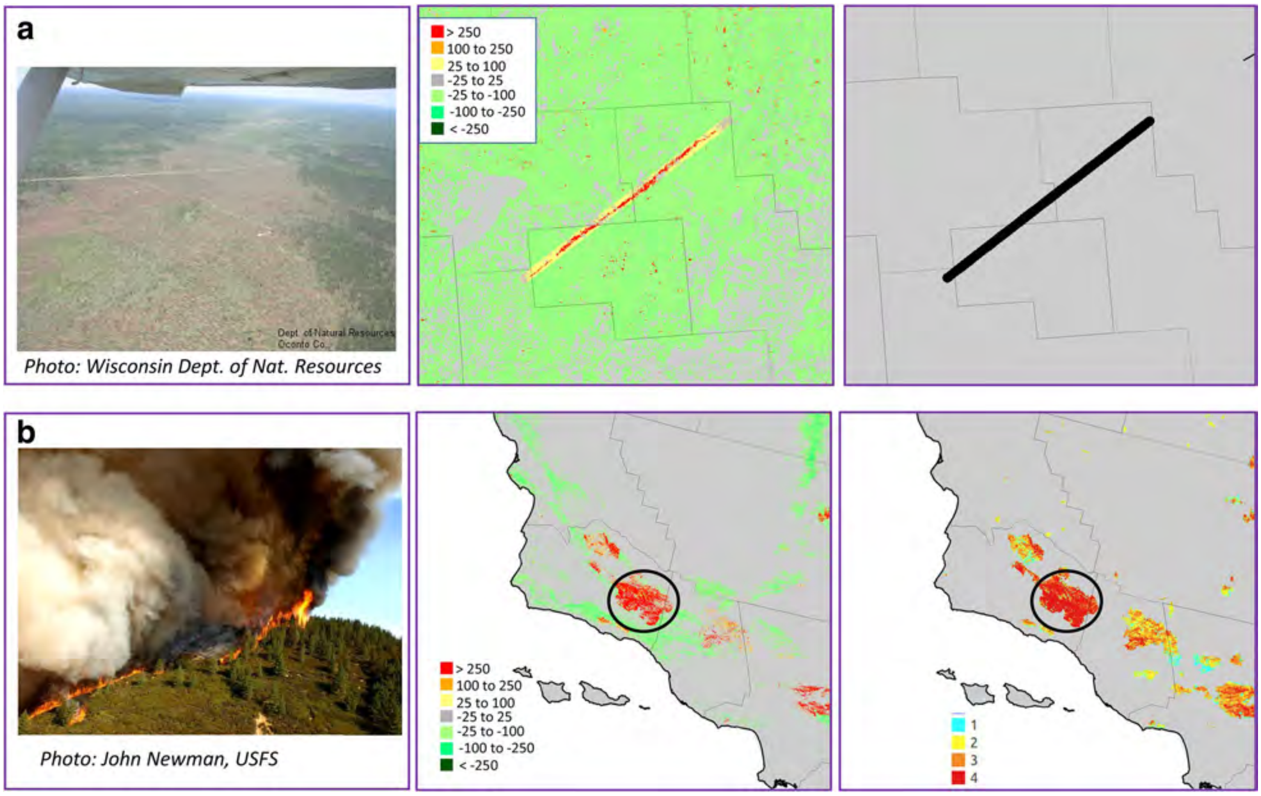

Fig. 5 The forest carbon accounting framework implemented here can be useful in assessing carbon impacts of localized disturbances. **a** 2007 tornado in Lakewood, Wisconsin. The tornado track from NOAA (*right*) resulted in extensive impacts to the forest, which is evident in an aerial photo (*left*) and in the resulting estimate of net carbon change (center, in units of Mg C ha^{-1}). **b** 2007 wild fire in southern California's Santa Barbara County, termed the "Zaca" fire. A photo of the blaze (*left*) highlights the fire intensity, which is mirrored in the burn severity map (*right*, MTBS) and the resulting net carbon change estimate (*center*, in units of Mg C ha^{-1})

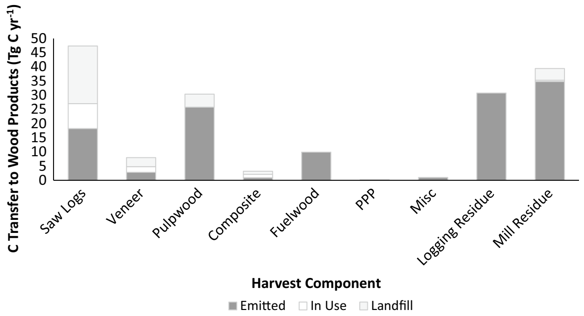

Fig. 6 Fate of C harvested from US forestlands in the year 2007, with some stored in use and landfills and the rest emitted within 100 years. *PPP* posts, poles and pilings

Priorities for FIA data collection

All forest inventory data used to estimate changes in the above- and belowground C stocks in this analysis come from FIA plots measured more than once. However, many more FIA plots have been re-measured in the North and South regions of the US than in the West. The limited number of re-measured FIA plots in the West resulted in higher uncertainties in net C stock change estimates and, in some disturbance categories, required the imputation of estimates obtained from other regions (Tables 1, 2). As the FIA program continues national implementation of an annual inventory (including re-measurement), the FIA data used in this analysis can be revised accordingly so that the sample size of plots per disturbance type increases and uncertainties decrease. Until the early 2000s, the FIA program measured only live tree attributes (e.g., tree diameter) allowing for the estimation of aboveground C and modelling of the other pools based on regions, live tree, and site characteristics (although the dead wood pool was measured in some states). Therefore, we estimated changes in the aboveground C pool using measured data while we relied on models to estimate belowground C. The FIA program is in the process of replacing model predictions of C in the dead wood, litter, and soil organic C pools with estimates obtained from measurements of these pools on a subset of FIA plots [40]. These pools, excluded from the current analysis, can be included in our framework as new data are collected.

Priorities for non-forest lands

Our analysis focused on forest areas defined in part by the NLCD data that is based on the interpretation of Landsat imagery. Comparison of our 1-ha map of carbon density of forestlands based on NLCD with high resolution lidar data over the state of Maryland has shown a significant underestimation of carbon stocks in highly fragmented and mixed urban and forest landscapes [41]. These small scale forests cover substantial areas of densely populated and fragmented landscapes of the eastern United States and appear to be highly dynamic. There is information on the disturbance and recovery of these forests over the time frame of our study, but our analysis has ignored carbon sources and sinks from these lands. By improving the carbon inventory and satellite observations to capture small scale changes, the uncertainty of carbon fluxes, particularly over the Eastern states, may be reduced. In the future (post-2020), planned satellite observations of the aboveground structure of forests by GEDI and NISAR from the National Aeronautics and Space Administration (NASA) and BIOMASS from the European Space Agency should improve the annual inventory of forest C change, as should the planned collection of FIA plot data in urban and woodland areas.

Priorities for UNFCCC reporting

Although the US has data on the magnitude of area change across land use categories, it does not have reliable and comprehensive estimates of C stocks across the entire reporting time series (e.g., 1990–2014 for the most recent UNFCCC submission) and full matrix of land use and land-use change categories to report these changes separately. For this reason, in its GHG inventory submission the US has historically deviated from IPCC guidance by reporting together C stock changes from afforestation and forest management as "forest land remaining forest land", while emissions associated with a land use conversion from forest land to a non-forest land use are reported in the non-forest land use category (per IPCC guidance). For the first time in its 2016 submission [16, 17], the US delineated net C stock changes from afforestation separately from forest land remaining forest land. An additional data need is refined C stock monitoring on non-forest lands and better coordination among land use categories to ensure complete accounting and avoidance of double counting. Our spatially resolved analysis approach allowed us to disaggregate net C change into subcategories of non-forest land to forest land (-8 ± 1 Tg C year^{-1}), forest land to non-forest land (6 ± 1 Tg C year^{-1}), and forest land remaining forest land (-267 Tg C year^{-1}). While the sole focus on net processes within the forest land use category in this study does not fully solve complete C accounting issues across all land uses, the methods used in this research are an incremental improvement toward resolving components of net C change within the forest land category, and these results can help inform and refine US reporting in the future.

Priorities for improving disturbance attribution

Insect and disease aerial detection surveys (ADS) are conducted annually using a variety of light aircraft by the USDA Forest Service in collaboration with other state and federal cooperators. Overview surveys map the current year's forest impact, and some regions have been conducting ADS for more than 60 years while others have become more active only within the last decade. Therefore, annual maps of insect damage with full coverage of all US forestlands are not available, but areas most likely to be affected by insect damage are surveyed more frequently. We accounted for the lack of continuous data coverage in our uncertainty analysis by assuming a 5% bias in underreported area. The Monitoring Trends in Burn Severity (MTBS) dataset, sponsored by the Wildland Fire Leadership Council, consistently maps the burn severity and perimeters across all lands of the US since 1984. Although 30 m resolution imagery is used for analysis, the minimum mapping unit for delineating fire perimeters is greater than 1000 acres (404 ha) in the West and 500 acres (202 ha) in the East. Therefore, burned forest areas smaller than these patch sizes were excluded from our analysis.

Priorities for wood harvest data collection

Information on the primary anthropogenic source of C loss in US forests—wood harvest—is available only at the level of combined counties. TPO data allow for the estimation of C losses from the extraction of wood products that are not readily detected by remote sensing observations, including the most recent Landsat based tree cover loss data from Hansen et al. [8]. We examined the relationship between TPO estimated C losses and a remote sensing-based estimate of C losses from forest disturbance that could not be readily linked to another disturbance type (i.e. wind, insect, fire, or conversion). For this comparative analysis, we assumed all tree cover loss pixels in Hansen et al. [8] data that could not be linked to another disturbance type were harvested, and subsequent C loss was estimated via our FIA look-up table approach. When aggregated to the state level, these two independent estimates of C loss associated with harvest were highly correlated (Fig. 7), and the remote

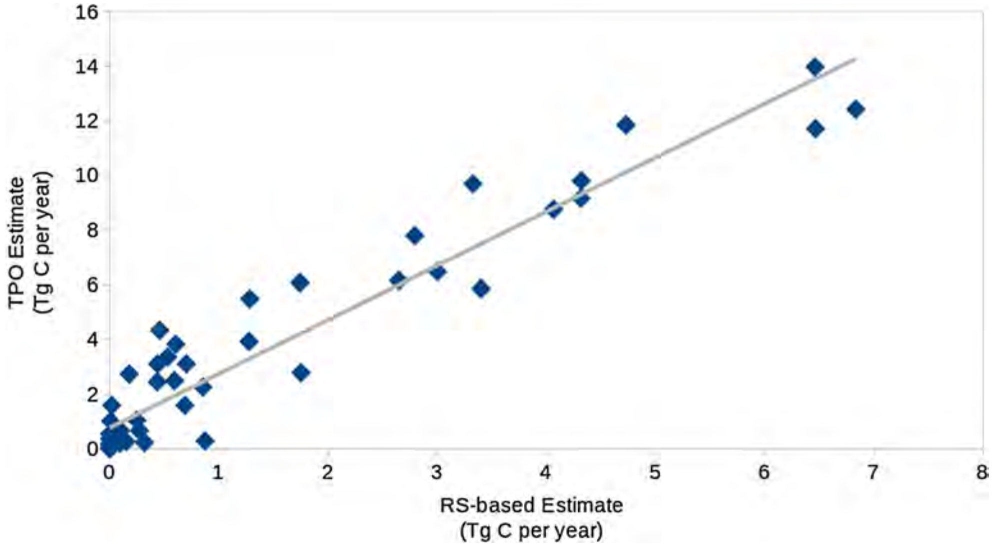

Fig. 7 Relation between C losses from harvest as estimated from timber product output (TPO) data and from an independent remote sensing-based estimate. TPO = 1.98 × RS + 767,777; $R^2 = 0.91$). Data points represent results aggregated to the state-level

sensing-based estimates of (net) C loss from harvest were approximately half of the (gross) TPO-based estimates. This provides indications that: (1) Landsat-based remote sensing observations likely miss a significant proportion of harvest activity due to partial loss, rather than full loss, of tree canopy cover; and (2) the additional C loss not identified by the remote sensing approach is spatially proximate to larger scale C losses from harvest, at least at the state scale. Increased transparency on the spatial location, timing and type of harvesting occurring across the US would allow more explicit attribution of forest C fluxes to specific forest management activities.

Managing US forests for climate change mitigation

Globally, the US ranks fourth in terms of forest area [42, 8]. Although large C losses occur from US forests as a result of an active wood products industry, particularly in the US South, 76% of the total US net carbon sink (342 Tg C year^{-1}) occurred within timberland areas, more than half of which are privately owned [43]. The income received by landowners from Intensive forest management may reduce the likelihood of forest conversion to development, but in the absence of all disturbance effects, we estimate a potential C sink between 2006 and 2010 of −460 and −436 Tg C year^{-1} if only non-harvest disturbance effects (fire, drought, wind, insect damage, land-use conversion) are considered. The US has also committed to restoring 15 Mha of forest land [44], which could further increase the C sink capacity of US forests. This implies that the US C sink could be increased substantially if existing forest land were managed to achieve this goal.

In addition to sequestering and storing atmospheric carbon, US forests also generate wood products that support the energy, industry, transport and building sectors both domestically and internationally. Given that wood harvest represents the majority of C losses from US forests, increasing the US net forest C sink would require shifts in current forest management practices as well as more refined and disaggregated information to reduce the uncertainty of these estimates and resolve these with correct estimation of net C change. For example, national debate has grown over the production of wood pellets as a renewable energy source, particularly from the southeast US, with demand driven by European policies to reduce emissions of greenhouse gases and increase the use of renewable energy. Georgia, Florida, Alabama and Virginia currently account for nearly all US wood pellet exports [45]. Although wood pellets are claimed by the industry to be made from residues at lumber mills or logging sites, the industry's growth could lead to a substantial increase in demand on Southern forests, potentially creating incentives to expand plantations. The potential of bioenergy to reduce greenhouse gas emissions inherently depends on the source of the biomass and its net land use effects; bioenergy reduces greenhouse gas emissions only if the growth and harvesting of the biomass used for energy sequesters carbon above and beyond what would be sequestered anyway [46]. This additional carbon must result from land management changes that increase tree C uptake or from the use of biomass that would otherwise decompose rapidly.

New global emphasis on climate change mitigation as one of the many benefits that forests provide gives US decision makers the opportunity to re-evaluate national and state policy agendas to consider not only the production of merchantable wood volume and biomass for bioenergy, but also enhanced C sequestration and storage for climate change mitigation. As recognized in the 2014 Farm Bill [47], there is a growing need to both reduce the uncertainty associated with estimating forest biomass and the associated monitoring of C dynamics across US forests. As it currently stands, the statistical power of detecting changes in forest C stocks exists only at large regional scales [48], disallowing the detection of C change at policy-relevant scales such as encountered in the pellet industry. Continued research to both downscale forest C inventories and correctly attribute C change to natural and anthropogenic disturbance events is needed to empower forest management policy decisions.

Conclusions

Achieving a global, economy-wide "balance between anthropogenic emissions by sources and removals by sinks" [1] will require both more emission reductions and more C sequestration from the forest sector. Results from this analysis indicate the location and estimated magnitude of C losses from different disturbances in absolute and relative terms, and can be used to track more explicitly which losses result from natural or anthropogenic disturbances. Our national net C change estimate of -269 ± 49 Tg C year^{-1} is within the range of previously reported estimates, and provides spatially explicit estimates and attribution of changes to different types of disturbances. Data are synthesized from various US agencies into a common framework, which could improve inter-agency dialogue to ensure complete accounting and to avoid double counting within and between land use categories. This work may also improve collaboration that drives a more efficient and participatory process for allocating resources towards activities that meet common goals, including an increased focus on climate change mitigation. The methodological framework and accompanying results allow US policymakers and negotiators to better understand the causes of forest C change more completely so that they can participate more effectively in domestic policy discussions about forest management and monitoring as well as in international negotiations. Integration of results from this and other studies should further enable the development of future US GHG inventories that include disturbance attribution and full land use change accounting in expectation of post-2020 commitment requirements.

Authors' contributions

NH, SH, SS, CW, SB and WS designed the study. SH, NH and TP conducted the analysis. CW, BW and GD compiled the FIA and TPO datasets. SS, YY and AF produced the biomass maps. SH implemented model runs and designed and conducted the uncertainty analysis. BB provided guidance on C modeling and on technical implementation of the methods. SH produced figures and tables. NH and SH wrote the paper. All authors reviewed the final manuscript. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets supporting the conclusions of this article are available on the ORNL DAAC website (http://daac.ornl.gov/).

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LETTER

Meeting GHG reduction targets requires accounting for all forest sector emissions

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Supplementary material for this article is available online

Abstract

Atmospheric greenhouse gases (GHGs) must be reduced to avoid an unsustainable climate. Because carbon dioxide is removed from the atmosphere and sequestered in forests and wood products, mitigation strategies to sustain and increase forest carbon sequestration are being developed. These strategies require full accounting of forest sector GHG budgets. Here, we describe a rigorous approach using over one million observations from forest inventory data and a regionally calibrated life-cycle assessment for calculating cradle-to-grave forest sector emissions and sequestration. We find that Western US forests are net sinks because there is a positive net balance of forest carbon uptake exceeding losses due to harvesting, wood product use, and combustion by wildfire. However, over 100 years of wood product usage is reducing the potential annual sink by an average of 21%, suggesting forest carbon storage can become more effective in climate mitigation through reduction in harvest, longer rotations, or more efficient wood product usage. Of the ~10 700 million metric tonnes of carbon dioxide equivalents removed from west coast forests since 1900, 81% of it has been returned to the atmosphere or deposited in landfills. Moreover, state and federal reporting have erroneously excluded some product-related emissions, resulting in 25%–55% underestimation of state total CO_2 emissions. For states seeking to reach GHG reduction mandates by 2030, it is important that state CO_2 budgets are effectively determined or claimed reductions will be insufficient to mitigate climate change.

Introduction

Heat trapping greenhouse gases (GHGs) are being added to the atmosphere at an accelerating rate by fossil fuel combustion and land use change. Climate change consequences were recently described by the Intergovernmental Panel on Climate Change (IPCC) and the United States National Climate Assessment (USGCRP 2018). The IPCC Special Report (IPCC 2018), Global Warming of 1.5 °C, concludes that to keep global average temperature below 1.5 °C by 2100, it is essential to reduce fossil fuel emissions by 45% by 2030, while substantially increasing the removal of atmospheric CO_2. Both reports emphasize the need to increase atmospheric CO_2 removal strategies by forests in addition to sustaining current forest carbon uptake (Houghton and Nassikas 2018). Some states in the US have set targets for reducing GHGs that include forest climate mitigation options (Anderson *et al* 2017, Law *et al* 2018), yet consistent, rigorous accounting methods are required for evaluating options. Challenges include determining the extent that forests, harvest operations, and wood products affect GHG budgets and emissions accountability.

The most recent global carbon budget estimate indicates that land-based sinks remove 29% of anthropogenic emissions (including land use change) with a significant contribution from forests (Le Quéré *et al* 2018). However, none of the agreements or policies (IPCC 2006, NRCS 2010, Brown *et al* 2014, Doe 2017, EPA 2017, Duncan 2017) provides clear and consistent procedures for quantitatively assessing the extent forests and forest products are increasing or reducing carbon dioxide concentrations in the atmosphere. Assessments are challenging because they involve components that require multiple types of expertise and accounting methods (i.e. forest ecosystem processes, wood products, and inherently uncertain substitution credits). Methods are often in disagreement over the wood product Life Cycle Assessment (LCA) assumption of *a priori* carbon neutrality, where biogenic emissions from the combustion and decomposition of wood is ignored because the carbon released from wood is assumed to be replaced by subsequent tree growth in the following decades (EPA 2016). Despite a multitude of analyses that recognize that the assumption is fundamentally flawed (Harmon *et al* 1996, Gunn *et al* 2011, Haberl *et al* 2012, Schulze *et al* 2012, Buchholz *et al* 2016, Booth 2018), it continues to be used in mitigation analyses, particularly for wood bioenergy.

Forests are sustainable *net* sinks as long as forest carbon uptake from the atmosphere exceeds emissions from harvesting, wood product use and decomposition, and wildfire. Wood products ultimately release CO_2 to the atmosphere as they are manufactured, disposed of, and decompose or are burned. However, because of concerns about double-counting, significant emissions associated with harvest and wood product use have not been counted for any sector (EPA 2018). These emissions are often not included in state CO_2 budget estimates (Brown *et al* 2014, Oregon Global Warming Commission 2017), even when they are included in national budgets (EPA 2017) (table S1 is available online at stacks.iop.org/ERL/14/095005/mmedia). If US states intend to use forests for mitigation strategies, they must account for all contributing sources and sinks of forests and forest-derived products (Stockmann *et al* 2012, IPCC 2014).

By focusing on a region with sufficient information to conduct a meaningful LCA, we demonstrate how a quantitative assessment of forests, management practices and wood products can assess the actual role played by forests and forestry practices in managing atmospheric CO_2. We calculate the regional forest carbon balance (from 2001 to 2016) using observations from over 24 000 forest inventory plots in Washington, Oregon, and California (states with GHG reduction mandates). Net forest sector carbon balance is quantified using an improved LCA including harvest, transportation, manufacturing, wood product pool storage and decay, emissions associated with fire, and substitution for both building construction and energy production. We specifically consider global warming potential associated with carbon dioxide and do not include additional GHGs such as nitrous oxide and methane. Our aim is to provide an accurate cradle-to-grave, transparent and transferable accounting method of all forest-derived carbon for other states and countries with GHG reduction mandates (figure 1; box 1; figure S1; tables S2–S6).

Results

Western US forest ecosystem CO_2 balance (2001–2016)

Forest carbon uptake and release (net ecosystem production (NEP); figure 1(a)) controlled by ecosystem biological processes is calculated as the balance between forest carbon uptake (net primary production (NPP)) and forest carbon release through the decomposition of dead organic matter (heterotrophic respiration; R_h). In this study, a negative number indicates a net carbon sink (removal from the atmosphere) and a positive number indicates a net carbon source (addition to the atmosphere). The coastal Western US states together are a strong forest carbon sink with NEP of -292 ± 36 million metric tonnes (MMT) CO_2e per year (-857 g CO_2e m^{-2} yr^{-1}) (table 1; table S1), and account for approximately 60% of total Western US forest NEP (coastal, southwestern, and intermountain regions).

In addition to NEP, disturbances from harvest and wildfire influence estimates of net ecosystem carbon balance (NECB = NEP minus losses Chapin *et al* 2006; figure 1(a)). In the Western US states, the significant carbon losses from the forest are primarily from removals of wood through harvest, decomposition or burning of aboveground and belowground harvest residues, and wildfire (Law and Waring 2015). Significant harvest has been occurring in the western US since the early 20th century (figure S2). Up to 40% of the harvested wood does not become a product and the products themselves decay over time, resulting in product accumulation much smaller than the total amount harvested (figure 2(a); solid line) (Harmon *et al* 1996, Dymond 2012, Williams *et al* 2016, EPA 2017). Emissions include combustion of wood that does not become a product, combustion for energy, decomposition and/or combustion at end-of-life (table 1; rows 5, 6, 9, and 10). When these carbon losses are accounted for, these forests remain significant carbon sinks at -187 ± 33 MMT CO_2e per year (-551 g CO_2e m^{-2} yr^{-1}), with the largest sink in California (40%) followed by Oregon (33%) and Washington (27%). Despite California having twice the fire emissions of the other states (~10 versus ~5 MMT CO_2e yr^{-1} per state) the ranking is due to much lower harvest removals in California (~12 MMT CO_2e yr^{-1}) compared to almost double in

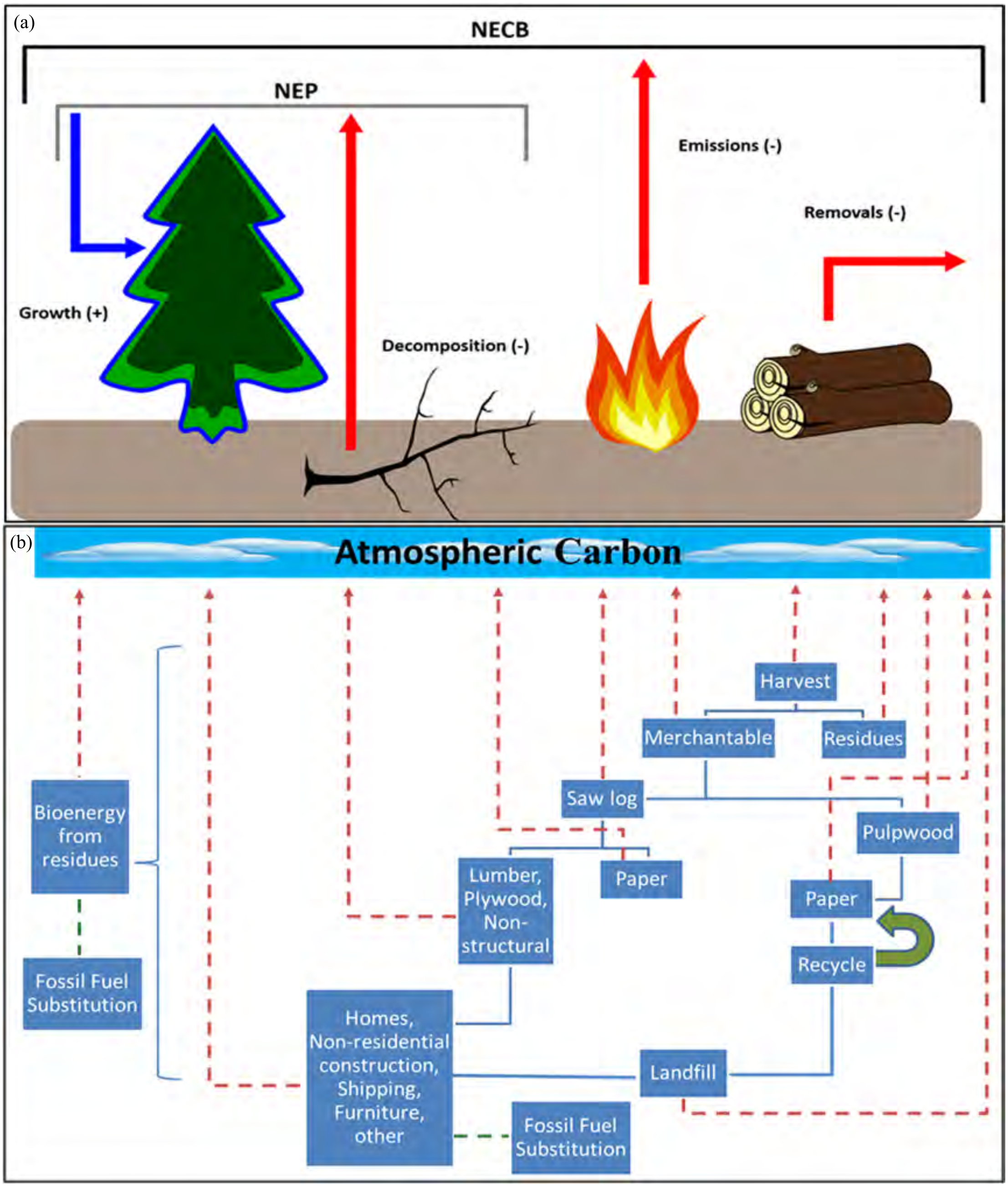

Figure 1. Conceptual diagram of Forest-GHG (a) describes the natural, land-based forest carbon sink where the net of growth and decomposition is net ecosystem production (NEP), and after accounting for removals from fire and harvest, the balance is net ecosystem carbon balance (NECB), (b) describes the cascade of wood products until eventual deposition in landfills or the atmosphere and shows the pathway of emissions.

Washington (~20 MMT $CO_2e\ yr^{-1}$) and triple in Oregon (~31 MMT $CO_2e\ yr^{-1}$). Fire emissions are a third of harvest removals region-wide.

Building on our earlier work (Harmon *et al* 1996, Hudiburg *et al* 2011, Law *et al* 2018), we developed a modified cradle-to-grave model (Forest-GHG) for combining the balance of carbon captured in forest ecosystems, wood product use, lifetime emissions, and eventual return to the atmosphere or long-term storage in landfills. Forest-GHG tracks emissions associated with harvest of wood and manufacturing, transport and use of wood products. Harvest removals result in immediate (combustion of residues on-site or as mill residues with and without energy recapture), fast (short-lived products such as paper), decadal (long-lived products such as wood) and centuries-long (older buildings and land-filled) timeframes before emissions are released back to the atmosphere (figures 1(b) and S1). Our model includes seven product pools and temporally dynamic recycling and landfill rates. Most importantly, we now include a more mechanistic representation of longer-term structural wood in buildings, by moving beyond a simple half-life with exponential decay (figure 3 and SI methods and SI tables 2–6). Our new building cohort-component method tracks decay of short- and

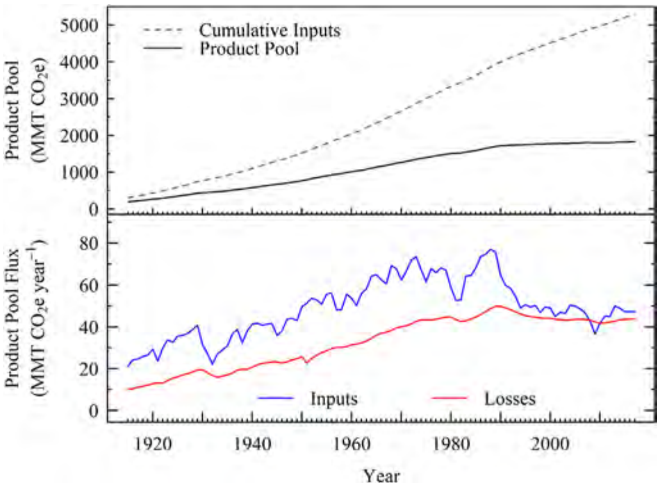

Figure 2. Wood product inputs and outputs from 1900 to 2016 for Washington, Oregon, and California. (A) Cumulative production in MMT CO_2e per year assuming no losses over time (dotted grey line) versus the realized in-use wood product pool over time after accounting for decay (losses). (B) Yearly product inputs over time (blue line) that represents the fraction of harvest (removed wood) that becomes a product versus the decay emissions from the pool over time (red line).

Table 1. Average annual total fluxes by state and region from 2001 to 2016. All units are in million MT CO_2e. Negative numbers indicate a carbon sink (CO_2 is being removed from the atmosphere). The more negative the number, the stronger the sink. Grey shading is used to indicate net values that represent carbon sink strength both before and after removals are accounted for.

Ecosystem	Washington	Oregon	California	Total
1. Forested area (million hectares)	9.7	12.4	11.9	34.0
2. Net ecosystem production (NEP)	**−89.9**	**−102.0**	**−99.8**	**−291.6**
3. Fire emissions	5.1	5.3	10.3	20.7
4. Harvest removals	18.5	30.5	11.5	60.5
Net ecosystem carbon balance (NECB) (sum of rows 1 through 4)	**− 66.4**	**−66.2**	**−78.0**	**−210.5**
Forest industry	**Washington**	**Oregon**	**California**	**Total**
5. Harvest residue combustion (onsite)	3.9	6.5	2.5	12.9
6. Harvest, transportation, manufacturing (FFE emissions)	2.8	4.6	1.6	9.0
7. Wood product pool annual inputs	−18.5	−30.5	−11.5	−60.5
8. Landfill annual inputs (from products)	−6.8	−11.9	−4.2	−22.9
9. Wood manufacturing losses	3.9	6.5	3.9	14.3
10. Wood product and landfill decomposition	21.4	36.2	13.3	71.0
Net forest sector carbon balance (NECB + sum of rows 5 through 10)	**−59.5**	**−54.7**	**−72.4**	**−186.6**
11. Wood product substitution (wood)	−3.0	−4.9	−1.6	−9.4
12. Wood product substitution (energy)	−1.8	−3.0	−1.8	−6.6
Net forest sector carbon balance (with credits; NECB + sum of rows 5 through 12)	**−64.3**	**−62.6**	**−75.8**	**−202.7**

long-lived building components annually, and the lag time associated with these losses (figure S3). Our wood bioenergy substitution credits (Sathre and O'Connor 2010) include wood waste from harvest, mill residues, and wood products displacement of more fossil fuel intensive materials.

Using our component tracking LCA, we found that of the ~10 700 MMT CO_2e of wood harvested in all three states since 1900 (figure 2), only 2028 MMT CO_2e are currently stored in wood products with half stored in Oregon (1043 MMT CO_2e). In just over 100 years, Oregon has removed the equivalent of all live trees in the state's Coast Range forests (Law *et al* 2018), and returned 65% to the atmosphere and transferred 16% to landfills. Even though these are some of the most productive and carbon dense forests in the world (Hudiburg *et al* 2009), the carbon accumulated in much of the removed biomass took up to 800 years to accumulate—and cannot be recovered if current management practices continue.

Forest harvest-related emissions have averaged 107 MMT CO_2e annually from 2001 to 2016 (table 1; row 5, 6, 9, and 10). Emissions are highest from decay of the wood product pool that has been accumulating for over 100 years (table 1 row 10; figures 3 and S3). This is after accounting for recycling and semi-permanent storage in landfills. Structural wood product decay for long- and short-term components (wood in buildings; figure 3) account for about 30%–35% of wood product and landfill decomposition while paper and non-building wood products account for about 65%–70%. Under this complete accounting, the

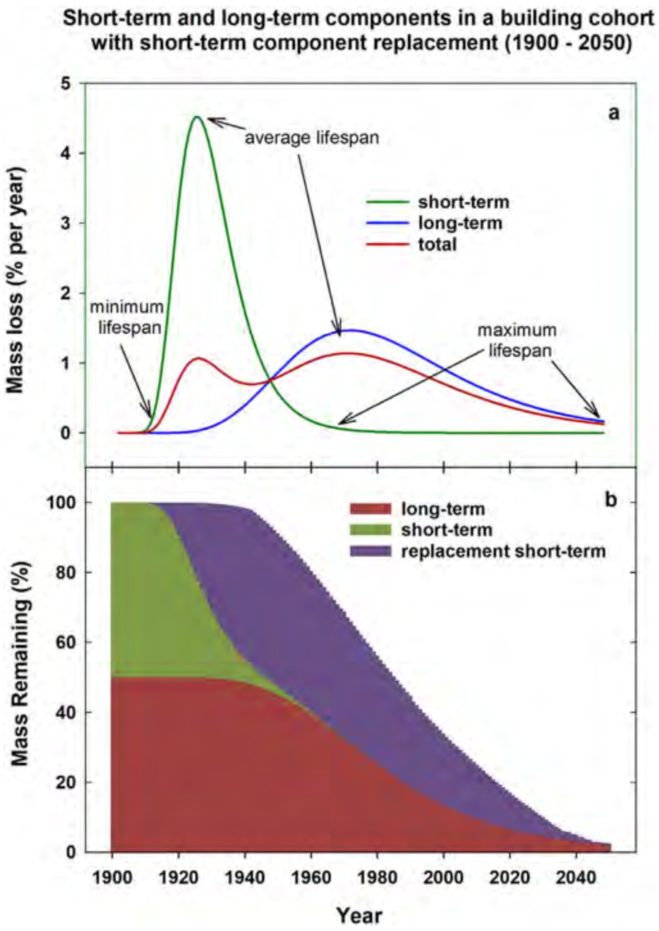

Figure 3. Conceptual models of the Forest-GHG cohort-component method for: (a) mass loss in a cohort of buildings with a 75 year average life span that accounts for the short and long-term portions of buildings and (b) mass remaining in a single building cohort over time (with replacement). Data presented is based on the 1900 cohort of single-family homes built in Oregon.

lowest contribution to overall emissions is from fossil fuel usage during harvest, transportation, and manufacturing, i.e. less than 10% of total wood product-related emissions in the three states.

We found that wood-related substitution for construction materials (0.54 fossil fuel carbon emissions avoided per unit carbon of wood; table 1 row 11) and energy (0.68 fossil fuel carbon emissions avoided; table 1 row 12) may offset 18% of forest industry emissions. This assumes 50% of wood-derived construction products are substituted for a non-wood product and that 75% of mill residues are substituted for fossil fuel energy (Berg *et al* 2016).

We varied the maximum average life spans of the wood products used in construction (e.g. buildings) to examine its effect on emissions estimates. Emissions are minimally reduced by 2%–4% in each state when a longer average maximum lifespan is used (100 years) for the long-term building components and minimally increased by 2%–3% when a shorter average maximum lifespan is used (50 years, which is the mean lifetime of buildings in the US EPA 2013).

Combined, the US west coast state forest sector (cradle-to-grave) is a net carbon sink, removing ~187 MMT CO_2e annually from the atmosphere and potentially reducing fossil fuel emissions by up to another 20 MMT CO_2e through product and energy substitution. Harvest-related emissions reduce the natural sink (NEP—Fire) by 34, 46, and 27% for Washington, Oregon, and California, respectively. When substitution credits are included, this changes to reductions of 27%, 37%, and 23%. Harvest rates have been highest in Oregon (table 1), contributing to increasing wood product emissions and the largest reductions to forest sink capacity.

Discussion

NECB is a good estimate of ecosystem carbon uptake, e.g. for carbon offsets programs (Anderson *et al* 2017), and can be compared spatially with changing environmental conditions or disturbances, but is an incomplete calculation of the entire forest sector emissions. It does not include emissions from wood products caused by machinery, transport, manufacturing and losses—emissions that can equal up to 85% of the total versus 15% from fire, insects, and land use change (Williams *et al* 2016). Nor does it account for the storage and subsequent release of carbon in varying end uses with varied product lifetimes. Given that not all harvested wood is an immediate source to the atmosphere and very little harvested wood is stored in perpetuity, it is essential to track associated emissions over time. For state- or region-level carbon budgets, a cradle-to-grave carbon LCA should be combined with the ecosystem carbon balance (NEP and NECB) to account for how much the forestry sector is contributing to or offsetting total carbon emissions.

If wood buildings are replaced by wood buildings, substitution is not occurring, and because wood is preferred for construction of single-family housing in North America, some of our substitution values are overestimated (Sathre and O'Connor 2010). Wood products store carbon temporarily, and a larger wood product pool increases decomposition emissions over time (figure 3). This emphasizes that increasing the wood product carbon sink will require shifts in product allocation from short-term to long-term pools such as reclaimed (re-used) wood products from demolition of buildings, and reduction of product manufacturing losses (EPA 2016). Clearly, there is potential for climate mitigation by using forests to sequester carbon in biomass and reduce losses associated with the wood product chain (Law *et al* 2018).

It is argued that there may be reductions in fossil carbon emissions when wood is substituted for more fossil fuel intensive building materials (e.g. steel or concrete) or used as an alternative energy source (Butarbutar *et al* 2016). Substitution is a one-time credit in the year of the input. Studies have reported a range of substitution displacement factors (from negative to positive displacement; Sathre and O'Connor 2010, Smyth *et al* 2017), but we found no study that has tracked the actual amount of construction product substitution that is occurring or has occurred in the past in the United States. This makes substitution one of the most uncertain parts of this carbon budget. It may be more easily tracked in the fossil fuel sector through a decrease in emissions because of reduction in product supply, in which case it would be double counting to then include it as a credit for the forest sector. We show results with and without the substitution credit (a decrease in forest sector emissions) because it cannot be verified. We show the potential impact it has on the overall forest sector carbon sink, even though the displacement factor may be unrealistically high (Smyth *et al* 2017, Dugan *et al* 2018). For forest sector emissions assessments, the uncertainty suggests exclusion of the credit.

Currently, state's GHG accounting budgets are incorrect because they are not full cradle-to-grave estimates of all CO_2 emissions associated with forest natural processes and human influences. For accurate GHG accounting, these emissions should be included in the forestry sector as they are not accounted for by state's energy and transportation sectors (IPCC 2006) (table S1). The US EPA reported average fossil fuel CO_2 emissions of 491 MMT CO_2e yr^{-1} for the three states combined (2013–2016). Forest industry harvest, transportation, and manufacturing fossil fuel emissions are included in this total. However, it is unclear to what extent wood product decay and combustion emissions are also counted in state budgets. In Oregon, they are not included at all, resulting in state CO_2 emissions that have been underestimated by up to 55% (Oregon Global Warming Commission 2017, Law *et al* 2018). Washington includes combustion emissions from the current year's harvest (table 1; Manufacturing losses; row 9), but not from wood product decay, resulting in up to a 25% underestimation of state CO_2 emissions. Because California's emissions from other sectors are so high (76% of regional total), and harvest rates have been historically lower than in Oregon and Washington, the impact of not including these emissions is very small as a proportion of the total. Although fire in California has received much attention, it only accounts for 3% of the state's total fossil fuel CO_2 emissions.

These underestimates are especially alarming for Oregon where GHG reduction targets are to be 10% below 1990 levels by 2020 and at least 75% below 1990 levels by 2050 (Pietz and Gregor 2014). California and Washington emissions are to be reduced to 1990 levels by 2020 (Nunez 2006), and 80% and 50% below 1990 levels by 2050 (Washington State 2008), respectively.

In contrast, the US EPA reports emissions from wood product decay and landfills (EPA 2017) per the IPCC guidelines (IPCC 2006) (table S1). However, combustion emissions from logging and mill residues are not reported (EPA 2017). Moreover, ecosystem carbon losses are indirectly estimated through changes in biomass pools with measurement uncertainty that can be greater than the change (Ferster *et al* 2015). So even at the national level, emissions (as a fraction of fossil fuel emissions) would be underestimated by 10% and 24% in Washington and Oregon, respectively. Undoubtedly, there are implications for reduction mandates when the magnitude of emissions themselves are incorrect.

Conclusions

The goal for all societies and governments as stated in Article 2 of the *United Nations Framework Convention on Climate* Change (Oppenheimer and Petsonk 2005) should be '…stabilization of GHG concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system.' The Paris Climate Agreement (UNFCCC 2015) aims to keep global average temperature from rising by no more than 2 °C above preindustrial levels, and if possible no more than 1.5 °C. Forests are identified as part of the strategy (UNFCCC 2015).

Although some US states have attempted to quantify a portion of forest-related emissions, improved estimates are essential to track emissions to meet reduction goals. We identified the main components that should be part of the forest sector state estimates. We found that emissions have been underestimated by up to 55% in Oregon and 25% in Washington, and that at present, these emissions are not reported in state GHG reporting guidelines. The accuracy of forest sector emissions estimates can be improved with sub-regional data on residential and commercial building lifespans, recycling, verifiable substitution benefits and accurate monitoring of growth rates of forests. However, verifiable substitution of one material for another may be more readily quantified in the fossil fuel sector.

The 2006 IPCC GHG guidelines provide three different approaches for calculating emissions from harvested wood products (IPCC 2006) (including reporting 'zero') and reporting of this component is not required by UNFCCC. To complicate accounting further, several studies have shown that using the different recommended approaches results in emissions that differ by over 100% (Green *et al* 2006, Dias *et al* 2007). Moreover, according to IPCC and UNFCCC, emissions of CO_2 from forest bioenergy are to be counted under land use change and not counted in the energy sector to avoid double counting. However, this provides a 'loophole' leading to their not being counted at all.

The United States government currently requires all federal agencies to count forest bioenergy as carbon neutral because the EPA assumes replacement by future regrowth of forests somewhere that may take several decades or longer (EPA 2018). While it is theoretically possible that a replacement forest will grow and absorb a like amount of CO_2 to that emitted decades or a century before, there is no guarantee that this will happen, and the enforcement is transferred to future generations. In any rational economic analysis, a benefit in the distant future must be discounted against the immediate damage associated with emissions during combustion. Furthermore, the goal for climate protection is not climate neutrality, but rather reduction of net GHGs emissions to the atmosphere to avoid dangerous interference with the climate system. Allowing forests to reach their biological potential for growth and sequestration, maintaining large trees (Lutz *et al* 2018), reforesting recently cut lands, and afforestation of suitable areas will remove additional CO_2 from the atmosphere. Global vegetation stores of carbon are 50% of their potential including western forests because of harvest activities (Erb *et al* 2017). Clearly, western forests could do more to address climate change through carbon sequestration if allowed to grow longer.

Since it is now clear that both CO_2 emissions and removal rates are essential to meet temperature limitation goals and prevent irreversible climate change, each should be counted and reported. We recommend that international agreements and states utilize a consistent and transparent carbon LCA that explicitly accounts for all forest and wood product storage and emissions to determine compliance with goals to lower atmospheric GHGs. Only by using a full accounting of GHGs can the world manage its emissions of heat trapping gases to achieve concentrations in the atmosphere that will support a stable climate.

Materials and methods

We calculated the 2001 to 2016 average net forestry sector emissions from cradle-to-grave, accounting for all carbon captured in biomass and released through decomposition by forest ecosystems and wood products industry in Washington, Oregon, and California. Building on our previous work (Harmon *et al* 1996, Hudiburg *et al* 2011, Law *et al* 2013, Law *et al* 2018), we developed a modified and expanded LCA method to combine with our ecosystem carbon balance, now called Forest-GHG (version 1.0; figure 1 and box 1). We accounted for all carbon removed from forests through fire and harvest. All harvested carbon was tracked until it either was returned to the atmosphere through wood product decomposition/combustion or decomposition in landfills, minus the amount semi-permanently stored in landfills (buried). This required calculating the carbon removed by harvest operations starting in 1900 to present day because a portion of the wood removed in the past century is still in-use or decomposing. In addition to carbon in biomass, we also accounted for all carbon emissions associated with harvest (equipment fuel, transportation, manufacturing inputs). Moreover, our wood product life-cycle assessment includes pathways for recycling and deposition in landfills. Finally, we give substitution credits for not using more fossil fuel intensive materials than wood used in construction of buildings and energy production.

Observed carbon stocks and fluxes (ecosystem carbon balance)

Carbon stock and flux estimates were calculated from over 30 000 forest inventory plots (FIA) containing over 1 million tree records in the region following methods developed in previous studies (Law *et al* 2018) (SI Methods). Flux calculations include NPP (Clark *et al* 2001) NEP, and NECB. The NECB represents the net rate of carbon accumulation in or loss from ecosystems.

Off-site emissions associated with harvest (LCA)

Decomposition of wood through the product cycle was computed using a LCA (Harmon and Marks 2002, Law *et al* 2018). A 117 year wood products pool (1900–2016) was simulated using reported harvest rates from 1900 to 2016 for Oregon and Washington (Harmon *et al* 1996, DNR 2017, Oregon Department of Forestry 2017) and from the California State Board of Equalization (CA 2018). Harvest was converted to

Box 1. Terminology and Flux Definitions for table 1

1. Forest Area = sum of all forest area in each state derived from US Forest Service forest area map (30 m resolution). Includes all ownerships.

1. NEP = Net Primary Production—heterotrophic respiration; microbial respiration as they decompose dead organic matter in an ecosystem.

1. Fire emissions = the emissions associated with *combustion* of organic matter at the time of the fire. Most of what burns is fine surface fuels, averaging 5% of aboveground biomass in mixed severity fires of Oregon and Northern California.

1. Harvest removals = Wood actually removed from the forest (not the total aboveground biomass killed). Removals are not equal to emissions but are the removed carbon from the forests at the time of harvest. This is subtracted from NEP along with fire emissions to calculate the net forest carbon balance from the viewpoint of the forest ecosystem.

NECB = NEP + Fire Emissions + Harvest Removals. The term is the simplest expression of forest carbon balance without tracking wood through the product life cycle. Although not all of the harvest removals will result in instant or near-term emissions, NECB still captures the impact of the removed carbon on the forest ecosystem carbon balance, and is consistent with international agreements (REDD+, conservation).

1. Harvest Residue Combustion = the emissions associated with combustion of slash piles; the branches, foliage, and non-merchantable wood left after harvest operations (remains in the forest) and burned onsite (assumed to be 50% of slash).

1. Harvest, Transportation, Manufacturing (FFE emissions) = the fossil fuel emissions associated with harvest (skidding, sawing, etc), transportation of logs to mills, manufacturing of wood and paper products, and transportation of products to stores (see table S5 for coefficients).

1. Wood Product Pool Annual Inputs = Harvest removals

1. Landfill Annual Inputs (from products) = The amount of wood and paper that is sent to landfills at end of life. In Forest-GHG, this occurs incrementally from 1950 to 1960 and then in 1961 is assumed to be constant at the current rate.

1. Wood Manufacturing Losses = fraction of wood that is lost at the mill (sawdust, etc) and is assumed to be returned to the atmosphere within one year through combustion (with 75% energy recapture) or decomposition.

1. Wood Product and Landfill Decomposition = fraction of the total wood product and non-permanent landfill carbon pools that is returned to the atmosphere annually.

Net Forest Sector Carbon Balance = sum of NECB and rows 5 through 10. Emission sources are rows 5, 6, 9, and 10. Sinks are rows 7 and 8.

1. Wood product substitution (Wood) = carbon credits that account for the displaced fossil fuel emissions when wood is substituted for a fossil fuel derived product in buildings (e.g. concrete or steel). We assume 0.54 g C fossil fuel emissions avoided per g of C of wood biomass used.

Box 1. (Continued.)

1. Wood product substitution (Energy) = carbon credits that account for the displaced fossil fuel emissions when wood is substituted for energy. In the Oregon, Washington, and California this primarily a mix of natural gas and coal. We include the biogenic emissions from combustion of forest-derived woody biomass and include an energy substitution credit if it is combusted with energy recapture.

Net Forest Sector Carbon Balance (with substitution credit) = sum of NECB and rows 5 through 12.

total aboveground biomass using methods from (Law *et al* 2018). The carbon emissions to the atmosphere from harvest were calculated annually over the timeframe of the analysis (1900–2016).

The coefficients and sources for the Forest-GHG LCA (figures 1(b) and S1) are included in table S1 through S6 with all units expressed as a function of the wood biomass being cut, transported, manufactured, burned, etc. We accounted for the fossil fuel emissions that occur during harvest (fuel for equipment) and the fossil fuel emissions associated with transport of wood to mills. Then, we accounted for the fossil fuel emissions associated with manufacturing of products followed by a second transportation emission for delivery of products to stores and warehouses. Wood that is not made into a wood or paper product (e.g. waste) is assumed to be combusted onsite at the mill (with 50% energy recapture as combined heat and power) or used in a product that will return the carbon to the atmosphere within one year (table 1 and box 1; Wood Manufacturing Losses).

Wood products are divided into varying product pools and are then tracked through the wood product cascade until end of life (figure 1(b)). Wood products are split into seven product pools: single-family homes, multi-family homes, mobile homes, non-residential construction, furniture and manufacturing, shipping, and other wood. We simulated wood product storage and emissions to 2050 for display purposes in the figures assuming a constant harvest rate after 2016.

We estimate the carbon pools and fluxes associated with buildings by separating buildings into components with different life spans (figures 3 and S3). This allows components and buildings to have a lag time before significant losses occur, and recognizes the difference between building life span and the residence time of carbon in a building. This also allows capacity for Forest-GHG to have component and building life spans evolve over time as construction practices and the environment (including biophysical, economic, and social drivers) change.

In Forest-GHG, a fraction of each year's new harvest is allocated to residential (single-family, multi-family, and mobile homes) and non-residential construction (Smith *et al* 2006). This fraction is further divided into the short-term (23%) and long-term (77%) components. The resulting pools are tracked independently, quantifying losses through decay and demolition from the year they start until then end of the simulation.

All the components created in a given year are considered a building cohort that is also tracked separately each year. All components are summed to give the total amount of building carbon remaining in a cohort at a given time (figure S3). For each year, the amount lost to the atmosphere or to the landfills through demolition, is simply the current year's total wood product carbon pool plus the current years inputs and minus last year's total wood product carbon pool.

Substitution

We calculated wood product substitution for fossil fuel derived products (concrete, steel and energy). The displacement value for product substitution was assumed to be 0.54 Mg fossil C/Mg C (Smyth *et al* 2017, Dugan *et al* 2018) wood use in long-term structures (Sathre and O'Connor 2010). Although the displacement value likely fluctuates over time, we assumed it was constant for the simulation period. We accounted for losses in product substitution associated with building replacement (Harmon *et al* 2009), but ignored the leakage effect related to fossil C use by other sectors. We assumed 75% of 'waste wood' was used for fuelwood in homes or at mills (wood manufacturing losses in table 1). We accounted for displacement of fossil fuel energy sources using a displacement factor of 0.68 assuming a mix of coal and natural gas replacement (Smyth *et al* 2017, Dugan *et al* 2018).

Uncertainty estimates and sensitivity analysis

We calculate a combined uncertainty estimate for NEP and NECB using the uncertainty in the observations and input datasets (climate, land cover, harvest amounts). For the biomass and NPP observations, we performed Monte Carlo simulations of the mean and standard deviations for NPP (Hudiburg *et al* 2011) derived for each plot using three alternative sets of allometric equations. Uncertainty in NECB was calculated as the combined uncertainty of NEP, fire emissions (10%), harvest removals (7%), and land cover estimates (10%) using the propagation of error approach. Sensitivity analysis was only used for the long-term wood product pool by varying the average life spans of buildings by ±25 years in our new cohort component method. Our estimates varied by 7%. This was combined with the uncertainty in NECB to calculate total uncertainty on the net forest sector carbon balance.

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Land use strategies to mitigate climate change in carbon dense temperate forests

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ENVIRONMENTAL SCIENCES

SUSTAINABILITY SCIENCE

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·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.

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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/).

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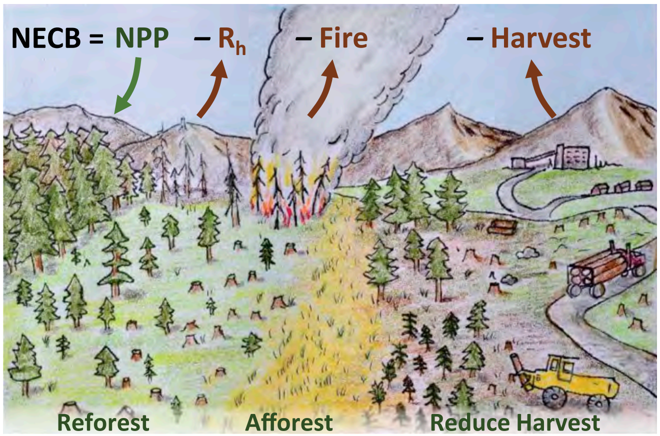

Fig. 1. Approach to assessing effects of mitigation strategies on forest carbon and forest sector emissions. NECB is productivity (NPP) minus Rh and losses from fire and harvest (red arrows). Harvest emissions include those associated with wood products and bioenergy.

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$_2$e 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$_2$e y^{-1} (0.97 Tg C y^{-1}) in 2011–2015 (Table S4). Note that 1 million tCO$_2$e equals 3.667 Tg C.

Our LCA showed that in 2001–2005, Oregon's net wood product emissions were 32.61 million tCO$_2$e (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$_2$e 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$_2$e 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$_2$e).

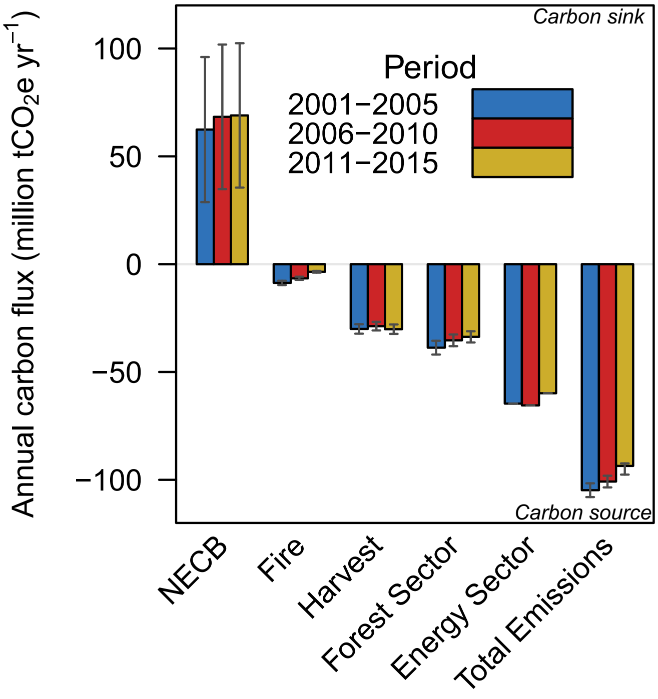

Fig. 2. Oregon's forest carbon sink and emissions from forest and energy sectors. Harvest emissions are computed by LCA. Fire and harvest emissions sum to forest sector emissions. Energy sector emissions are from the Oregon Global Warming Commission (14), minus forest-related emissions. Error bars are 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·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·y^{-1} and 516 mm·y^{-1}. Under current climate conditions, the observations suggest an increase in annual water availability of 260 billion m^3· 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,

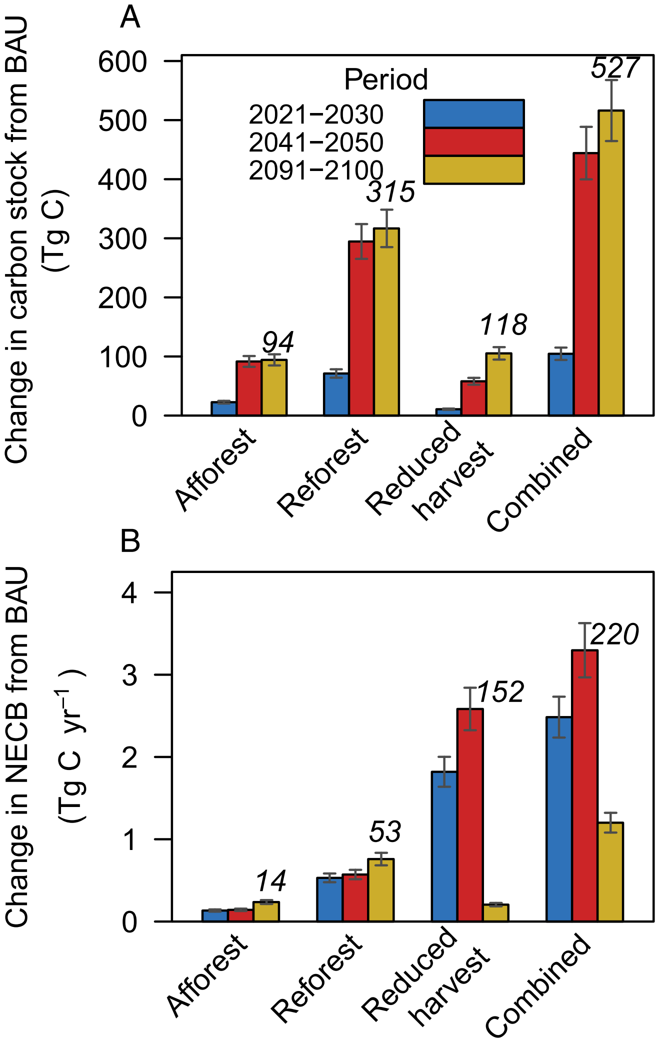

Fig. 3. Future change in carbon stocks and NECB with mitigation strategies relative to BAU management. The decadal average change in forest carbon stocks (*A*) and NECB relative to BAU (*B*) are shown. Italicized numbers over bars indicate mean forest carbon stocks in 2091–2100 (*A*) and cumulative change 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.

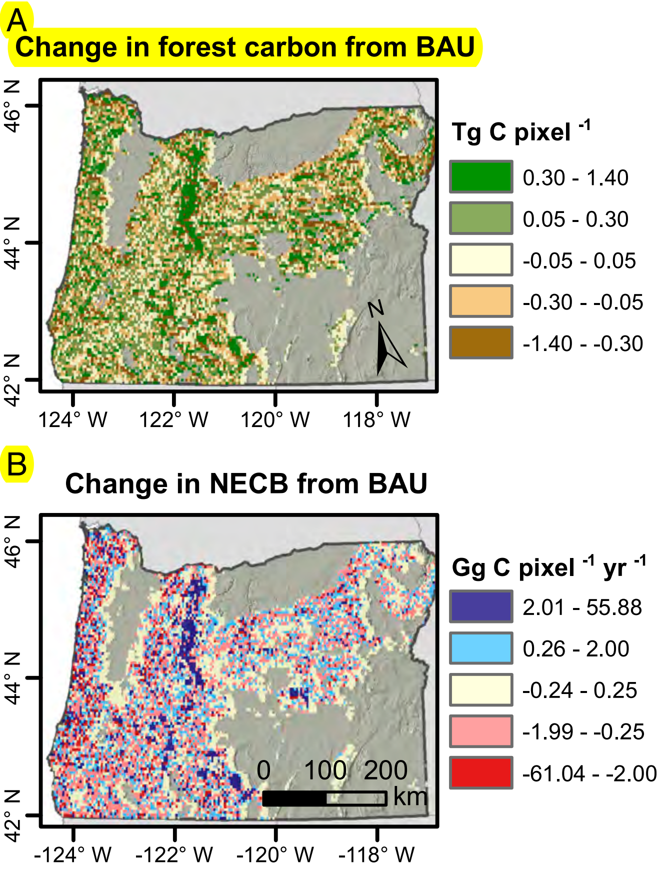

Fig. 4. Spatial patterns of forest carbon stocks and NECB by 2091–2100. The decadal average changes in forest carbon stocks (*A*) and NECB (*B*) due to afforestation, reforestation, protected areas, and lengthened harvest cycles relative to continued BAU forest management (red is increase in NECB) are shown.

Oregon has a legislated mandate to reduce emissions, and is considering an offsets program that limits use of offsets to 8% of 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$_2$e of total emissions by 2025 and 2050, respectively (Table S6). The combination of afforestation, reforestation, and reduced harvest would provide 13 million metric tCO$_2$e 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).

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Fire Ecology

ORIGINAL RESEARCH

Open Access

Northern spotted owl nesting forests as fire refugia: a 30-year synthesis of large wildfires

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Abstract

Background: The northern spotted owl (*Strix occidentalis caurina*) is an Endangered Species Act-listed subspecies that requires coniferous forests with structurally complex and closed-canopy old-growth characteristics for nesting. With climate change, large wildfires are expected to become more common within the subspecies' range and an increasing threat to these types of forests. Understanding fire severity patterns related to suitable nesting forest will be important to inform forest management that affects conservation and recovery. We examined the relationship between fire severity and suitable nesting forest in 472 large wildfires (> 200 ha) that occurred in the northern spotted owl range during 1987–2017. We mapped fire severities (unburned-low, moderate, high) within each fire using relative differenced normalized burn ratios and quantified differences in severity between pre-fire suitable nesting forest (edge and interior) and non-nesting forest. We also quantified these relationships within areas of three fire regimes (low severity, very frequent; mixed severity, frequent; high severity, infrequent).

Results: Averaged over all fires, the interior nesting forest burned at lower severity than edge or non-nesting forest. These relationships were consistent within the low severity, very frequent, and mixed severity, frequent fire regime areas. All forest types burned at similar severity within the high severity, infrequent fire regime. During two of the most active wildfire years that also had the largest wildfires occurring in rare and extreme weather conditions, we found a bimodal distribution of fire severity in all forest types. In those years, a higher amount—and proportion—of all forest types burned at high severity. Over the 30-year study, we found a strong positive trend in the proportion of wildfires that burned at high severity in the non-nesting forests, but not in the suitable nesting forest types.

Conclusions: Under most wildfire conditions, the microclimate of interior patches of suitable nesting forests likely mitigated fire severity and thus functioned as fire refugia (i.e., burning at lower severity than the surrounding landscape). With changing climate, the future of interior forest as fire refugia is unknown, but trends suggest older forests can dampen the effect of increased wildfire activity and be an important component of landscapes with fire resiliency.

Keywords: Northern spotted owl, *Strix occidentalis caurina*, Wildfire severity, RdNBR, Climate change, Fire refugia

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Resumen

Antecedentes: La lechuza moteada del norte (*Strix occidentalis* caurina) es una subespecie listada como en peligro de extinción por la ley sobre especies amenazadas, ya que requiere de bosques de coníferas con características estructurales complejas, doseles cerrados y prístinos para poder anidar. Con el cambio climático, se espera que los grandes incendios sean más comunes dentro del hábitat de la subespecie y se incremente la amenaza a estos tipos de bosques. Entender los patrones de severidad del fuego relacionados con las condiciones apropiadas para anidar en el bosque podrían ser muy importantes para informar al manejo forestal que se ocupa de la conservación y la recuperación. Examinamos la relación entre la severidad del fuego y las condiciones apropiadas para anidar en el bosque en 472 grandes incendios (> 200 ha), que ocurrieron en el hábitat de la lechuza moteada del norte entre 1987–2017. Mapeamos distintas severidades del fuego (sin quemar, bajo, moderado, alto) dentro de cada incendio, utilizando relaciones de diferencias relativas normalizadas, y cuantificamos las diferencias de severidad entre bosques con condiciones apropiadas antes del fuego (borde e interior) y bosques sin condiciones para anidar. También cuantificamos estas relaciones entre áreas de tres regímenes de fuego (severidad baja, muy frecuente; severidad mixta, frecuente; y severidad alta, infrecuente).

Resultados: Promediando todos los fuegos, la parte interior del bosque para anidar se quemó a más baja intensidad que en el borde exterior o en el bosque no apto para anidar. Estas relaciones fueron consistentes dentro de áreas con régimen de fuegos frecuentes dentro de la severidad baja, muy frecuente, y severidad mixta. Dentro del régimen de fuegos infrecuente de alta severidad, todos los tipos de bosque se quemaron con una severidad similar. Durante dos de los años más activos de incendios, que también presentaron los fuegos más grandes y que ocurrieron en condiciones meteorológicas extremas y raras, encontramos una distribución bimodal de severidad del fuego en todos los tipos de bosque. En esos años, una cantidad más grande -y proporción – de todos los tipos de bosque se quemaron a altas severidades. Durante los 30 años de estudio, encontramos una fuerte tendencia positiva de fuegos que quemaron a altas severidades en los bosques no aptos para anidar, pero no en los tipos de bosque apropiados para anidar.

Conclusiones: Bajo la mayoría de las condiciones de fuego, el microclima del interior de los parches en bosques apropiados para anidar, probablemente mitigaron la severidad del fuego y así funcionaron como refugios de fuego (por ej., quemando a severidades más bajas que el paisaje de alrededor). Con el cambio en el clima, el futuro del bosque interior como refugios de fuego se desconoce, pero las tendencias sugieren que los bosques prístinos pueden aminorar el efecto de la actividad en incremento de los fuegos y ser un componente importante de paisajes con resiliencia al fuego.

Background

The effect of wildfire on individual species and wildlife communities can range from highly beneficial to strongly negative depending on species-specific adaptability to disturbance and fire characteristics such as vegetation type burned, fire size, return interval, seasonality, and severity (Smith 2000). For example, many wildfires can be beneficial for some avian species (e.g., woodpeckers) because post-fire conditions enhance forage and nesting opportunities (Hutto 2008), but wildfire can remove many important habitat requirements for other species (e.g., greater sage-grouse *Centrocercus urophasianus*) (Coates et al. 2015; Foster et al. 2019). It is common within large wildfires to have a mix of fire severities, ranging from unburned-to-low severity to areas with nearly complete mortality of forest vegetation (high severity). For many forest-adapted species, the effects of wildfire trend more negatively with increasing severity, such that low severity being neutral or beneficial and high-severity fire negatively affecting species (Fontaine and Kennedy 2012). At the population scale, negative effects of high severity wildfire can be serious for forest wildlife facing extinction or extirpation. For example, wildfires in Australia in 2020 burned critical habitat for as many as 100 threatened species (Pickrell and Pennisi 2020), and wildfire is listed as one of the main threats to greater sage-grouse habitat, though rangewide habitat has been fragmented from other causes (USFWS 2015).

The northern spotted owl (*Strix occidentalis caurina*) inhabits coniferous forests of the Pacific Northwest of North America. It requires late-successional, multistoried, closed-canopy forests with large trees for nesting, roosting, and foraging (Forsman et al. 1984; Wilk et al. 2018; Sovern et al. 2019). Barred owls (*Strix varia*) also inhabit these forests and are an important competitor and severe threat to northern spotted owls (Wiens et al. 2014; Jenkins et al. 2019b; Yackulic et al. 2019; Wiens et al. 2021). Due primarily to loss of older forests from timber harvest, the northern spotted owl was listed as threatened in 1990 under the US Endangered Species

Act (USFWS 1990). The Northwest Forest Plan (NWFP) was then designed and has been implemented in part to conserve and recover enough late-successional forest on federally administered lands to support recovery of the subspecies (USDA and USDI 1994). The standards and guidelines of the NWFP on federal lands have been critical to northern spotted owl conservation but further management interventions are likely needed for successful population recovery (Lesmeister et al. 2018). Due primarily to continued loss of old forest and barred owl competition, northern spotted owl populations have continued to decline since the mid-1990s (Franklin et al. 2021) and were found to warrant reclassification to endangered in 2020 (USFWS 2020). Older forests that are suitable for nesting by northern spotted owls are monitored as a component of the NWFP effectiveness monitoring program (e.g., Davis et al. 2016). Based largely on NWFP monitoring results, large wildfires have been identified as one of the primary and increasing threats affecting northern spotted owl habitat (Lesmeister et al. 2018), and the occurrence and extent of large wildfires in the Western US is predicted to increase due to climate change (Westerling et al. 2006; Abatzoglou and Williams 2016; Davis et al. 2017; Wan et al. 2019).

High-severity fire, especially when combined with post-fire salvage logging, resets forest succession (e.g., Thompson et al. 2007) and removes forest cover suitable for nesting by northern spotted owls, resulting in negative effects on territory occupancy and survival (Clark et al. 2011; Clark et al. 2013; Rockweit et al. 2017; Lesmeister et al. 2019). Conversely, low severity fire has little effect on species composition or structure of suitable nesting forest, and vital rates are not altered (Rockweit et al. 2017; Lesmeister et al. 2019). Mixed-severity fires in landscapes with extensive northern spotted owl habitat result in diffuse forest edges that are preferentially selected for foraging and thus potentially beneficial to populations (Comfort et al. 2016). In a relatively coarse-scale analysis throughout the western USA, Bradley et al. (2016) found that fire severity was lower on lands with less active management which generally corresponded to more mature forests and higher biomass and fuel loading. For one mixed-severity wildfire that burned in a mixed-ownership landscape during a drought year and with severe fire weather conditions, younger forests (mean age 52.2 years) that were intensively managed for timber production burned at higher severity than older forests (mean age 108.8 years) with complex structure and designated as late-successional reserves under the NWFP (Zald and Dunn 2018). In that same fire complex, Lesmeister et al. (2019) found that northern spotted owl nesting forest with old forest characteristics had the lowest odds of burning at high severity compared to other forest types. However, it is unknown if those patterns of burn severity related to suitable nesting forest and management were unique to that landscape and those weather conditions, and perhaps findings would differ if many fires occurring over many years were included in the analyses.

Fire refugia can be defined as landscape elements that remain unburned, burn less frequently, or burn at lower severity than the surrounding landscape (Meddens et al. 2018). We sought to determine if northern spotted owl nesting forest may be considered fire refugia by burning at lower severity than non-nesting forest types (i.e., surrounding landscape) over many large wildfires that occurred during a 30-year period. Understanding the patterns of fire severity as related to the different forest types and spatial patterns over the entire range of the northern spotted owl can provide valuable information on how best to manage those forests for the subspecies' conservation and recovery. Forests used by northern spotted owls for nesting (i.e., suitable nesting forest) have old-growth characteristics that are typically older coniferous forests with large trees and moderate to closed canopy (Forsman et al. 1984). Non-nesting forests were distinct from suitable nesting forest in species composition or structure, or both (Franklin and Dyrness 1973; Swanson et al. 2011; Lesmeister et al. 2018; Spies et al. 2018). We mapped edge and interior suitable nesting forest and non-nesting forest for each year of the three-decade study and quantified wildfire severity in each of the three forest types across all large wildfires rangewide and within each of the three fire regimes of the region.

To elucidate the role northern spotted owl nesting forest may have played as fire refugia, our objectives were to (1) examine the pre-fire pattern of suitable nesting forest in relation to observed wildfire severity, (2) compare wildfire severity between suitable nesting forest and other forest types in the fire perimeter, and (3) examine temporal trends in wildfire severity in each forest type over the duration of the study. Compared to other forest types, the interior portions of old forest (> 30 m from an edge) can have milder microclimates during summer with lower wind speeds and temperature, and higher humidity (Chen et al. 1995). Therefore, we hypothesized that interior nesting forest would function as fire refugia by burning at lower fire severities compared to other forest types during large wildfires but that this relationship would be less prominent in the low severity, very frequent fire regime areas due to more rapid drying of vegetation during fire seasons.

Methods

Study area

We conducted our study of wildfire severity within the USA portion of the range of northern spotted owls (Fig.

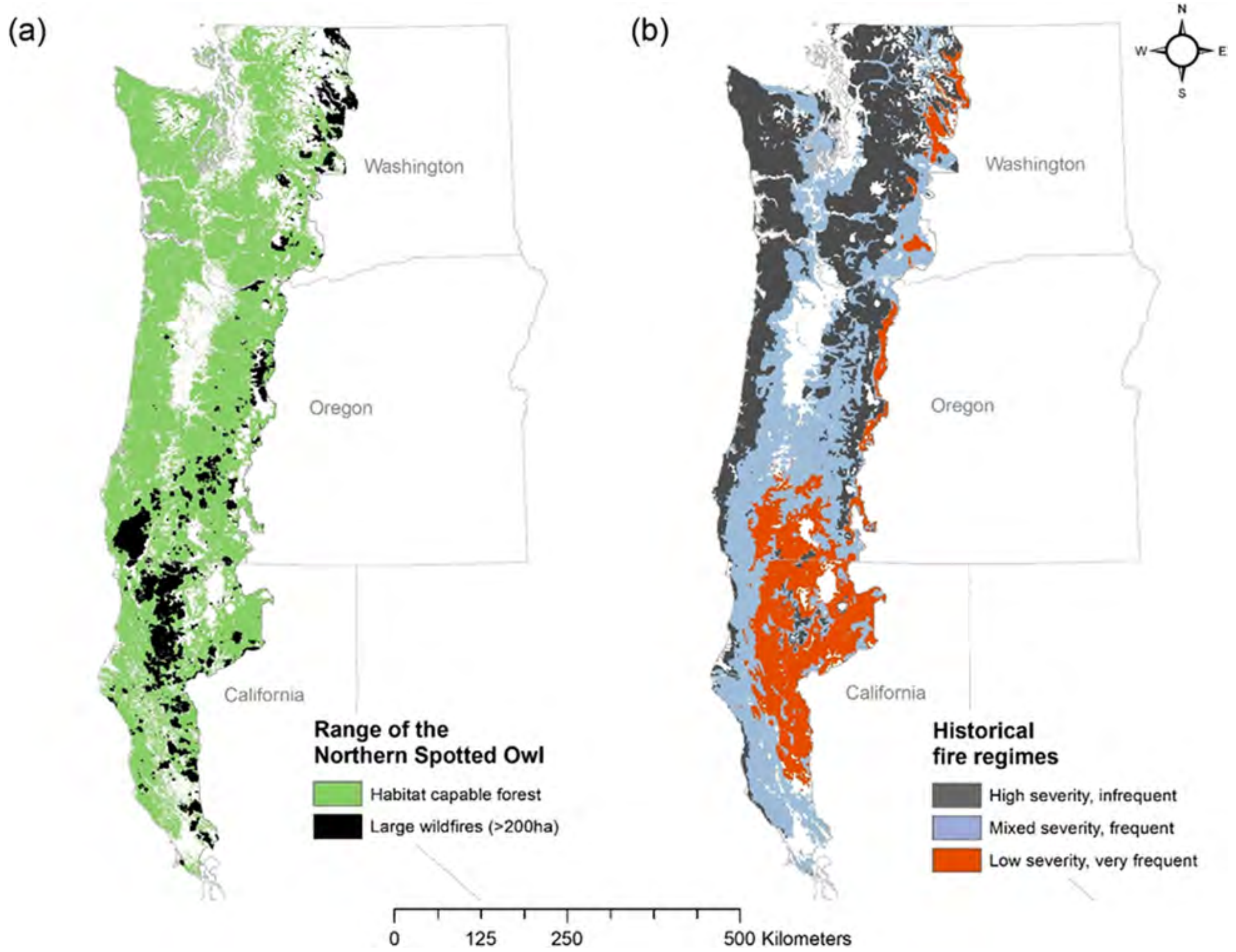

Fig. 1 The range of the northern spotted owl range in the USA. Map **a**: potential nesting forest (i.e., habitat capable forest) and coverage of large (> 200 ha) wildfires from 1987 to 2017. Potential nesting forests were those areas with environmental conditions of elevation (< 2000 m) and soil types that without disturbance (e.g., timber harvest) could develop into suitable forest for nesting and roosting by spotted owls given time for succession. Map **b**: the extent of three historical fire regimes modified from Spies et al. (2018). The high severity, infrequent regime are those areas that typically experience large to very large patches of high-severity fire on > 200-year return intervals. The mixed severity, frequent regime were those areas typically burning with a relatively even mix of severity and relatively frequent return interval (15–200 years). Prior to effective fire exclusion during the past century the low severity, very frequent regime areas would have experienced short return intervals (5–25 years) and were dominated by low-severity fire

1). Within this area, 472 large wildfires (> 200 ha) occurred from 1987 to 2017 over the full range of fire regimes extending across approximately 162,000 km^2 from western Washington to northwest California (Fig. 1a). A diversity of forest ecosystems composed the study area, with old-growth conifer forests being the most common climax communities. The major biophysical driving variables of extent, structure, composition, and dynamics of these old-growth forests were climate, topography, soils, succession processes, and disturbance events (Franklin and Dyrness 1973; Oliver 1981). Historically, landform, soil conditions, and relatively stable regional climate resulted in somewhat predictable biotic communities, pathways of forest development, levels of ecosystem productivity, and spatial patterns of disturbance regimes (Franklin and Dyrness 1973).

An area's fire regime is most strongly influenced by the normal frequency and severity of wildfires but is complex and can include area burned, spatial distribution of fire, fire season, and duration of burning (Agee 1993; Reilly et al. 2017; Sugihara et al. 2018). Spies et al. (2018) mapped four historical fire regimes within the NWFP area: infrequent-high severity, moderately frequent-mixed severity, frequent-mixed severity, and very frequent-low severity. We used this fire regime classification to explore the relationship between fire severity and suitable nesting forest rangewide and for each fire regime (Fig. 1b). Given burn pattern similarities in the two mixed-severity regimes, we combined them as the mixed severity, frequent regime for our analyses. The other regimes we termed as high severity, infrequent and low severity, very frequent. The high severity, infrequent regime were those areas experiencing > 200-year return intervals with large to very large patches of high-severity and stand-replacing fire. The mixed severity, frequent regime were those areas with a relatively frequent return interval (15–200 years) and wildfires typically burning with mixed severity and medium to large patches of high-severity fire. Prior to effective fire exclusion during the past century the low severity, very frequent regime would have experienced short return intervals (5–25 years) and been dominated by low-severity fire with large high-severity patches rarely occurring (Agee 1993; Spies et al. 2018). The extent and frequency of wildfires throughout the duration of our analyses indicated that fire was less common in the low severity, very frequent regime than would be expected under historical fire regimes (Spies et al. 2018).

Forest type classification

Forests used by northern spotted owls for nesting and roosting are typically more than 125 years of age with average tree diameters at breast height > 50 cm (often high diversity of sizes and some trees are > 75 cm diameter) and multi-layered canopies with > 60% canopy cover (Davis et al. 2016). Here we refer to this as suitable nesting forest, which differed in species composition or structure, or both, from the surrounding landscape consisting of other forest types (Franklin and Dyrness 1973; Franklin and Hemstrom 1981; Swanson et al. 2011). Within the study area, there were large areas not capable of developing into suitable nesting forest, mainly due to soil type, plant association, or elevation (Davis and Lint 2005). Therefore, we restricted our classification of forest types to potential nesting forest areas which had the capability (e.g., suitable abiotic and biotic characteristics) to develop into suitable nesting forest in the absence of disturbances that reset successional stage (Fig. 1a).

Information on pre-fire forest species composition and structure is critical for examining relationships between forest types and wildfire effects (Meigs and Krawchuk 2018; Lesmeister et al. 2019). We used newly developed maps of suitable nesting forests that were generated by the NWFP northern spotted owl habitat monitoring program (Davis et al. In Press). These monitoring maps have been used in many publications on northern spotted owl population dynamics and resource selection (e.g., Wiens et al. 2014; Dugger et al. 2016; Jenkins et al. 2019a; Franklin et al. 2021; Jenkins et al. 2021). Suitable nesting forest maps were produced using open source software Maxent (Phillips et al. 2006; Phillips et al. 2017) following NWFP monitoring methods (Fig. 1a, Davis et al. 2011; Davis et al. 2016). The maps were evaluated for predictive accuracy using nesting/roosting owl pair locations that were held out from the modeling. Models predicted these test locations well with Area Under the Curve estimates ranging from 0.78 to 0.92 and predicted versus expected ratio curve Spearman rank correlation coefficients from 0.87 to 0.98 ($P < 0.001$; Fielding and Bell 1997; Hirzel et al. 2006; Davis et al. In Press). Using Google Earth Engine (Gorelick et al. 2017), we applied suitable nesting forest algorithms to Landsat-based (30 m pixel resolution) annual time series (1987–2017) of forest structure and species composition maps (Bell et al. 2021). The resulting dynamic annual maps of suitable nesting forest spanned all years analyzed here, which we classified into binary maps of suitable nesting forest and used program GUIDOS (Soille and Vogt 2009) to classify suitable nesting forest pixels as either INTERIOR or EDGE forest (Fig. 2). The INTERIOR forest pixels were > 30 m from NON-NESTING forest and the EDGE forest pixels were adjacent to ≥1 NON-NESTING forest pixel(s). The NON-NESTING pixels were within the potential nesting forest area but not suitable for nesting because they were primarily younger forests, thinned older forest, or pre-forest conditions (Table 1) (Davis et al. 2016; Davis et al. In Press). The smallest patch size of suitable nesting forest that could contain an INTERIOR class was a 3 × 3 pixel configuration (0.81 ha), large enough to contain microclimates distinct from NON-NESTING forests (Heithecker and Halpern 2007). We summarized forest age and structure metrics for each forest type within each historical fire regime using data generated through gradient nearest neighbor imputation mapping, which is a multivariate analysis of forest inventory, remote sensing, and environmental data and is the standard tool for forest structure and species composition mapping and monitoring in the Pacific Northwest (Ohmann and Gregory 2002; Bell et al. 2021).

Wildfire data

Northern spotted owl territories are on average 700 ha (range 180 to 1390 ha) in size (Dugger et al. 2016), so we focused on wildfires that were ≥ 200 ha in size, large enough to impact > 25% of an average territory. Based on these criteria, we used 472 wildfires that totaled 20,970 km^2, with 17,273 km^2 burned in the extent of potential nesting forests (Fig. 3). This allowed us to examine fire severity encompassing various forest types and arrangements, as well as temporal trends in severity over a 30-year period.

We used a Landsat-based time series (1986–2017) of forest disturbance maps produced by the Landscape Change Monitoring System (LCMS; Healey et al. 2015) to measure extent and severity of wildfire. LCMS data

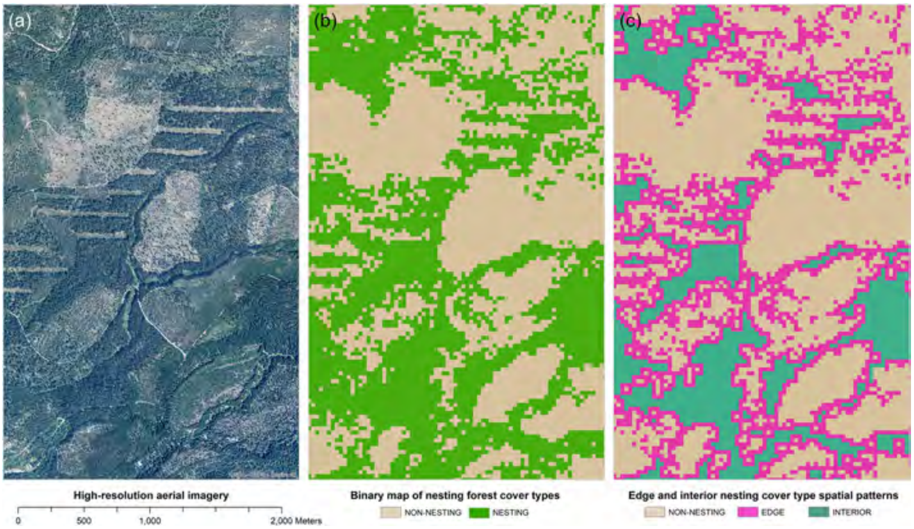

Fig. 2 Maps of forests that are suitable for nesting and roosting by northern spotted owls. Map **a**: high-resolution aerial imagery of an area with clear-cuts, younger forest, closed-canopy old forest, and thinned old forest. Map **b**: the same area with an example binary map identifying nesting forest and non-nesting forest. Map **c**: same area showing nesting forest classified as edge and interior pixels

are analogous to Monitoring Trends in Burn Severity (MTBS) but calibrated to local conditions and available for all wildfires in our time series. LCMS maps used forest disturbance data collected with TimeSync software (Cohen et al. 2010) and an ensemble LandTrendr disturbance mapping algorithm (Cohen et al. 2018; Healey et al. 2018) to produce annual disturbance maps with magnitude quantified by relativized difference in the normalized burn ratio (RdNBR) (Miller and Thode 2007). We used Reilly et al. (2017) classifications of fire severity based on RdNBR within fire perimeters for unburned-low (RdNBR < 235, < 25% basal area mortality), moderate (RdNBR 235–649, 25–75% basal area mortality), and high (RdNBR ≥ 649, > 75% basal area mortality) severity classes (Additional file 1: Appendix 1).

Wildfire selection ratios

We selected wildfires with ≥50% of the forested area within their perimeters classified as potential nesting forest (n = 472; 17,273 km^2) to compare fire severity relationships between INTERIOR, EDGE, and NON-NESTING forest types. Most wildfires had > 90% of the area within their perimeter classified as potential nesting forest. We used selection ratios (Manly et al. 2002) to compare wildfire severity in our three forest types, taking into account the proportion of each forest type within each wildfire perimeter (Moreira et al. 2001;

Table 1 Mean (standard deviation) of forest age and structure metrics within forest types (NON-NESTING, EDGE, INTERIOR) of potential nesting forests for northern spotted owls by fire regime [high severity, infrequent (HIGH); mixed severity, frequent (MIXED); low severity, very frequent (LOW)]

Stand structure metrics	NON-NESTING			EDGE			INTERIOR		
	HIGH	MIXED	LOW	HIGH	MIXED	LOW	HIGH	MIXED	LOW
Stand age[a]	59 (54)	63 (41)	81 (34)	155 (86)	125 (68)	122 (46)	212 (83)	184 (77)	153 (48)
Canopy cover[b]	59 (28)	47 (26)	36 (22)	80 (14)	68 (17)	60 (15)	85 (9)	74 (13)	63 (12)
Live conifer d.b.h.[c]	33 (21)	36 (21)	39 (18)	61 (24)	60 (24)	59 (20)	71 (22)	72 (22)	72 (20)
Diameter diversity[d]	3 (2)	3 (2)	4 (2)	6 (2)	6 (1)	6 (1)	7 (1)	7 (1)	7 (1)
Stand height[e]	18 (10)	17 (9)	14 (6)	31 (10)	27 (10)	22 (7)	35 (8)	34 (9)	27 (7)
Large conifer density[f]	4 (10)	4 (8)	4 (7)	22 (19)	18 (16)	15 (12)	31 (18)	30 (18)	24 (14)

[a] Average stand age based on field-recorded ages of live dominant and codominant trees
[b] Percent canopy cover of live conifer trees
[c] Diameter (cm) at breast height of live conifer trees
[d] Index of structural diversity based on live conifer tree densities in different diameter classes (Davis et al. 2016)
[e] Average height (m) of live dominant and codominant trees
[f] Density (trees/ha) of large (> 75 cm d.b.h.) live conifer trees

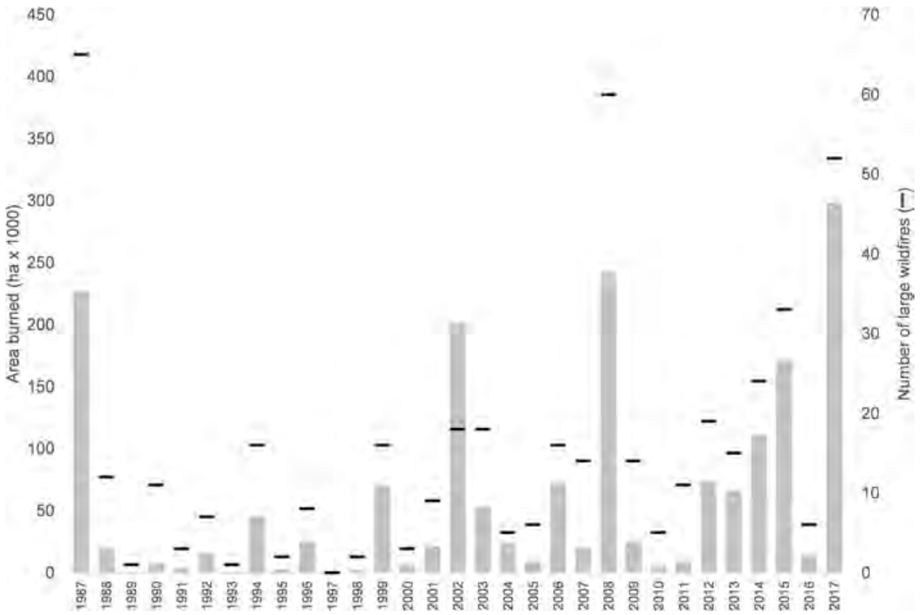

Fig. 3 Total area of potential nesting forest that burned each year during large wildfires (≥ 200 ha). Potential nesting forests were those areas with environmental conditions of elevation (below 2000 m) and soil types that without disturbance (e.g., timber harvest) could develop into suitable forest for nesting and roosting by spotted owls given time for succession. On secondary *y*-axis are the number of large wildfires per year (black markers) within the range of the northern spotted owl, USA, 1987–2017

Moreira et al. 2009; Lesmeister et al. 2019). We defined our selection ratios as the area burned:area available for burning (B/A) ratio. We estimated B/A for forest type i burning at severity class j (w_{ij}) by $w_{ij} = o_{ij} / \pi_i$, where o_{ij} = the proportion area burned at severity j that was forest type i, and π_i is the proportion of forest type i available to burn (i.e., within wildfire perimeter). Values for w_{ij} = 1 indicated the forest type burned at a given severity in proportion to its availability, $w_{ij} > 1$ indicated the forest type burned at a given severity greater than expected by chance, and $w_{ij} < 1$ indicated the forest type burned at a given severity less than expected.

We calculated the mean B/A ratios and 95% confidence intervals (CI) for all 472 wildfires rangewide and within areas of the three fire regimes (low severity, very frequent; mixed severity, frequent; high severity, infrequent). We used the amount of overlap in CIs to evaluate differences in B/A ratios for fire severity and forest type combinations. For example, if CI for a B/A ratio did not overlap 1, we considered the area in each forest type to have burned at a given severity more or less than expected by chance. Due to non-normal distribution of B/A ratios, we also conducted a Tukey post hoc comparison of contrasts between fire severity and forest types.

Fire severity patterns and trends

For each of the three forest types, we calculated the annual proportion of area burned at each of the three fire severities. We used linear regression to analyze long-term trends in yearly proportion of each forest type burning at high-severity fire. We considered slope estimates with CIs not overlapping 0 to indicate strong evidence of a trend in average percent of high-severity fire.

We examined normalized burned area frequency distribution patterns of observed fire severity based on RdNBR by forest type using kurtosis and skew statistics for the four wildfire seasons with the most area burned during our observation period: 1987, 2002, 2008, and 2017. We interpreted skewness values of > 1.0 or <-1.0 to indicate a substantially skewed distribution in RdNBR by forest type. Increasing positive skewness indicated greater frequency of a forest type burning at lower severity classes, while negative skewness indicated greater frequency of burning in higher severity classes. Higher kurtosis values in RdNBR indicated narrow distribution with a given severity and lower kurtosis suggested more flat distribution over fire severities (Thode et al. 2011; Sugihara et al. 2018).

Results

Across all fire regimes NON-NESTING forests were consistently younger, more open, less structurally complex and had fewer large trees compared to INTERIOR and EDGE forests (Table 1). EDGE forests were consistent with northern spotted owl nesting conditions and generally had similar forest structure as INTERIOR forest albeit were on average younger and had greater variability in forest structure metrics by fire regime (Table 1).

Burned/area ratios

When combining all wildfires rangewide throughout the study, we found that INTERIOR forest had higher average odds of burning at unburned-low severity (B/A = 1.17, CI = 1.13–1.22) and lower average odds of burning at moderate (B/A = 0.84, CI = 0.79–0.90) or high (B/A = 0.89, 95% CI = 0.81–0.96) fire severity (Fig. 4a). Conversely, NON-NESTING forest had lower average odds of burning at unburned-low severity (B/A = 0.97, CI = 0.95–0.98) and higher average odds of burning at moderate (B/A = 1.04, CI =1.03–1.06) or high (B/A = 1.05, CI =1.02–1.07) fire severity (Fig. 4a). The average B/A ratios for EDGE forest was near 1.0 with CI overlapping 1 for each fire severity class (Fig. 4a). The Tukey post hoc comparison of B/A ratios among the forest types revealed similar results as the assessment of CIs overlapping 1 (Additional file 2: Appendix 2).

Of the 472 fires, 307 fires had all or a portion of the perimeter (1,110,031 ha total area) in the low severity, very frequent fire regime area, 309 fires (1,027,364 ha) were in the mixed severity, frequent regime, and 114 fires (309,205 ha) were in the high severity, infrequent fire regime. In the low severity, very frequent regime, INTERIOR forest had higher odds of burning at low severity (B/A = 1.25, CI = 1.18–1.31) and lower odds of burning at moderate (B/A = 0.81, CI = 0.72–0.89) or high severity (B/A = 0.86, CI = 0.74–0.99; Fig. 4b). EDGE forest had lower odds of burning at moderate severity (B/A = 0.95, CI = 0.92–0.98), but B/A ratios were near 1 for unburned-low (B/A = 1.02, CI = 0.99–1.05) and high severity (B/A = 1.04, CI = 0.94–1.13; Fig. 4b). The NON-NESTING forest had low odds of burning at unburned-low severity (B/A = 0.95, CI = 0.93–0.96) but was more likely to burn at moderate (B/A = 1.06, CI =

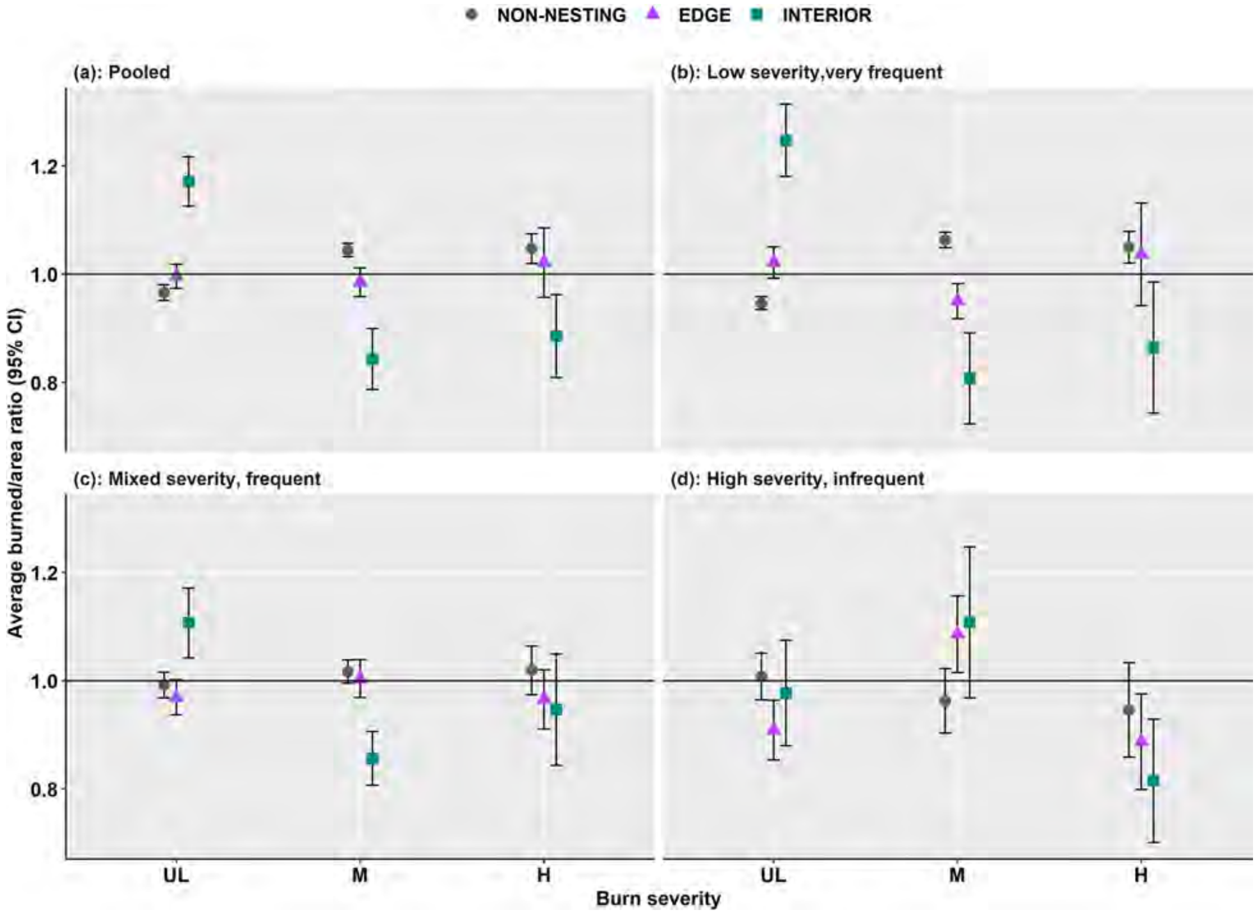

Fig. 4 Burned/area (B/A) ratios with 95% confidence intervals for forest types burned by severity class for 472 large (≥ 200 ha) wildfires in the range of the northern spotted owl, USA, 1987–2017. Forest types were INTERIOR nesting (cyan squares), EDGE nesting (orchid triangles), and NON-NESTING forest (gray circles), and fire severity classes were unburned-low (UL), moderate (M), and high (H) severity. Panels are the B/A ratios for all large wildfires rangewide (**a**) and within the three fire regime areas of low severity, very frequent (**b**), mixed severity, frequent (**c**), and high severity, infrequent (**d**)

1.05–1.08) or high severity (B/A = 1.05, CI =1.02–1.08; Fig. 4b).

Within the mixed severity, frequent regime, INTERIOR forest had higher odds of burning at unburned-low severity (B/A = 1.11, CI = 1.04–1.17) but less than expected in the moderate severity (B/A = 0.86, CI = 0.81–0.91). The B/A ratio for INTERIOR forest burning at high severity was < 1, but CI overlapped 1 (CI = 0.84–1.05; Fig. 4c). EDGE and NON-NESTING forest types had B/A ratios near 1.0 and CI overlapping 1.0 for each fire severity (Fig. 4c).

For fires in the high severity, infrequent fire regime, INTERIOR forests burned at high severity less than expected (B/A = 0.82, CI = 0.70–0.93), but CIs overlapped 1.0 at the two lower fire severities (Fig. 4d). The EDGE forest had low odds of burning at high severity (B/A = 0.89, CI = 0.80–0.98) and unburned-low severity (B/A = 0.91, CI = 0.85–0.96), but high odds of burning at moderate severity (B/A = 1.09, CI = 1.02–1.16). The CIs for the NON-NESTING forest overlapped 1.0 for all three severity classes. A Tukey post hoc comparison of B/A ratios among severity classes and forest types indicated that INTERIOR forest tended to burn at unburned-low severity compared to EDGE and NON-NESTING forests (Additional file 2: Appendix 2).

Fire severity patterns and trends

The number of fires and area burned varied greatly among years studied, with higher number of fires corresponding with more area burned (Fig. 3). Exceptions to this were the years 2002 and 2017, where two large fires (2002 Biscuit Complex = 200,444 ha; 2017 Chetco Bar = 77,103 ha) accounted for most of the area burned.

The proportion of area burned each year differed among years for all forest types (Fig. 5). For most years, the proportion of area burned at high severity was less than area burned at moderate or unburned-low severity (Fig. 5). All forest types had some evidence of increasing linear trends in the average yearly percent of area burned at high severity (Fig. 5), but only in the NON-NESTING forest was there strong evidence of an increase (Fig. 5d). The slope estimates for NON-NESTING forest indicated a 0.7% (CI = 0.29–1.05%) annual increase in average area burned at high severity.

For each of the four largest wildfire seasons, each burning over 200 000 ha of potential nesting forests, the fire severity frequency distribution patterns differed between forest types (Fig. 6). Frequency distributions for INTERIOR were consistently most positively skewed (2.3–3.3) and had the greatest kurtosis (5.0–10.9) toward low severity, with most of the area burning at lower severities (Fig. 6). Although less pronounced than for INTERIOR, EDGE forest was positively skewed (1.1–2.6) and had greater kurtosis (1.1–2.6), exhibiting a low to moderate severity pattern (Fig. 6). Skew and kurtosis for EDGE was intermediate to INTERIOR and NON-NESTING. For NON-NESTING forest, skewness was moderately positive (0.8–1.4) and little kurtosis (− 1.2–0.6), indicating a relative even distribution across the RdNBR spectrum (Fig. 6). Fire severity frequency distributions were the most bimodal during the 2002 and 2017 fire seasons (Fig. 6). These were the years with two largest wildfires during our

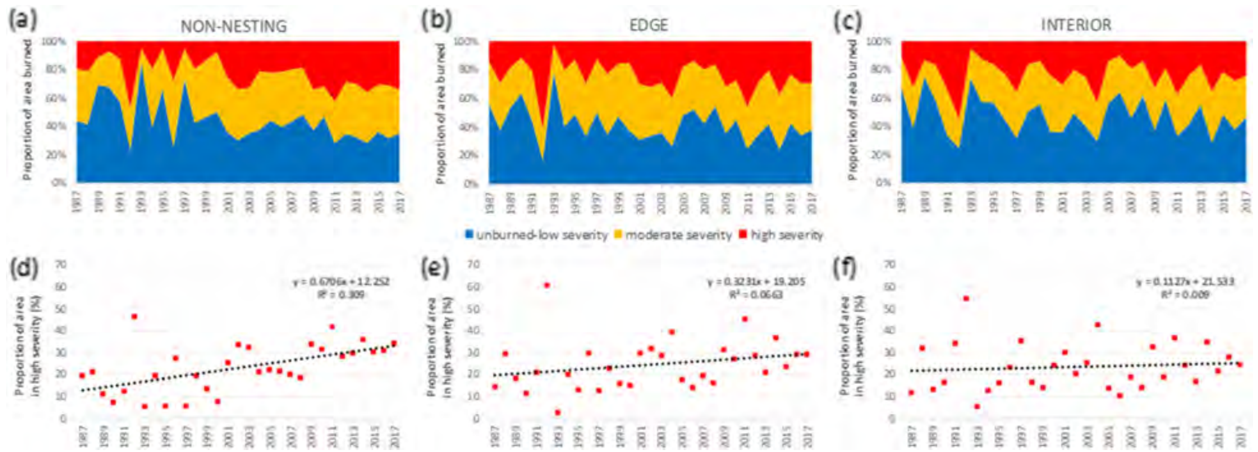

Fig. 5 Proportion of annual area of potential nesting forest burned at three fire severities [unburned-low (UL), moderate (M), and high (H)] in three forest types [NON-NESTING (**a**), EDGE (**b**), and INTERIOR (**c**)]. Also are the linear trends in annual proportion of fires burning at high severity in NON-NESTING (**d**), EDGE (**e**), and INTERIOR (**f**) forest types. Data are from 472 large (≥200 ha) wildfires occurring throughout the range of the northern spotted owl, USA, 1987–2017. Potential nesting forests were those areas with environmental conditions of elevation (below 2000 m) and soil types that without disturbance could develop into suitable forest for nesting and roosting by spotted owls given time for succession

Fig. 6 Frequency distributions of relative differenced normalized burn ratio (RdNBR) values, skewness, and kurtosis measures for nesting/roosting cover type in the 4 years with the highest area burned among 472 large (≥ 200 ha) wildfires in the range of the northern spotted owl, USA, 1987–2017. Higher RdNBR values indicate higher burn severity

study period (2002 Biscuit Complex and 2017 Chetco Bar Fire) and had the highest area burned per wildfire (Fig. 3).

Discussion

Here, we analyzed the likelihood of different forest types burning at three fire severities during 472 large wildfires that occurred over a span of 30 years throughout the range of northern spotted owls in the Pacific Northwest, USA. The spatial and temporal expanse of our dataset and the ability to generate annual maps of northern spotted owl nesting forest afforded us the ability to gain unprecedented insights into the function of suitable nesting forest as fire refugia. Strong evidence indicates that large wildfires are a severe threat to northern spotted owl habitat and populations (Clark et al. 2011; Davis et al. 2011; Clark et al. 2013; Rockweit et al. 2017; Lesmeister et al. 2019), yet the issue has been debated in the scientific literature, especially when also considering other spotted owl subspecies (e.g., Hanson et al. 2009; Spies et al. 2010; Ganey et al. 2017; Lesmeister et al. 2018). In some cases, published literature contains errors and bias, which was highlighted recently by Jones et al. (2020a). The primary natural fire regimes and fire severity patterns differ between northern spotted owls and the other spotted owl subspecies (California and Mexican spotted owls); therefore, caution should be used in assuming that our findings on northern spotted owls are applicable to forests used by those other subspecies. We also posit that population response and burn severity patterns within the range of the other subspecies are likely different than what should be expected for northern spotted owls and their habitat.

In addition to wildfire, multiple other stressors, especially barred owls, play a role in degrading the prognosis for persistence of northern spotted owl populations (Lesmeister et al. 2018; Miller et al. 2018; Wiens et al. 2019; Franklin et al. 2021; Jenkins et al. 2021). We approached this study to better understand the long-term and broadscale patterns of risk that large wildfires (especially high-severity fire) pose to northern spotted owls and their habitat because the extent and frequency of wildfires is expected to increase with climate change (McKenzie et al. 2004; Davis et al. 2017; Halofsky et al. 2020). We observed consistent patterns of fire severity in different forest types used by this old forest obligate and found that suitable nesting forest played an important role as fire refugia in the face of increasing wildfire activity.

Our findings from broadscale and long-term data were similar to those from Douglas Complex wildfires that burned in a mixed-ownership landscape of the Klamath-Siskiyou ecoregion of southwestern Oregon, USA (Zald and Dunn 2018; Lesmeister et al. 2019). The Douglas Complex burned an area of 38,000 ha in mixed-severity with large patches of high-severity fire. Older forests in late-successional reserves (i.e., suitable nesting forest) burned at lower severity despite having higher fuel loading than other forest types within the fire perimeters (Lesmeister et al. 2019). Ownership patterns were also a strong predictor of fire severity for the Douglas Complex, where federally managed lands were primarily comprised of late-successional forest reserves that burned at lower severity compared to plantation forests with homogenous fuel loads on private timber industry lands (Zald and Dunn 2018). Those studies suggested that, in addition to the contribution to northern spotted owl conservation, older forests functioned as fire refugia and had an added benefit of buffering the effects of climate change-induced increases in wildfire occurrence.

In our study, interior nesting forest tended to burn at lower severity compared to other forest types, especially when compared to the non-nesting forest type that was primarily younger or open-canopied forest (Table 1). Edges and fragmented nesting forest burned at intermediate severities, with edges presumably buffering interior forest from higher fire severity in non-nesting forest. Contrary to our predictions, these patterns of burn severity were strongest in the low severity, very frequent regime and least evident in the high severity, infrequent fire regime. We expected to observe a largely flat distribution of fire severity across forest types in the low severity, very frequent regime because these are primarily dry forest types that tend to have lower moisture levels during the fire season and, owing to fire exclusion for the past century, have higher fuel loading and susceptibility to high-severity fire compared to historic levels (Agee 1993; Spies et al. 2018). In dry forest types of Oregon, tree densities are more than four times greater, average canopy cover has increased, and species composition has shifted from a century ago (Hagmann et al. 2014; Hagmann et al. 2017). In many dry forests, these altered conditions have been associated with increased fire severities (e.g., Bigio et al. 2010; Hagmann et al. 2019; Marlon 2020). Baker (2015) suggested that some northern spotted owl habitat was historically maintained as fire refugia within the dry forests (with historical frequent fire return interval) of the study area. Therefore, the patterns we observed may have been relatively natural dynamics of fire severity in those dry forests. Fire refugia persisting through multiple fires in these landscapes typically have topography, elevation, and slope that result in moister conditions that facilitate development of older, intact, and closed-canopy conifer forest (Downing et al. 2021). Additionally, fire refugia capacity is enhanced in forests that are left unmanaged post wildfire because they burn at lower severity than areas salvage-logged following wildfires (Thompson et al. 2007; Thompson and Spies 2010).

Several interacting factors may have caused the differences in the patterns we observed with northern spotted owl nesting forests tending to burn as lower severity. We hypothesize one of the important mechanisms potentially driving the fire severity patterns of lower severity fire in suitable nesting forest was the long-known relationship (see Hursh and Connaughton 1938; Countryman 1955) between differing microclimates of forests and susceptibility to high-severity wildfire. In the moist forests of the Pacific Northwest, closed-canopy, structurally complex late-successional conifer forests with high biomass (i.e., northern spotted owl nesting forest) maintain cooler, more temperate microclimates and provide an insulating effect on temperatures (Chen et al. 1995; Frey et al. 2016; Downing et al. 2021) and result in lower fire severity (Meigs et al. 2020). Our findings of fire severity patterns suggest these factors may also reduce fire severity of older forests in the mixed- and low-severity fire regimes of the study area. Fire behavior and severity is largely driven by interactions among wind, humidity, temperature, fuels, and topography (Countryman 1964; Thompson and Spies 2009; Halofsky et al. 2011). Some open-canopied forests and younger even-aged and densely stocked stands have hotter, drier, and windier microclimates, and those conditions decrease dramatically over relatively short distances into the interior of older forests with multi-layer canopies and high tree density (Chen et al. 1995; Heithecker and Halpern 2007; Arroyo-Rodríguez et al. 2016).

Our objectives were to quantify burn severity patterns specific to suitable nesting forest over many wildfires and years, thus we did not include effects like drought, topography, weather, multiple spatial scales, and previous fires that could have explained some of the variance in area burned by severity classes (Keyser and

Westerling 2019; Meigs et al. 2020). For example, on the 2011 Wallowa Fire in the range of the Mexican spotted owl, the relationship between burn severity and pre-fire nesting forest suitability varied with spatial scale (Wan et al. 2020). A multi-scale evaluation of fire severity patterns warrants additional attention and could provide further insights into the interaction between northern spotted owl nesting forest and fire severity. An assumption in our B/A ratio analysis was that all forest types were equally available to burn at each severity, but other factors that affect wildfire severity could have also influenced the amount of forest types within fire perimeters. Lower severity wildfire tends to occur in areas with gentler topography (Skinner 1995; Heyerdahl et al. 2001; Alexander et al. 2006). If a particular forest type tends to be more prevalent in gentler topography, then reasoning suggests fire severity would tend to be lower in that forest type. In our study, the non-nesting forest typically occurred in gentler slopes compared to interior and edge forest types (Additional file 3: Appendix 3). Additionally, fire suppression efforts, including road access and tactical decisions for the location of fire lines and burnout activities, could affect fire spread and behavior on large wildfires. The effect of fire suppression activities on the fire severity patterns we observed is unknown but these activities are enhanced by road access that is more readily available on highly managed forest lands. As such, if fire suppression or slope affected burn severity patterns, they would likely function to decrease severity and extent on the non-nesting forest type. Further testing of hypotheses for independent and interacting drivers in fire severity patterns is needed.

We found an increasing trend in the proportion of annual area burned by high-severity fire over the duration of our study, but the trend occurred most strongly in the non-nesting forest type. These findings suggest that the effects of climate change on the occurrence of high-severity wildfires may be most pronounced in non-nesting forests and interior nesting forest appears to function as fire refugia buffering the trend of increasing wildfire activity. Forests functioning as fire refugia can support ecosystem resilience to disturbances as well as postfire ecosystem recovery and biodiversity (Meddens et al. 2018). Our findings are consistent with recent research that found a higher amount and quality of fire refugia in closed-canopy older forests compared to younger and more open-canopied forest cover types (Meigs and Krawchuk 2018; Andrus et al. 2021). In conifer forests of the Pacific Northwest, old-growth and late-successional forests have the highest likelihood of burning at low severities especially in landscapes with high topographic variability (Meigs et al. 2020; Downing et al. 2021), even during drought years with high-fire weather conditions (Lesmeister et al. 2019). Interior forests functioned as fire refugia during our observed timespan, but it remains unknown if they are ephemeral refugia or will function as persistent refugia with a changing climate and shorter fire return intervals. However, mature forests have higher resiliency to fire effects and climate variability, especially when not subject to fragmentation in a matrix of young flammable patches that can shift mature forests to an alternative steady state more prone to repeat high-severity fire (Thompson and Spies 2010; Kitzberger et al. 2012). Similarly, examining forests in Australia, Duff et al. (2018) showed that older forests had higher resilience to drought conditions that increased flammability of vegetation, thus functioned as fire refugia. Intact old forest with less fragmentation in Amazonian forests also function as refugia by ameliorating the effects of fire (Silva Junior et al. 2018; Silva et al. 2018; Maillard et al. 2020).

In the years with extremely large wildfires (2002 and 2017), there was a bimodal distribution in fire severity in all forest types, potentially degrading the function of suitable nesting forest as fire refugia. The 2002 fire season was dominated by the Biscuit Fire, which at over 200,000 ha was the largest fire in our study. The 2017 fire season had the greatest amount of area burned of the years we sampled and was dominated by the Chetco Bar Fire which burned over 190,000 ha. The bimodal patterns we observed in these 2 years were consistent with theorized fire severity distributions when extremely large fires (i.e., megafires), that occur very infrequently, produce large patches of high-severity burns (van Wagtendonk and Fites-Kaufman 2006). Strong dry foehn winds were the primary factor driving the extent and severity of the 2002 and 2017 megafires with katabatic heating that carried westward from high-density air from higher elevations in the deserts east of the Cascade Mountains (Ustin et al. 2009; Halofsky et al. 2011). Extreme wind events occurring episodically are also primary predictors of spatial variation in large wildfires in other regions (e.g., Moritz et al. 2010). These rare and extreme weather conditions have been the primary driver of the most well-known megafires during recorded history of the region, including the 1902 Yacolt burn, 1933 Tillamook burn, and 1936 Bandon fire, (Dague 1930; Dague 1934; Martin et al. 1974; Herring and Greene 2001; Zyback 2004; Potter 2012). One or a few very infrequent, wind-driven crown fires can shift severity distributions to more and larger high-severity patches, creating a bimodal distribution and increasing loss of old forest (Thode et al. 2011; Cansler and McKenzie 2014). If the occurrence of these extreme weather events increases with climate change then suitable nesting forest and northern spotted owl populations will be further threatened. Early evidence from recent megafires occurring in the most extreme years suggests there may be a further shift to a more equal distribution of fire severities. In September 2020, five megafires in Oregon burned about 329,000 ha in relatively equal distribution of severity (low = 31%, moderate = 28%, high = 42%) during a sustained and historic windstorm that caused the record-setting fire season (Antczak et al. 2020; Higuera and Abatzoglou 2020, R. J. Davis unpublished data; Mass 2020). In these megafires, extreme easterly foehn winds resulted in extraordinary fire growth in all forest types regardless of management history. During extreme fire weather events, the relative importance of fuels influencing burn severity diminishes because the effects of weather (fuel moisture, temperature, and wind speed) primarily determine fire intensity and crown fire development (Bessie and Johnson 1995).

Timber harvest remains one of the primary threats to suitable nesting forests used by northern spotted owls (Lesmeister et al. 2018), but on federal lands managed under the Northwest Forest Plan, the threat from wildfire is now greater than the threat from timber harvest (Davis et al. 2016). These are concerning trends, especially considering that the extent and frequency of large wildfires is expected to increase with climate change (Davis et al. 2017; Wan et al. 2019). Forest management plans—even some with stated goals to enhance northern spotted owl conservation—may seek to reduce wildfire risk by thinning forest stands of all ages using practices that modify forest structure by increasing canopy base height, reducing crown contiguity and bulk density, and reducing forest fuels. These actions can degrade the suitability of the forest for nesting by northern spotted owls and may decrease wildfire severity in the short term (Agee and Skinner 2005; Martinson and Omi 2013; Kalies and Yocom Kent 2016; Prichard et al. 2020). However, these actions are less effective at reducing wildfire extent and severity on a large scale beyond a short time window, so need to be repeatedly managed to maintain effectiveness (Stone et al. 2003; Reinhardt et al. 2008; Barnett et al. 2016; Schoennagel et al. 2017).

Converting older, closed-canopy forests that function as fire refugia to more open, managed forests does not assure a dampening effect on wildfire severity, due in part to the complex changes in the microclimate of forest stands after thinning. Recently disturbed forests have higher and more variable shortwave radiation, temperature, and windspeed (Chen et al. 1999), all of which can increase fire severity (Estes et al. 2017). Fuel loads and arrangement are a component of the fire environment, so forest thinning that alters microclimates may increase flammability if fuel loading is not repeatedly maintained. Variable retention harvesting, which aims to mimic natural forest disturbance regimes and retains old forest structures, including snags and logs, is becoming more commonplace (Franklin and Donato 2020). These silvicultural prescriptions may retain enough forest structure to function as edge nesting forest and thus be less prone to high-severity fire than non-nesting forest. These actions may be especially effective if the resulting landscape has extensive areas of interior nesting forest. Additional research is needed to predict the conditions under which northern spotted owl nesting forest is likely to remain fire refugia in the face of increasing fire activity with climate change.

Conclusions

We present evidence that suitable nesting forests for northern spotted owls tend to burn at lower severity than the surrounding landscape and thus may be more resilient to increasing trends of wildfire. We do not infer that our results trivialize the threat to northern spotted owls from large wildfires because high-severity fires result in the loss of suitable nesting forest and lower survival (Rockweit et al. 2017; Lesmeister et al. 2019). Particularly in the face of barred owl competition, loss of suitable nesting forest is concerning because widespread old-growth forest helps to dampen northern spotted owl territory extinction rates, improves colonization and survival rates, facilitates resource partitioning, and decreases breeding dispersal distance and rates (Jenkins et al. 2019a; Jenkins et al. 2019b; Franklin et al. 2021; Jenkins et al. 2021). Therefore, barred owl management coupled with conservation of suitable nesting forest and restoration efforts to promote forest resilience to climate change are likely necessary for successful recovery of northern spotted owl populations and other biodiversity goals of the NWFP (Lesmeister et al. 2018; Spies et al. 2019; Yackulic et al. 2019; Wiens et al. 2021). Wildfires that remove large swaths of suitable nesting forest are of particular concern because it may take over a century for forest structure to recover and become suitable for nesting by northern spotted owls. Jones et al. (2016) found clear evidence for detrimental impact of a megafire on a California spotted owl population, and other research showed landscape use decreasing with larger patches of high-severity fire (Jones et al. 2020b; Kramer et al. 2021). Although high-severity fires have been an important ecological process in Pacific Northwest forests for at least 11,000 years with frequent fires steadily increasing over the past 4000 years (Walsh et al. 2015), periodic megafires that result in extremely large losses of nesting forest pose a conservation concern for northern spotted owls. The historic landscape with millions of hectares of intact old-growth forest could incur these occasional events and maintain function, but the contemporary amount and spatial extent of suitable nesting forest is a small percentage of what existed historically and primarily confined to federal lands making the landscape less resilient to megafires.

Under most fire weather, suitable nesting forests burn at lower severity compared to the surrounding landscape but are at increased risk of burning at high-severity when fragmented and surrounded by non-nesting forests (primarily younger forests) which are most susceptible to loss due to wildfire. These findings support the recovery actions in the 2011 northern spotted owl Recovery Plan that call for conservation of existing high-quality northern spotted owl nesting forest and, outside those areas, focused treatments to increase the extent of forest types with large diameter trees, high amounts of canopy cover, and decadence components such as broken-topped live trees, mistletoe, cavities, large snags, and fallen trees (USFWS 2011). By identifying the potential role that intact old-growth and late-successional forests may play to enhance fire resiliency in the face of climate change, this study highlights the potential benefits of adaptive management and landscape-scale restoration.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-021-00118-z.

Additional file 1: **Appendix 1**. Example of wildfire perimeters juxtaposed against our owl nesting/roosting cover type model (Map A) and burn severity from Landscape Change Monitoring System (Map B) for the Douglas complex fires which burned 20 479 ha in Oregon, USA, in 2013.

Additional file 2: **Appendix 2**. Tukey post hoc comparison of burned/area (B/A) ratios of severity (UL, M, H)-forest type (INTERIOR, EDGE, NON-NESTING) combinations for 472 large (≥ 200 ha) fires within the range of the Northern Spotted Owl, 1987-2017. Fire severity codes are UL= unburned-low, M = moderate severity, H = high severity.

Additional file 3: **Appendix 3**. Figures of the frequency distribution of slope (30 m pixels) within each forest cover type for the large wildfire years of 1987 (a) and 2017 (b). The NON-NESTING forests had high distribution and occurred on gentler slopes compared to EDGE and INTERIOR forest types.

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Authors' contributions

DBL developed the analysis concept, secured funding, interpreted statistics, and did the majority of manuscript writing; RJD developed the analysis concept, compiled data, created figures, and contributed to manuscript writing; SGS performed GIS analysis, compiled and analyzed data, and contributed to manuscript writing; ZY developed the original spatial datasets, assisted in interpreting statistics, and contributed to writing the manuscript. The authors read and approved the final manuscript.

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Availability of data and materials

If this paper is accepted, we will make the code and datasets used in our analyses available in a public repository.

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.

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Publisher’s Note

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Mixed-severity wildfire and habitat of an old-forest obligate

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Abstract. The frequency, extent, and severity of wildfire strongly influence the structure and function of ecosystems. Mixed-severity fire regimes are the most complex and least understood fire regimes, and variability of fire severity can occur at fine spatial and temporal scales, depending on previous disturbance history, topography, fuel continuity, vegetation type, and weather. During high fire weather in 2013, a complex of mixed-severity wildfires burned across multiple ownerships within the Klamath-Siskiyou ecoregion of southwestern Oregon where northern spotted owl (*Strix occidentalis caurina*) demographics were studied since 1990. A year prior to these wildfires, high-resolution, remotely sensed forest structural information derived from light detection and ranging (lidar) data was acquired for an area that fully covered the extent of these fires. To quantify wildfire impact on northern spotted owl nesting/roosting habitat, we fit a relative habitat suitability model based on pre-fire locations used for nesting and roosting, and forest structure variables developed from 2012 lidar data. Our pre-fire habitat suitability model predicted nesting/roosting locations well, and variable response functions followed known resource selection patterns. These forests had typical characteristics of old-growth forest, with high density of large live trees, high canopy cover, and complex structure in canopy height. We projected the pre-fire model onto lidar data collected two months post-fire to produce a post-fire suitability map, which indicated that >93% of pre-fire habitat that burned at high severity was no longer suitable forest for nesting and roosting. We also quantified the probability that pre-fire nesting/roosting habitat would burn at each severity class (unburned/low, low, moderate, high). Pre-fire nesting/roosting habitat had lower probability of burning at moderate or high severity compared to other forest types under high burning conditions. Our results indicate that northern spotted owl habitat can buffer the negative effects of climate change by enhancing biodiversity and resistance to high-severity fires, which are predicted to increase in frequency and extent with climate change. Within this region, protecting large blocks of old forests could be an integral component of management plans that successfully maintain variability of forests in this mixed-ownership and mixed-severity fire regime landscape and enhance conservation of many species.

Key words: forest structure; habitat; lidar; mixed-severity fire regime; northern spotted owl; old forest; pre-fire vegetation condition; *Strix occidentalis caurina*.

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INTRODUCTION

Climate and land-use patterns are strong predictors of disturbance regimes that ultimately influence the structure and function of an ecosystem (Sousa 1984). Globally, forest ecosystems are at risk of large disturbance regime shifts (frequency and severity) and ultimately a range of possible alternative stable states due to climate change-induced drought and heat stress, and associated interactions with insect disease outbreaks and wildfire (Dale et al. 2001, Allen et al. 2010, Kitzberger et al. 2012). In the case of fire regimes, their frequency and severity are typically negatively correlated, such that frequent fires are of lower severity, and strongly influence community dynamics and successional pathways (Agee 2005). Fire regimes play a key role in species adaptations as well as community structure and distribution of ecosystems, including the availability of several key components of wildlife habitat (Bunnell 1995, Noss et al. 2006, Pausas and Keeley 2009). Persistence of native wildlife species that are adapted to historical fire regimes may be at risk given climate change and land management practices that alter patterns in fire frequency and intensity relative to historical patterns. For example, in many dry forests the extent of areas impacted by high-severity fire is increasing, with concern for sensitive wildlife species that rely on forest types altered by fire (Westerling et al. 2006, Miller et al. 2008, Miller and Safford 2012, Reilly et al. 2017, Rockweit et al. 2017).

The fire regime of an ecosystem is defined as the natural patterns of wildfire in a given area including fire frequency, seasonality, extent, severity, and synergistic effects with other disturbances (Agee 1993, Halofsky et al. 2011). Forest successional theory suggests that in most areas, the interval length between disturbances should influence outcomes of succession, such that early-seral stands, low stature, and open microclimates are common in ecosystems with short-interval fires, whereas those with long-interval fires generally are dominated by mature forests with relatively closed canopies (Donato et al. 2009, Halofsky et al. 2011). Low-severity regimes are most often associated with dry forest types which experience frequent and predominantly low-severity fires where loss of biomass due to fire is low, and <30% mortality of trees is typical (Agee 1993). This disturbance regime results in stands with open canopies and an understory dominated by sprouting and rhizomatous shrubs and herbaceous plants, which are described in historical accounts as open, parklike forests (Agee 2013). The extent of these forest types was often overrepresented in historical records due to the ease of traveling through them and the opportunities for pleasing photographs (Van Pelt 2008). In truth, these open, parklike forest conditions do not represent many forests in western North America (Odion et al. 2014). Forests in high-severity fire regimes experience infrequent (>200-yr return intervals) but high-severity fires. Large patches of total mortality occur within the fire events and overall mortality is high (>70%), though areas of low- and moderate-severity fire are also common (Agee 1993, Turner and Romme 1994). In western North America, these forest types associated with high-severity fire regimes are characteristic of high-elevation, lodgepole pine (*Pinus contorta*)-dominated stands, some spruce (*Picea* spp.)-dominated forests, and moist Douglas-fir (*Pseudotsuga menziesii*)/western hemlock (*Tsuga heterophylla*) forests of the Pacific Northwest (Agee 1993).

Within mixed-severity fires, 30–70% tree mortality is common; however, the mixed-severity regime is not simply intermediate between low- and high-severity fire regimes (Agee 1993, Perry et al. 2011). The resulting pattern of low-, moderate-, and high-severity fire patches within a given area is highly variable and difficult to predict (Agee 2005), although at a large enough spatial scale (e.g., watersheds), nearly all fires are mixed-severity (Turner and Romme 1994, Baker et al. 2007, Halofsky et al. 2011). This variability can occur at fine spatial and temporal scales dependent on previous fire history, topography, fuel continuity, vegetation type, and weather (Heyerdahl et al. 2001, Donato et al. 2009, Thompson and Spies 2009, Krawchuk et al. 2016). Because of the spatiotemporal variability across the landscape, mixed-severity fire regimes are the most complex and least understood fire regimes, unique in terms of patch metrics and the life history attributes of native species (Schoennagel et al. 2004, Agee 2005, Halofsky et al. 2011). Fire histories in mixed-severity regimes, in particular, are difficult to determine because most fire history techniques have been developed to study either the low- or high-severity extremes in fire regimes (Agee 2005). Short-interval severe fires are an important characteristic of mixed-severity fire regimes and are typically considered extreme events and expected to be deleterious to forest succession and diversity (Donato et al. 2009). However, many native plants within these forests possess functional traits (e.g., persistent seed banks, vegetative sprouting, rapid maturation) lending to resilience to short-interval severe fires that result in distinct vegetation assemblages that enhance landscape heterogeneity inherent to mixed-severity fire regimes (Donato et al. 2009). Furthermore, high diversity of vegetation types, driven by short-interval repeat fires in a mixed-severity fire regime landscapes, plays an important role in conservation and the structure of avian communities (Fontaine et al. 2009).

Fire behavior is most strongly influenced by weather, topography, and fuels (i.e., above-ground vegetation biomass) interacting through multiple pathways and at multiple spatial scales (Agee 1993). Weather is perhaps the most important factor controlling fire behavior and severity, especially in mixed-severity regimes (Bessie and Johnson 1995, Collins et al. 2007, Thompson and Spies 2009, Bradstock et al. 2010). In moderate fire weather, topographical complexity and position (east- and south-facing, upper- and mid-slopes) have been shown to strongly influence fire intensity, with pre-fire vegetation condition and fire history also important predictors of severity (Estes et al. 2017). Under these conditions, shrubs and younger forests were more likely to burn at higher intensity than mature forests. In very high and severe fire weather, the amount (fuel loads), type (e.g., younger vs. older forest), and vertical and horizontal spatial arrangement of fuels (contiguous vs. unconnected) can be the primary driver of spatial patterns in mixed-severity fire (Zald and Dunn 2018). Furthermore, previous fires and post-fire management can set up the landscape for patterns of self-perpetuating high-severity fire in mixed-severity regimes (Donato et al. 2009, Thompson and Spies 2010). Even in drier forest types with high frequency of fire, certain topographic settings have lower fire frequencies where patches of dense, old forest can develop and persist as islands in a matrix of open, older forests (Camp et al. 1997, Krawchuk et al. 2016). With changing climates and land management practices, the size of patches of high-severity fire is increasing relative to historical patterns, with concern for sensitive species that rely on forests dramatically altered by fire (Westerling et al. 2006, Miller et al. 2008, Miller and Safford 2012, Reilly et al. 2017, Rockweit et al. 2017).

Northern spotted owls (*Strix occidentalis caurina*) are an obligate species of old forests in the Pacific Northwest of the United States and southwest Canada and typically nest in large old conifer trees (Wilk et al. 2018). The subspecies was listed as threatened under the U.S. Endangered Species Act because populations declined primarily as result of habitat loss due to large-scale harvest of late-successional forests (USFWS 1990). A variety of forest types are used by northern spotted owls for foraging, but nesting and roosting primarily occur in forests older than 125 yr of age. These older forests have average tree diameters above 50 cm and many trees exceed 75 cm diameter, canopy cover is usually >60%, and the forest has multiple canopy layers (Davis et al. 2016). The Northwest Forest Plan (NWFP) was designed to protect most remaining old forest and, after several decades, provide enough habitat on federal lands for viable populations of several old-forest species, primarily through a network of late-successional forest reserves (USDA and USDI 1994). On federal lands, loss of northern spotted owl habitat due to timber harvest has declined, but losses due to wildfires have increased in recent decades (Davis et al. 2016). Studies focused on the subspecies of northern spotted owls suggest that occupancy and survival generally decline after fire, especially if post-fire logging occurs (Clark et al. 2011, 2013, Rockweit et al. 2017). The effects of fire on individual northern spotted owls and habitat quality are complex and not fully understood (Lesmeister et al. 2018), but clearly suitability of forests for nesting and roosting decreases if canopy cover is reduced and with spatial aggregation of high-severity fire (Davis et al. 2016, Rockweit et al. 2017, Sovern et al. 2019).

Fire regimes within the range of northern spotted owls range from infrequent/high severity in the northern and coastal regions to frequent/low severity in the eastern and southern regions (Spies et al. 2018). In between these two extremes is a broad area of mixed-severity regimes, including the Oregon Klamath, where recent wildfires have caused high rates of loss of old forests and threaten species associated with them (Spies et al. 2006, 2018). Wildfires within this regime are comprised of a mix of burn severities, with low-severity ranging from 45% to 54% of the burned area, moderate-severity from 24% to 36%, and high-severity fire from 23% to 26% (Reilly et al. 2017). While the frequency and extent of high-severity fire have been increasing due to a general increase in large wildfires within the owls range, there is no strong evidence that high-severity wildfire comprises a higher proportion of burned areas than it did historically (Miller and Safford 2012, Reilly et al. 2017).

Within the Klamath-Siskiyou ecoregion of southwestern Oregon, an area characterized as moderate-frequency, mixed-severity fire regime (Spies et al. 2018), northern spotted owl demographics have been studied on the Klamath demographic study area since 1990 (Dugger et al. 2016). In and near the study area, lightning from a thunderstorm on 26 July 2013 started 54 fires that burned under very high fire weather conditions and were managed as the Douglas Complex and Big Windy Fires (Zald and Dunn 2018). Most of the fires joined into several large fires that burned with mixed severity over an area of about 38,000 ha. Within the fire perimeter were large patches of high-severity fire and subsequent salvage logging, primarily on private lands and along roads on federal lands. The non-overlapping—but nearby—large mixed-severity wildfires burning simultaneously in a mixed-ownership and management landscape presented a unique landscape experiment to evaluate interactions between severity classes (unburned/low, low, moderate, and high) and vegetation condition (e.g., suitable or unsuitable forest for nesting and roosting by northern spotted owls). Further, the study area provided an exceptional opportunity to study responses of vegetation to fire because high-resolution remote sensing data of vegetation height provided by aerial light detection and ranging (lidar) were available pre- and post-fire, which provided an unprecedented ability to measure forest attributes before and immediately following the fires.

Our objectives were to (1) quantify the immediate impact of various wildfire severities on northern spotted owl nesting/roosting habitat, which has typical characteristics of old-growth forests in the Pacific Northwest; and (2) analyze the relative susceptibility of northern spotted owl nesting/roosting habitat to higher or lower severity fire. We hypothesized that northern spotted owl nesting/roosting habitat would be degraded as severity increased, but the relationship would be non-linear where habitat would not be degraded at low severity, only slightly degraded with moderate severity, and highly degraded with high severity. Because the area was in drought and fire weather was very high to severe, we expected the high fuel loading of northern spotted owl nesting/roosting habitat may cause these stands to burn at higher or equal severity than other forest types with less fuel (Weatherspoon et al. 1992). However, several lines of evidence suggest older forests with dense, multi-storied canopies are more resistant to high-severity wildfire during severe fire weather (e.g., Countryman 1955).

METHODS

Study site

The study was conducted in the Klamath-Siskiyou ecoregion, which extends from northwestern California into southwestern Oregon (Fig. 1). The Douglas Complex and Big Windy Fires burned mostly within the boundary of the Klamath northern spotted owl demography study area (1422 km^2; Fig. 1) with elevations ranging from 610 to 1680 m. Annual precipitation ranged from 1500 to 3000 mm over the study area (http://prism.oregonstate.edu/), with <15% falling from May to September. The region is among the top global hotspots of species rarity and richness, identified as a global center of biodiversity, a World Wildlife Fund globally outstanding ecoregion (www.worldwildlife.org/publications/global-200), and an IUCN area of global botanical significance (Olson and Dinerstein 1998, Noss 2000). The complexities of climate, topography, biogeographic patterns, geology, and mixed-severity fire regime in the Klamath and Siskiyou Mountains create one of the four richest temperate coniferous forests in the world with high endemism, species richness, and unique community assemblages (Noss et al. 1999, Vance-Borland

1999). Forests were dominated by Douglas-fir, ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana*), and incense cedar (*Calocedrus decurrens*) and mixed with a variety of other conifers (*Pinus* spp. and grand fir *Abies grandis*) and hardwoods (e.g., Pacific madrone *Arbutus menziesii*, golden chinquapin *Castanopsis chrysophylla*, and oak *Quercus* spp.).

Within the Klamath-Siskiyou ecoregion, a complex and variable fire regime prevails, dominated by frequent mixed-severity and very frequent mixed-severity fires (Fig. 1; Spies et al. 2018). Historical fire severity varied in spatial scale, patchiness, and fire-return intervals (c. 5–75 yr), but overall exhibiting mixed severity over time and space (Agee 1993, Taylor and Skinner 1998, Perry et al. 2011). When a stand-replacing fire occurs, rapid recovery of vegetation and fuel continuity, coupled with dry summers and frequent lightning, create the potential for recurrent high-severity fires over decadal timescales (Thompson et al. 2007). Thus, short-interval severe fires have likely been a component of the complex fire regime and a factor structuring vegetation in the region (Agee 1993, Donato et al. 2009).

Fire data

We used daily fire perimeter map data for the Douglas Complex Fires that burned with mixed

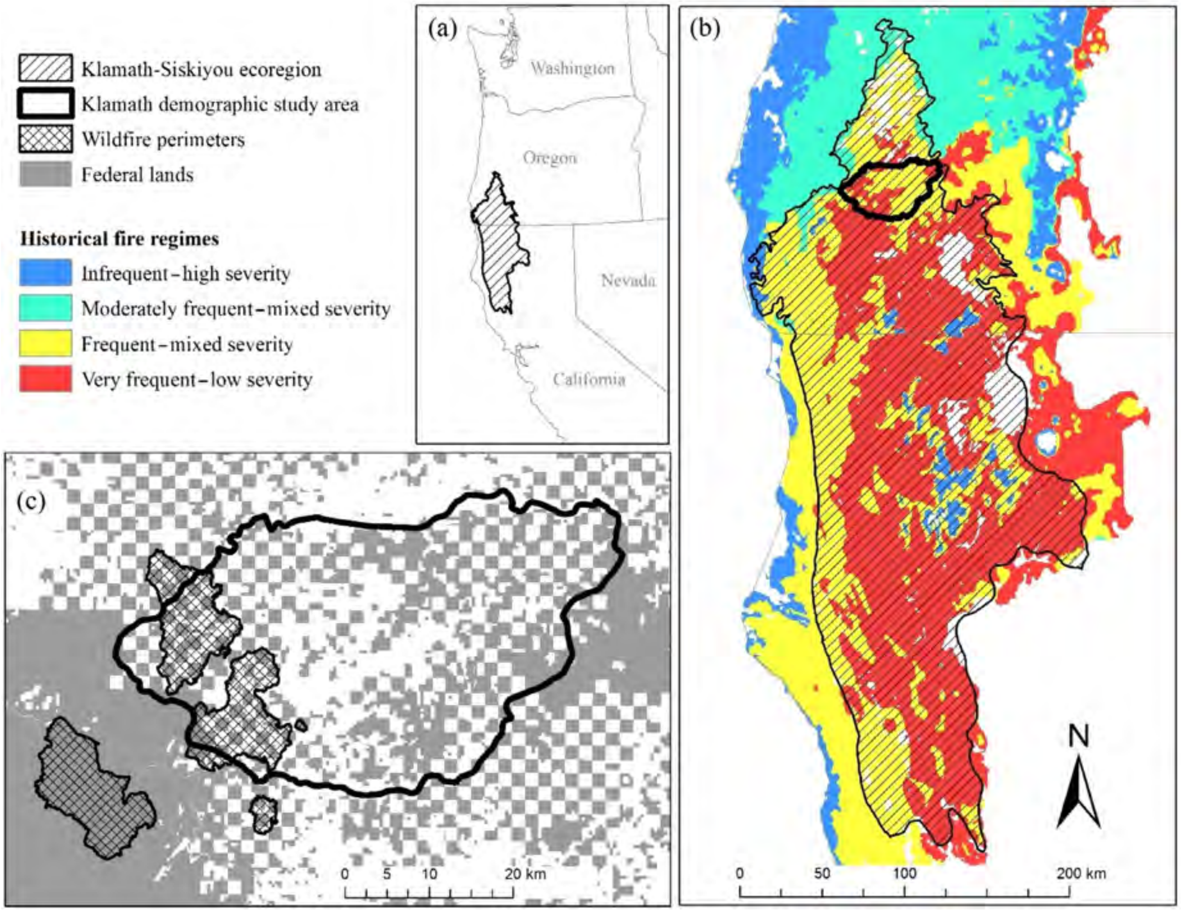

Fig. 1. Maps showing (a) the Klamath-Siskiyou ecoregion of California and Oregon, USA (hatched area); (b) historical fire regimes in the Klamath-Siskiyou ecoregion (Spies et al. 2018), Klamath northern spotted owl demography study area (1422 km^2; center = 123.315° W, 42.782° N, heavy black border); and (c) landownership (federal land, gray; private land, white) and the 2013 Douglas Complex and Big Windy Fires (cross-hatched area).

severity: Dads Creek (final perimeter = 9890 ha), Rabbit Mountain (9706 ha), and Brimstone (928 ha); and for the Big Windy Fire (10,799 ha; Fig. 2). Low precipitation in 2013 resulted in moderate-to-severe drought conditions in southern Oregon (NDMC 2018) and contributed to active fire behavior in the early burning period of these fires. Zald and Dunn (2018; and unpublished data) summarized weather data for the first 4 d of the Douglas and Big Windy Complexes (see Fig. 2 for fourth-day fire perimeters) from three Remote Automatic Weather Stations near fires and found maximum temperature was 25–32°C, minimum relative humidity was 17–30%, and maximum wind speed was 19–29 kmh. After the fourth day of the fire, a temperature inversion developed—a common occurrence in this region (Estes et al. 2017)—which dramatically changed fire behavior and greatly improved the effectiveness of suppression efforts. Mean daily burning index (BI) for the first 4 d of the fire was 52–76, which was above the

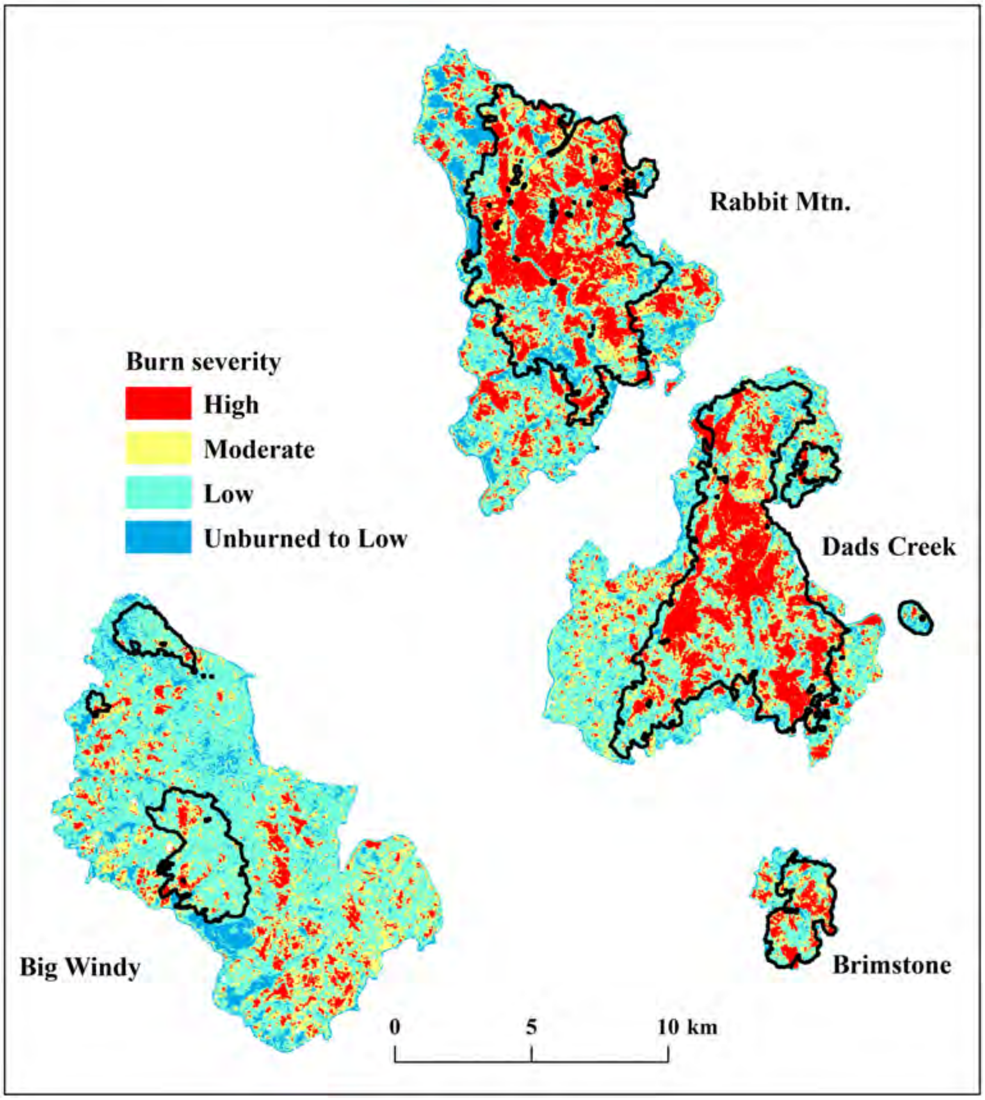

Fig. 2. Map of monitoring trends in burn severity (Eidenshink et al. 2007) data for the Big Windy and Douglas Complex Fires in southwest Oregon, USA, 2013. Severity is based on change in normalized burn ratio (dNBR) from Landsat-8 images from pre- and post-fire. The perimeter of the fires after the fourth day is outlined in black.

historic (1991–2017 1 June–30 September) 90th percentile for this period (Zald and Dunn 2018). Mean daily energy release component (ERC) values ranged from 49 to 67, also above the 90th percentile for this area (Dalton et al. 2015) for 3 of 4 d. Burning index is a fire behavior index proportional to flame length that incorporates wind speed estimates, and ERC is an index of fire energy that includes the cumulative drying effect of weather in the days prior to the estimate and measures live and dead fuel moisture (Bradshaw et al. 1983, Cohen and Deeming 1985). Post-fire logging occurred over much of the high-severity portions of the private lands, but most federal land was unlogged post-fire because the area was designated as a late-successional reserve under the NWFP. The areas of the Douglas Complex Fires were primarily composed of Oregon and California Railroad Lands with federal lands, managed by the U.S. Bureau of Land Management, in a checkerboard pattern with private lands (Fig. 1; Zald and Dunn 2018). The Big Windy Fire burned within an intact landscape of federally managed forest lands (Fig. 1).

Pre- and post-fire habitat suitability

We used program MaxEnt version 3.3.3k (Phillips et al. 2006) to produce a pre-fire relative nesting/roosting habitat suitability model of forests used by northern spotted owls and applied the model algorithm to post-fire forest conditions to map post-fire suitability. MaxEnt is based on the maximum information entropy theory and is widely used to develop resource selection functions through the use of machine learning applied to known species locations (i.e., model training data) and relevant environmental predictor variables (Harte and Newman 2014). Previous efforts also used machine learning to develop nesting/roosting cover type models in several northern spotted owl studies and monitoring reports (Davis et al. 2011, 2016, Glenn et al. 2017). We followed Ackers et al. (2015) by using lidar-derived forest structure variables to develop a model of suitable forest for northern spotted owl nesting and roosting.

We used site locations where northern spotted owls nested and roosted within the demographic study area as training and testing data for relative habitat suitability models. These location data were collected during long-term research of northern spotted owl demography, including survival rates, reproductive rates, and annual rate of population change. The protocol used to determine site occupancy, nesting, and reproductive status for this study followed the guidelines specified by monitoring effectiveness of the NWFP (Franklin et al. 1996, Dugger et al. 2016).

We derived our pre- and post-fire model predictor variables from multiple-return discrete lidar data acquired in 2012 (1 yr pre-fire) and 2013 (2 months post-fire) by Quantum Spatial (previously Watershed Sciences, Corvallis, Oregon, USA) using aircraft-mounted Leica ALS 50 and/or Leica ALS 60 sensors with an average point density of ≥10 points per square meter. The 2012 data were collected as part of the Oregon Lidar Consortium (OLC) Rogue River lidar acquisition, covering an area of ~567,000 ha. Within this OLC Rogue River collection area, ~50,000 ha of lidar data were acquired again in 2013 post-wildfire, encompassing the Douglas complex and Big Windy Fires. We processed all lidar metrics from delivered point clouds, creating 1-m-resolution models of highest (i.e., first) return and bare earth digital elevation models (DEMs) with FUSION/LDV software (McGaughey 2015).

Following Ackers et al. (2015), we derived four metrics from the lidar data known to be important drivers in northern spotted owl nesting and roosting ecology: percentage overstory canopy cover (CANOPY), mean overstory canopy height (HEIGHT), density of large live trees (LARGE TREES), and rumple index (RUMPLE; Parker et al. 2004). We calculated the percent CANOPY taller than 2 m and the mean vegetation height using only first returns at 30 m resolution. We calculated RUMPLE, a measure of stand structure diversity where higher values represent stands with more horizontal and vertical complexity, using a 3 × 3 window focal mean of the 1-m canopy height model (CHM; Ackers et al. 2015). We matched the resolution of the HEIGHT and CANOPY metrics using a cell multiplier of 30 and then derived RUMPLE from the surface area ratio output. We calculated LARGE TREES from point files representing large live tree (≥31 m tall) locations from the 1-m CHM and CanopyMaxima in FUSION/LDV (McGaughey 2015). The tree height threshold of 31 m was the average height of 80-yr-old trees based on a height–age relationship of trees in forest inventory plots from the study area. To minimize the chance of having multiple points for the same tree, we created 10 m radius buffers around all points in ArcGIS 10.1 (ESRI, Redlands, California, USA), dissolved overlapping buffers, and then created a new point layer from the centers of the dissolved buffers. Any trees that were mapped only in the post-fire LARGE TREES map were added to the pre-fire model (with the assumption that large trees present after the fire were present prior to fires).

Northern spotted owl presence data for model training and testing were based on 107 nesting or roosting locations from 27 territories. Given that presence data originated from a long-term northern spotted owl study area, we were confident that we met sampling assumptions of minimal sampling bias and high probability of detecting owls when they were present. We followed standard procedures for presence-only modeling to avoid multi-collinearity between model variables by restricting modeling response functions that were overly complex, using stepwise calibration, and testing of bootstrapped model replicates (O'Brien 2007, Phillips and Elith 2013, Merow et al. 2014). We followed the model selection method used by Ackers et al. (2015) by using a random subset of our owl location data (75%) and 10,000 random modeling region locations to develop bootstrapped replicate models that related location data to random environmental conditions. We used the held-out 25% of northern spotted owl locations to test model predictions. We made stepwise adjustments to the model regularization multipliers that serve as a penalty parameter in machine learning by eliminating model coefficients and keeping only those that increase model gain, which relates to the likelihood ratio of an average species location to average background environmental conditions. Higher gains produce better differentiation of species locations from background conditions. The best model was based on balancing two criteria: (1) minimizing the difference between regularized training gain and test gain to avoid over-fitting the models, while (2) maximizing model test statistics (area under the curve [AUC] and Spearman rank correlation [Rs]). Once the best model was selected, we used the predicted vs. expected (P/E) curve to classify the model into a binary map of suitable and unsuitable nesting/roosting habitat (Hirzel et al. 2006).

Burn severity and change in suitability

We assumed most of the negative effects of wildfire on northern spotted owl nesting/roosting habitat would result from loss of canopy cover and mortality of large trees. To capture changes in the large, live tree component (LARGE TREES), we needed to estimate the proportion of LARGE TREES that suffered mortality by fire severity to adjust our post-fire LARGE TREES variable for the post-fire nesting/roosting habitat model. However, initial examination of the lidar data indicated that the post-fire lidar data could not differentiate live vs. dead trees ≥31 m height, leading to a bias in the lidar-based LARGE TREES variable. Previous research has indicated that lidar variables are better predictors for live and total basal area while multispectral imagery variables (e.g., Landsat data) are better predictors for dead and percent dead basal area (Bright et al. 2014). For example, changes in normalized burn ratio (NBR) are commonly used for mapping forest disturbance, especially timber harvest and wildfire (Miller and Thode 2007, Kennedy et al. 2010, 2012, Schroeder et al. 2011). In particular, changes in NBR have been widely used to assess fire severity (Miller et al. 2009, 2012, Cansler and McKenzie 2012, Lydersen et al. 2016). Furthermore, changes in NBR have been effectively related to changes in canopy cover (Miller et al. 2009) and basal area (Reilly et al. 2017). In this study, we used changes in satellite-based NBR from Landsat-8 to assess changes in canopy cover, and thus tree mortality, in live trees ≥31 m height to avoid biases produced by directly calculating changes in LARGE TREES from pre- and post-fire lidar data.

To assess canopy cover losses, and thus large live tree mortality associated with the fire, we acquired two spatial datasets to be used for mapping vegetation change within the fire perimeters: (1) We used Google Earth Engine (Google Earth Engine Team 2015, Gorelick et al. 2017) to collect 30-m-resolution Landsat-8 LaSRC imagery for the study area from 1 May to 1 August of 2013 and 2014 to generate pre- and post-fire NBR maps; and (2) we used post-fire high-resolution (7.62 cm) imagery acquired concurrently with lidar acquisition to estimate tree canopy cover. For all 30 × 30 m (900 m^2) pixels in the study area, we calculated NBR in 2013 (pre-fire) and 2014 (post-fire) as the normalized differences between near-infrared and shortwave-infrared bands (bands 5 and 7, respectively; Li et al. 2013) for each Landsat-8 image. For our study area, no single image was optimal (e.g., cloud cover over part of the area on a given date), so we created a median composite image of NBR for each growing season (May–August; Kennedy et al. 2012). Large, live trees represented by LARGE TREES were only located in older forests; therefore, we measured live tree canopy cover visible in the high-resolution aerial photographs at 200 randomly generated 30 × 30 m (900 m^2) plots within older forests (95th percentile lidar return height ≥30.8 m) inside the study area snapped to the 2014 Landsat-8 pixel boundaries. Within each plot, 36 systematically distributed sampling points were established and tree canopy cover was measured as the proportion of sampling points where we observed live tree crowns in the high-resolution imagery. Plots co-located with roads, timber salvage, young plantations, or lacking clear imagery (e.g., steep slope in shadow) were excluded from our analysis, resulting in a final sample size of $n = 181$ that included post-fire canopy cover in forests experiencing a variety of fire severity conditions. Note that canopy cover measurements collected at these sample locations represent only live tree canopy cover and were independent from lidar-based canopy cover estimates that include both live and dead trees.

Statistical models relating NBR change and forest change (e.g., basal area mortality; Reilly et al. 2017) are available, but we did not have reliable measurements of canopy cover change based on both pre- and post-fire aerial photographs upon which we could parameterize a model. Pre-fire aerial imagery could not be used in conjunction with post-fire aerial imagery to calculate change in canopy cover directly because of the lower resolution images and differing parallax (i.e., an apparent shift in the position of objects as viewed from differing vantage points) between pre- and post-fire images. Therefore, an accurate assessment of cover change between photographs was unreliable. Additionally, published models were not parameterized for our landscape, but rather broad regional datasets for California (Miller et al. 2009) or Oregon and Washington (Reilly et al. 2017). Because only post-fire reference data for canopy cover (high-resolution aerial photographs) were available, we developed a mortality algorithm based on changes in forest canopy cover predicted from NBR data. The algorithm (1) predicted live canopy cover based on post-fire NBR and canopy cover measurements from aerial photography, (2) calculated the change in predicted canopy cover from the pre-fire to post-fire conditions, and (3) assigned mortality to LARGE TREES with probability proportional to the change in Landsat-based canopy cover.

Because tree canopy cover data were non-negative, we modeled tree canopy cover as a function of NBR with a zero-truncated regression model (Fig. 3). The model was fit to the 2014 NBR (post-fire) and tree canopy cover data in the R statistical environment version 3.3.1 (R Core Team 2016) with the function tobit (AER package; Kleiber and Zeileis 2009). For each 30-m Landsat pixel, tree canopy cover predictions for pre- and post-fire were generated by applying the fitted model to 2013 (before fire ignition) and

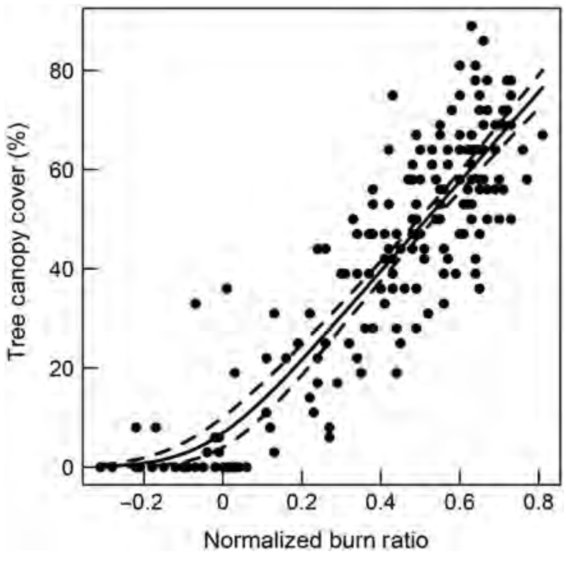

Fig. 3. Mean (solid line) and 95% confidence intervals (dashed lines) for predicted live tree canopy cover as a function of normalized burn ratio within the Douglas Complex and Big Windy Fires in southwest Oregon, USA, in 2013 based on the zero-truncated regression model.

2014 NBR data, respectively. To minimize differences between 2013 and 2014 canopy cover maps, we normalized the 2013 NBR data so that the differences between 2013 and 2014 NBR outside the fire perimeter were minimized. We transformed the 2013 NBR image by creating a mask of high NBR (stable forest, both 2013 and 2014 NBR were >0.75) outside the fire boundaries, and within the study area, which served as the population for creating a normalization between the two image dates. We then created a simple least-squares linear fit between NBR 2013 and NBR 2014 based on all pixels in the mask population, with a slope of 0.845 and intercept of 0.119 based on estimated coefficients. We created the transformed NBR 2013 by applying slope/intercept from linear fit, thereby transforming the 2013 image calibrated to the values in the 2014 image and quantified differences.

Pre- and post-fire predictions of canopy cover were differenced and divided by the predicted pre-fire canopy cover to calculate the proportional change in canopy cover (ΔC). The probability of mortality for a given 30-m pixel on the landscape was taken to be $1 - \Delta C$ (i.e., canopy cover-weighted tree mortality). Areas with canopy cover increases (i.e., $\Delta C > 0$) were assumed to have no tree mortality. We assessed the performance of the canopy cover-weighted mortality by comparing our predictions for each pixel with a large live tree with an independent basal area-weighted mortality prediction generated using existing models (Appendix S1; Reilly et al. 2017). We use these data for validation because the models produced by Reilly et al. (2017) predict basal area-weighted tree mortality from a regional forest inventory network based on RdNBR ($r^2 = 0.68$) and perform particularly well in identifying patches of forest experiencing basal area-weighted mortality >75% (classification accuracy = 82.8%).

Large tree mortality within each pixel was assigned proportional to $1 - \Delta C$. For a given pixel with n canopy dominant trees identified based on lidar imagery, a sample $n \times (1 - \Delta C)$ trees, rounded to the nearest integer, was taken and recorded as having died during the fire, with the remaining $n \times \Delta C$ trees surviving. This assumes that the number of trees dying during the fire was proportional to the canopy cover losses and that the identity of trees dying does not matter. For canopy dominant trees examined in this paper, such an assumption seems reasonable. We, therefore, used the mortality algorithm to modify our post-fire point file of tree stems to estimate which trees mapped by lidar suffered mortality. We then used the post-fire live tree point file to generate our post-fire LARGE TREES density variable for nesting/roosting habitat modeling.

We recognize that by leveraging multiple datasets and modeling techniques—lidar-based LARGE TREES and satellite-based canopy cover-weighted mortality—there is the opportunity to propagation of error from one step to another. For example, errors in estimating forest carbon stocks may arise from field data collection, allometric equations, and modeling errors (Clough et al. 2016). In the case of this study, errors associated with canopy cover modeling, the calculation of canopy cover-weighted mortality, and the application of that mortality to attribute tree death to individual trees all contribute to overall errors.

Pre-fire vegetation vs. fire severity analysis

Our main interest was to examine the relationship between fire severity and nesting/roosting habitat with limited confounding effects of fire suppression activities and differences in fire weather during the time the fire burned. Though it is difficult to separate the confounding effects of suppression efforts when analyzing almost all fires, we reasoned we could minimize this effect by examining the early days of the fire before more extensive backfiring occurred and suppression activities had limited effect. Thus, we used the spatial extent of daily fire growth (as mapped using aerial IR technology each night) throughout the first 4 d after ignition. Starting at approximately day 5 of the fire, changes in atmospheric temperature altered fire weather conditions and suppression efforts included igniting backfires in some areas (K. Kosel, *personal communication*; Fig. 2). Additionally, by focusing on these rapid fire growth days we believe there is little to no alteration of natural fire behavior or severity across the spectrum of northern spotted owl nesting/roosting habitat suitability. To quantify the odds of forest types burning in 1 of 4 severity types, we evaluated the ratios of the proportion of suitable and unsuitable nesting/roosting habitat that burned (B) at each fire severity to what was available to burn (A). Fire severity types were taken from Monitoring Trends in Burn Severity (MTBS 2017) data, a map product based on changes in NBR commonly used by forest management agencies. The types include high severity, moderate severity, low severity, and unburned to low severity. By using the same fire severity classifications commonly used by land managers, communication and application of results from this research will be more straightforward. A value of B/A < 1 indicates that the forest type burned less than would have been expected by chance, and a ratio B/A > 1 indicates it burned more than would be expected by chance (Moreira et al. 2001, 2009, Manly et al. 2010). While the canopy cover-weighted mortality modeling we used to attribute large tree mortality depends on NBR and is thus likely related to the MTBS fire severity classes, we use the MTBS classes for summarizing across severity classes because of their widely accepted use in forest planning.

Results

Pre- and post-fire habitat suitability

Our best model of nesting/roosting habitat suitability predicted nesting/roosting locations well with an AUC statistic of 0.89 and a P/E curve Spearman rank correlation of 0.92. The binary classification of the habitat model into suitable and unsuitable was based on P/E = 1 (0.32). Model variable response functions (Fig. 4) followed known resource selection patterns by owls (Ackers et al. 2015, Glenn et al. 2017).

Burn severity and change in suitability

Post-fire nesting/roosting habitat suitability decreased with increasing fire severity (Table 1),

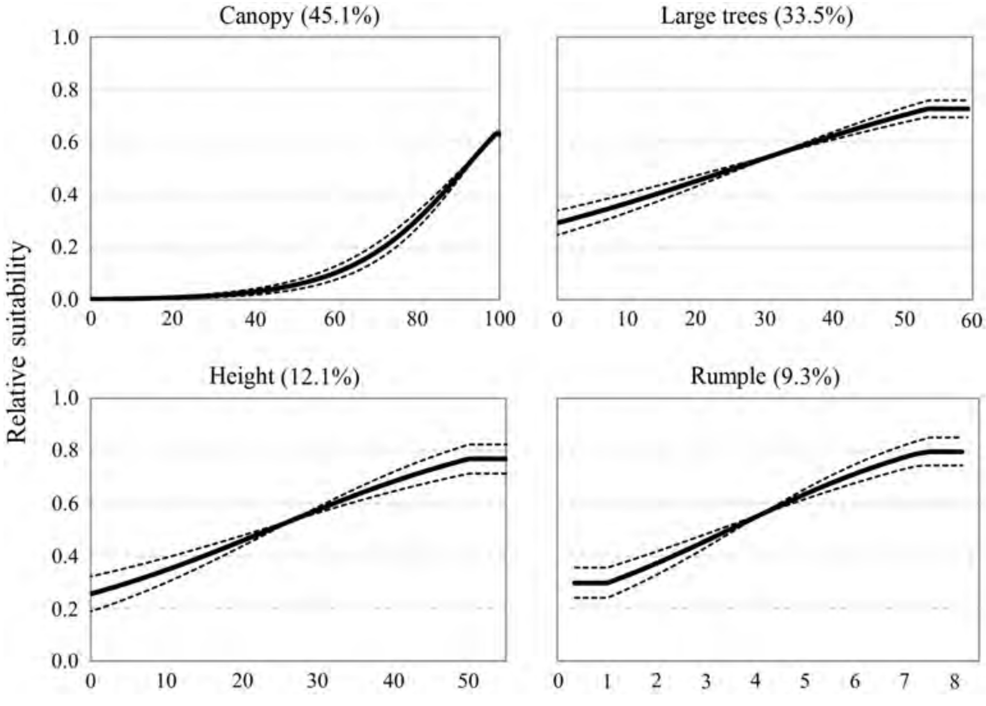

Fig. 4. Variable response functions with percent contribution (%) to pre-fire nesting/roosting habitat suitability model for northern spotted owls in the Klamath demographic study area in southwest Oregon, USA, where the Douglas Complex and Big Windy Fires burned in 2013. The solid line represents the mean, and the dashed lines represent 95% confidence intervals. Variables were derived from lidar data, and the variables included were CANOPY (percent canopy cover), LARGE TREES (large live trees per hectare), RUMPLE (rumple index), and HEIGHT (mean tree height [m]).

Table 1. Metrics within areas burned at four severity classes based on Monitoring Trends in Burn Severity (MTBS) measurements.

Fire severity	Pre-fire live trees	Trees killed	% Mort	Mean pre-fire NBR	Mean post-fire NBR	Δ Mean NBR (%)	Mean pre-fire suitability	Mean post-fire suitability	% Loss suitable habitat
Unburned to low	66,015	2830	4	0.75	0.68	−9.2	0.22	0.20	4.5
Low	251,356	49,413	20	0.74	0.56	−24.6	0.22	0.21	25.5
Moderate	71,826	40,038	56	0.72	0.30	−58.3	0.10	0.08	63.9
High	67,897	62,348	92	0.75	−0.04	−104.9	0.12	0.03	93.7

Notes: Reported are estimated number of large live trees pre-fire, estimated number large live trees killed during fire, percentage of large live trees killed, mean normalized burn ratio (NBR) pre (2013)- and post-fire (2014), percent change in NBR, pre (2012)- and post-fire (2013) mean nesting/roosting habitat suitability, and percent loss of suitable nesting/roosting habitat for northern spotted owls in the Douglas Complex and Big Windy wildfires in southwest Oregon during 2013.

mainly owing to fire-caused decreases in LARGE TREES and CANOPY. Low-severity fire had little effect on nesting/roosting habitat suitability. High-severity fire resulted in 75% decrease in mean suitability and >93% loss of suitable nesting/roosting habitat (Table 1) and commonly converted pre-fire suitable forests to conditions that were unsuitable for nesting and roosting (Fig. 5). Overall, most pre-fire habitat was lost if it burned at moderate severity (Table 1), but depending on the pre-fire suitability, moderate-severity fire produced mixed effects on nesting/roosting habitat suitability and did not consistently result in a loss of suitability. The forests that burned at unburned to low severities had pre-fire suitability values approximately two times higher than suitability of forests that burned at moderate or high severity (Table 1); thus, moderate- to high-severity fire had the greatest effect on pre-fire areas with low habitat suitability for northern spotted owls (Fig. 6).

Tree mortality and pre-fire vegetation vs fire severity

Canopy cover-weighted mortality (Appendix S1: Fig. S1) generated as the basis of attributing post-fire tree mortality for large trees exhibited a slight positive bias (mean error = 2.42% mortality) and root mean square deviation of 5.82% compared to an existing basal area-weighted mortality model based on regional forest inventory datasets co-located with large wildfires (Reilly et al. 2017). Despite these errors, our canopy cover-weighted mortality predictions were highly correlated with the existing basal area-weighted mortality predictions (Pearson correlation = 0.99).

Based on lidar tree mapping and the post-fire NBR analysis, we estimated the fires directly killed a total of 154,629 large live trees (51.1% of total pre-fire estimate). Tree mortality increased with fire severity and percent change in NBR (Table 1). There were 2.27 times more large live trees in areas that experienced unburned to low-severity fire compared to those areas that burned at moderate and high severity (Table 1). The susceptibility of forests to moderate- and high-severity fire was lower in suitable nesting/roosting habitat and higher in unsuitable forest than would be expected by chance (Fig. 6). The differences between low and moderate/high severity were more pronounced in suitable nesting/roosting habitat than unsuitable forest. The odds that suitable nesting/roosting habitat would burn at lower severity was 2–3 times higher than the odds it would burn at moderate-to-high severity. There were significant differences (based on non-overlapping 95% confidence intervals) between odds of burning at low severity and burning at moderate/high severity among forest types. There was no evidence for a difference between the odds (i.e., B/A index) of burning at moderate or high severity within suitable nesting/roosting habitat or unsuitable forest types, but there were differences between suitable and unsuitable forest types (Fig. 6). The odds that unsuitable forest burned at moderate-to-high severity was about twice that of suitable nesting/roosting habitat.

DISCUSSION

Here, we used newly developed tools and lidar data to examine the interaction between mixed-severity fires and northern spotted owl

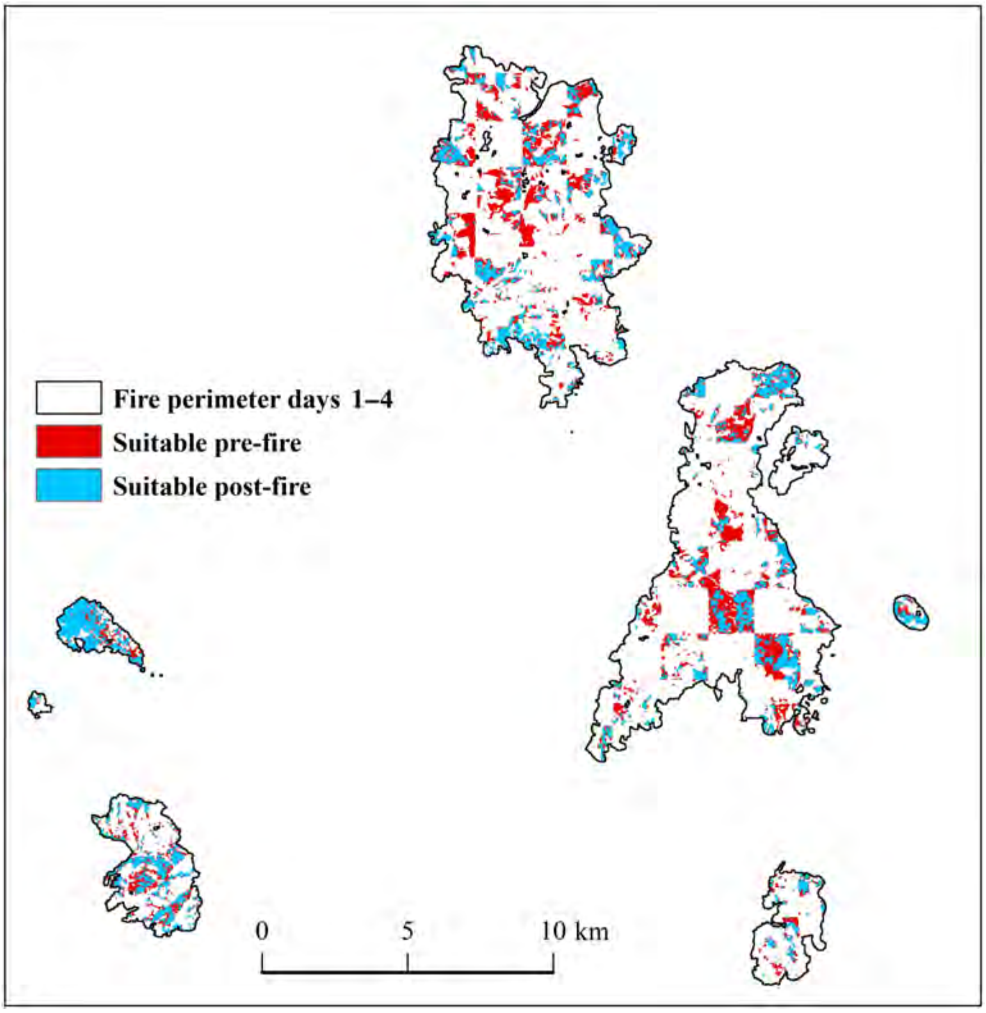

Fig. 5. Patterns of conversion from suitable habitat to unsuitable conditions for northern spotted owl nesting and roosting in the Douglas Complex and Big Windy Fires that burned in southwestern Oregon, USA. Binary classification of nesting/roosting habitat was based on predicted vs. expected ratio threshold of 0.32, and lidar metrics of live vegetation height, canopy cover, stand complexity (rumple index), and large tree density. Area shown is the perimeter of the fires 4 d after the fire ignited on 26 July 2013.

nesting/roosting habitat under high fire weather conditions in a landscape characterized by the interactions between land-use patterns and a mixed-severity fire regime. Because of high site fidelity, northern spotted owls may continue to use areas if suitable nesting/roosting cover remains and prey are available. However, survival decreases through time in areas with a high proportion of high-severity fire likely because post-fire habitat quality decreases to the point that territories are only marginally capable of supporting northern spotted owls (Rockweit et al. 2017). Within a few years post-fire, areas opened up by tree mortality change structurally (i.e., standing dead trees transitioning to fallen logs) and prey may be less accessible with high density of shrubs and herbaceous understory in high-severity burn areas. As expected, in our study the suitability of northern spotted owl nesting/roosting habitat decreased with increasing fire severity, to the degree that much of the pre-fire habitat that burned at high severity was no longer suitable cover for nesting or roosting. The greatest impacts from moderate- and high-severity fire

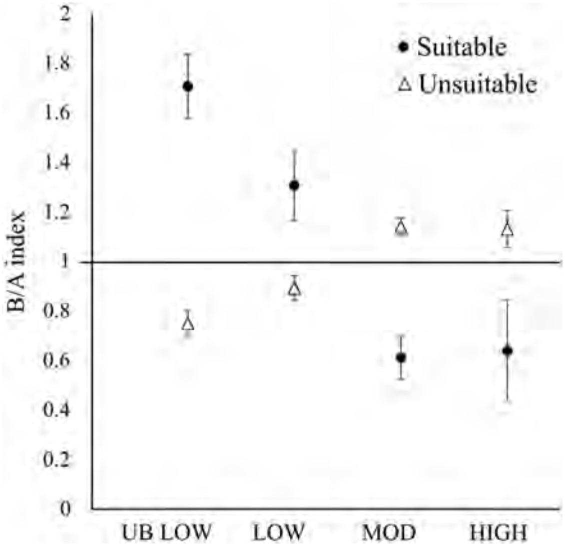

Fig. 6. Ratio of proportion of suitable and unsuitable nesting/roosting habitat that burned (B) at each fire severity to what was available (A) to burn (B/A index) with 95% confidence intervals, Douglas Complex and Big Windy Fires, southwestern Oregon, USA, 2013. We used Monitoring Trends in Burn Severity (MTBS 2017) to determine fire severity types (UB LOW, unburned to low severity; LOW, low severity; MOD, moderate severity; HIGH, high severity) and separated into suitable nesting/roosting habitat for northern spotted owls or unsuitable forest types based on lidar metrics. B/A index < 1 indicates that the forest type (suitable or unsuitable) burned at the severity class less than would have been expected by chance, and B/A index > 1 indicates forest type burned at the class more than by chance alone.

were observed in those forests exhibiting low habitat suitability for northern spotted owl nesting and roosting before the fire.

We found that the old-forest conditions associated with northern spotted owl habitat burned at lower severity despite having higher fuel loading than other forest types on the landscape. The microclimate and forest structure likely played a key role in lower fire severity in nesting/roosting habitat compared to other forest types. As succession progresses and canopy cover of shade-tolerant tree species increases, forests eventually gain old-growth characteristics and become less likely to burn because of higher relative humidity in soil and air, less heating of the forest floor due to shade, lower temperatures, lower wind speeds, and more compact litter layers (Countryman 1955, Chen et al. 1996, Kitzberger et al. 2012, Frey et al. 2016, Spies et al. 2018). In addition, as the herbaceous and shrub layer is reduced by shading from lower to mid-layer canopy trees, the connection between surface fuels and the canopy declines, despite possible increases in canopy layering (Halofsky et al. 2011, Odion et al. 2014). Alexander et al. (2006) found that in the Klamath-Siskiyou ecoregion, southern aspects tended to burn with greater severity, but exogenous factors also played an important role because areas with large trees burned less and had less fire damage than areas dominated by smaller trees. On the 2002 Biscuit Fire that burned near our study area, Thompson and Spies (2009) concluded that weather and pre-fire vegetation conditions were the primary determinants of crown damage. They found that forests with small-stature vegetation and areas of open tree canopies and dense shrubs experienced the highest levels of tree crown damage, while older, closed-canopy forests with high levels of large conifer cover were associated with the lowest levels of tree crown damage. The moisture content of air and soil in a forest affects the amount of fuel moisture, and thus the probability of ignition and burning temperature (Heyerdahl et al. 2001). In addition to the potential to mitigate negative effects of climate warming at local scales by creating refugia and enhancing biodiversity (Frey et al. 2016), we suggest that northern spotted owl nesting/roosting habitat also has the potential to function as fire refugia (i.e., areas with higher probability of escaping high-severity fire compared to other areas on landscape) in areas with mixed-severity fire regimes under most weather conditions. Thus, in these landscapes, management strategies to conserve old-growth characteristics may also reduce risk of high-severity wildfire (Bradley et al. 2016) and serve as buffer to negative effects of climate change (Betts et al. 2018).

Although it has long been recognized that older forests have lower flammability than other forest types (Countryman 1955), federal agencies are often criticized for not extensively managing old forests to reduce risk of high-severity fire (OFRI 2010). The perception is that forest succession leads to increased flammability with age

(Kitzberger et al. 2012, Duff et al. 2017). Where this view may be correct is in dry forests with historically very frequent fire-return intervals (<10 yr), and contemporary increased fuel continuity has resulted from fire exclusion and led to increased sizes of high-severity patches when fires burn under extreme weather (Reilly et al. 2017). In the driest forest types, fire exclusion converts open forests with grassy understories to dense forests with high fuel loads, and the increased fuel continuity can result in larger patches of high-severity fire than would have occurred historically. In other forest types, succession likely decreases risk of high-severity fire. Compared to older forest, younger forests have lower canopies and thinner barked trees that reduce resistance to fire, and thinned young forests can be susceptible to high mortality from fire unless surface fuels are treated with prescribed fire (Raymond and Peterson 2005). Thinned forests have more open conditions, which are associated with higher temperatures, lower relative humidity, higher wind speeds, and increasing fire intensity. Furthermore, live and dead fuels in young forest or thinned stands with dense saplings or shrub understory will be drier, making ignition and high heat more likely, and the rate of spread higher because of the relative lack of wind breaks provided by closed canopies with large trees.

Primarily as inputs to fire models that estimate likely fire behavior, fuel models involve typing forested stands according to fuel loading and are often used to explore or inform management directions because fuels are under the purview of forest managers (Deeming and Brown 1975, Anderson 1982, Bradshaw et al. 1983, Finney 2004, Scott and Burgan 2005, Andrews 2009). Suitable nesting/roosting habitat often falls in classes rated as highly burnable, with fast rates of fire spread, high flame lengths, and intense fire behavior (Anderson 1982). Thus, fire model results can show nesting/roosting habitat has higher burn probabilities and higher crown fire potential than adjacent areas (Ager et al. 2007, 2012). The results of this study as well as other recent studies show that these older forests in mixed-conifer forest environments are less susceptible to high-severity fire than other successional stages, even under high fire weather conditions and with short return intervals <15 yr (Donato et al. 2009). Running fire models for our study area based on conditions during the Douglas Complex and Big Windy Fires would be a worthwhile exercise to evaluate model predictions relative to the actual behavior of those fires. However, based on the findings of this study and many others (see review by Duff et al. 2017), we contend that fire models that continue to use fuel models that rate older forests with higher relative fire behavior will likely overestimate fire severity and inflate estimated loss of old forests in the Pacific Northwest. An alternative is to consider forest fuels in a more holistic manner and alternative age–flammability models (Kitzberger et al. 2012, Duff et al. 2017).

Intensive management (especially on timber industry lands) that results in reduced fuel loading does not always equate to less frequent or severe fire. Results by Charnley et al. (2017) in southcentral Oregon showed that private industry lands had more than three times the percentage area of open-canopy forest compared to U.S. Forest Service-managed lands that included thinning trees <53.3 cm diameter, prescribed fire, and no active management. Federal land management practices resulted in forests with more resilience to high-severity wildfire as opposed to management on private lands (Charnley et al. 2017). Furthermore, Zald and Dunn (2018) found that ownership patterns were the best predictor for high-severity fire in the Douglas Complex Fires, where federal lands, with primarily older forests in late-successional reserves, burned at lower severity than non-federal forests that were primarily private timber industry lands.

Gradual changes in temperature or precipitation patterns may have little effect until a disturbance-driven threshold is reached at which a large shift occurs that might be difficult or impossible to reverse (Scheffer and Carpenter 2003). Peterson (2002) described "ecological memory" and how previous patterns of disturbance can predispose an area to follow a certain disturbance pathway. For example, a landscape that experiences severe disturbance (e.g., high-severity fire, clear-cut logging, post-fire salvage logging) can be predisposed to high-severity fire in a mixed-severity fire regime (Thompson et al. 2007, Donato et al. 2009, Thompson and Spies 2009, Zald and Dunn 2018). High-severity wildfire can alter soil and successional pathways and potentially shift the system into an alternative stable state (Peterson 2002). A key component of overall ecosystem function and sustainability occurs belowground, and with high-severity fire, changes in the soil physical, chemical, and biological functions can be deleterious to the entire ecosystem caused by changes in successional rates and species composition (Neary et al. 1999). Conversely, low-severity fire effects on soil can promote herbaceous flora, increase plant diversity, increase available nutrients, and thin over-crowded forests, all of which can enhance healthy forest ecosystems (Neary et al. 1999). The time for recovery of belowground systems is a key driver of ecosystem processes and depends on burning intensity and on previous land-use practices. Soils are greatly altered and degraded in young intensively managed forest and post-salvage logged sites, which are more susceptible to repeat and short-interval high-severity wildfire, and these forests that experience multiple rapid successions of natural and human-derived disturbances may cross thresholds and be changed catastrophically (Lindenmayer and Noss 2006).

The Klamath-Siskiyou ecoregion is currently dominated by biodiverse temperate coniferous forest and may be near a tipping point toward an alternative stable state (shrub/hardwood chaparral) with extensive loss of conifer forest, dominance by deciduous trees and shrubs, and recurring early-seral and young forest conditions (Tepley et al. 2017, Serra-Diaz et al. 2018). The region has experienced short intervals between recent high-severity fires coupled with intensive timber management in this mixed-severity fire regime area, and the likelihood of further shortening of fire-return intervals with climate change (Davis et al. 2017). Even where climate is suitable to sustain dense mature forests, early-seral and non-forest conditions may perpetuate because of a cycle of short-interval repeat burning and timber harvest and have dramatic impacts on biodiversity and wildlife habitats (Lindenmayer et al. 2011, Tepley et al. 2017). Under this scenario, the persistence of old-forest associated species, including northern spotted owls, within the Klamath-Siskiyou ecoregion would be further threatened.

It was recognized early in the history of northern spotted owl conservation that fire would play a major role in determining the success of management plans (Agee and Edmunds 1992). The 2011 federal northern spotted owl recovery plan calls for increasing fire resiliency in dry forests with focus on active management outside of northern spotted owl core areas to meet project goals (USFWS 2011). For many dry forests in the western United States that historically experienced frequent, low- to moderate-severity fire regimes, prescribed fire and mechanical treatments have been effective at reducing surface fuel loads, forest structure, and potential fire severity (Stephens et al. 2009). In mixed-severity landscapes, the fire severity mosaic is highly variable and the effects of topography and climate are strong predictors for this regime, but forest conditions also are important and much less predictable and stable (Beaty and Taylor 2001), further complicating management decisions aimed at increasing fire resiliency of forests. Management actions employed in dry forest types to reduce wildfire risk may not work equivalently in mixed-severity regimes. Active management actions that include mechanical treatments degrade suitability of forests for nesting and roosting by northern spotted owls (Lesmeister et al. 2018) and may not always decrease risk of high-severity fire. Further, considering trends and forecasts for earlier spring snowmelt and longer fire seasons, climate change may exacerbate the effects of wildfire (Dale et al. 2001, Westerling et al. 2006), and thus the framed conundrum between northern spotted owl habitat and fire management in mixed-severity regimes. Our results indicate that older forest in late-successional reserves (i.e., northern spotted owl nesting/roosting habitat) with no active management can serve as a buffer to the effects of climate change and associated increase in wildfire occurrence. These multi-storied old forests in these environments enhance biodiversity and have the highest probability to persist through fire even in weather conditions associated with high fire activity.

Fuel-reduction treatments such as mechanical thinning can effectively reduce fire severity in the short term, but these treatments, by themselves, may not effectively mitigate long-term dynamics of fire behavior under severe weather conditions and may not restore the natural complexity of historical stand and landscape structure (Schoennagel et al. 2004). On the other hand, prescribed fire that mimics severity and return intervals of natural fire regimes in forests that historically experienced fire can result in landscapes that are both self-regulating and resilient to fire (Parks et al. 2015). Prescribed fire is generally considered to be the most effective way to reduce the likelihood of high-severity fire in combination with mechanical treatments (Stephens et al. 2009). The 2013 Rim Fire in the Sierra Nevada, California, USA, burned with low severity in areas previously treated with prescribed fires, suggesting that prescribed burning was an effective management tool to reduce fire severity (Harris and Taylor 2017). Many fire-prone forests will require active management to restore ecosystem function, but no single prescription will be appropriate for all areas and, in some portions of the forests, minimal maintenance may be more sustainable in the long term (Noss et al. 2006). Within the Klamath-Siskiyou ecoregion, flexible and multi-scale land management approaches that promote diversity of forest types will likely enhance conservation of a range of species requiring different forest conditions for long-term persistence. An integral component of these approaches could include resistance strategies (i.e., no active management) to protect high-value older forest (Millar et al. 2007) and prescribed fire to promote and maintain a mix of forest conditions in this landscape characterized by mixed-ownership and mixed-severity fire regime. Ultimately, spatial heterogeneity that includes the buffering effects of northern spotted owl nesting/roosting habitat may serve as a stabilizing mechanism to climate change and reduce tendency toward large-scale catastrophic regime shifts.

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SUPPORTING INFORMATION

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From the archive

The disquieting theories of modern physics, and a stealthy attack from an inconspicuous fish.

100 years ago

The problems of physics are manifold, and tend to increase in number and in difficulty. Fifty years ago there was a general feeling that we had only to proceed steadily in the application of familiar dynamical principles to explain all the phenomena of inanimate nature … How different is the position to-day! … The outstanding problems of our time, that of radiation on one hand and of atomic structure on the other, have been at least partially solved by the electro-magnetic theory of Clerk Maxwell and the electron theory which owes so much to his successors at the Cavendish Laboratory. But the still greater problem of relating these theories satisfactorily to one another and to the disquieting results embodied in the modern theories of quanta and relativity still awaits the revealing power of the master mind.

From *Nature* 4 August 1923

150 years ago

The John Dorée … although of shy and retiring habits, has already yielded many points of interest in connection with its life history. The ordinary position assumed by this fish is the neighbourhood of the some projecting rock near the bottom of its tank, and … it is only when on rare occasions it rises high in the water, that the beautiful mechanism that guides its movements can be appreciated. It may then be seen that the only organs called into action are the narrow and delicate membranes of the posterior dorsal and anal fins, each of which vibrates in a similar manner to the single dorsal of the pipefish; the long filamentous first dorsal, pectorals, ventrals, and caudal fins meanwhile remaining perfectly motionless. Thus this wary fish, with an almost imperceptible action, silently and stealthily advances upon its intended prey, engulphing it in its cavernous mouth almost before the hapless victim is aware of its enemy's approach.

From *Nature* 31 July 1873

Environmental science

A call to reduce the carbon costs of forest harvest

William R. Moomaw & Beverly E. Law

Economic modelling of the global carbon cost of harvesting wood from forests shows a much higher annual cost than that estimated by other models, highlighting a major opportunity for reducing emissions by limiting wood harvests. **See p.110**

Forests accumulate and store vast amounts of carbon dioxide from the atmosphere and protect biodiversity[1], giving them a defining role in controlling the global average temperature. By contrast, human activity typically increases carbon emissions to the atmosphere and diminishes species populations and diversity. Nowhere is this distinction more obvious than in the harvesting of wood from forests, but the carbon cost of this practice has been overlooked – until now. On page 110, Peng *et al.*[2] report the true carbon cost of wood harvests, which have reduced more carbon storage in vegetation and soils than any other practice except agriculture[3,4].

The authors estimate that emissions from wood harvests will add 3.5 billion to 4.2 billion tonnes of CO_2 to the atmosphere each year between 2010 and 2050. This estimate approaches the increase in emissions expected to result from land-use change as a result of the expansion of agriculture. To determine forest carbon emissions by tracking the life cycle of harvested wood, it is essential to quantify the carbon stocks in forest ecosystems and to understand how they change with harvests. It is also crucial to quantify emissions associated with the decay and combustion of residues left at the harvest site, and the decay of wood products in landfill, as well as emissions from the combustion of harvest residues at timber mills[5].

> **"Converting mature forests to young forests results in a considerable loss of carbon stocks."**

In practice, however, many people estimate carbon cost using an approach known as net accounting, which offsets carbon emissions from one source to another. For example, fossil-fuel emissions are commonly offset by the carbon sink provided by forest ecosystems. Forest-harvest emissions are similarly offset by crediting the growth of forests in other locations. But net accounting of forest stocks has been shown to undervalue the importance of actual increases in these stocks[6]. Peng *et al.* describe several forest carbon-offset systems that have been used that allow forest-harvest emissions to go uncounted.

The authors make the essential point that carbon costs from harvested forests are substantially underestimated by the common practice of counting offsets from forests growing elsewhere. The authors consider different scenarios for the future supply and demand of wood, and use them to establish a carbon-cost accounting system that discounts the value of future carbon emissions and removals by using a common rate. In this scheme, a tonne of carbon emitted in one year is valued 4% higher than the same amount emitted the following year – a discount designed to account for the future carbon value of recovering harvested forests.

However, the authors do not consider several findings[7–9] that older forests continue to accumulate substantial amounts of carbon. Indeed, in mature forests that contain trees of different ages, the largest trees hold a disproportionately large amount of the carbon: a 2018 survey of 48 forests found that the largest 1% of trees held half the above-ground carbon[10].

Peng *et al.* argue that harvested forests regain lost carbon quickly because they grow faster than forests that have not been harvested. However, this doesn't affect the outcome. Converting mature forests to young forests results in a considerable loss of carbon stocks through harvesting, even when carbon storage in wood products is included, as the authors make clear, and future carbon stocks will always be less than those retained if no harvest occurs. Modelling has shown previously that the density of carbon expected to be stored in a mature unharvested forest is much higher than that in a mature harvested forest 120 years after harvest – even when the carbon in wood products is combined with the carbon storage after harvest[8].

Wood harvests are increasingly used as a

Figure 1 | The felling of giant ancient cedars in the Caycuse region in western Canada.

TJ WATT/ANCIENT FOREST ALLIANCE

source of bioenergy, for electricity and for community and large commercial heating systems (for example, Drax power station, the largest in the United Kingdom, sources 69% of its wood fibre in the United States and 11% in western Canada; go.nature.com/3ptahnk). Burning wood for both of these uses is often mistakenly claimed to be carbon neutral. In 2020, global bioenergy emissions for heat and electricity generation were about 1.7 billion tonnes of CO_2, which is 40–50% of the projected annual emissions from global wood consumption between 2010 and 2050 (refs 2, 11, 12). It is not clear whether all modern bioenergy emissions are accounted for in global estimates of carbon emissions.

In 2014, the Intergovernmental Panel on Climate Change (IPCC) found that the perception that bioenergy is carbon neutral was based on a misinterpretation of the guidelines for how greenhouse-gas emissions are calculated[13]. Many European countries import wood pellets from North America and say that they generate zero emissions from burning them because the emissions occur in a different location from where the wood was harvested. One of the authors of the paper by Peng *et al.* identified this loophole in 2009 (ref. 14). Yet several calls from scientists to fix this carbon-accounting problem have been ignored. Instead, a massive and growing industrial harvest, along with increasing numbers of wildfires, has turned Canada's managed forests, most of which are in the west of the country (Fig. 1), from a net sink to a net source of CO_2 emissions[15].

To ensure that reduced harvests and increased forest growth lower the carbon cost of forests, there must be carbon-management practices and accounting rules that lead to substantial carbon accumulation and storage. To implement an effective policy for reducing forest harvests, existing carbon stocks, as well as their annual change and harvest-related emissions, must be accurately measured, verified and reported. The current system of national self-reporting has proved inadequate and would be more reliable if replaced by an independent scientific body.

Fewer harvests would mean substantially less direct CO_2 emissions to the atmosphere. Reduced harvesting would also enable 'proforestation', a term used to describe the practice of leaving forests to achieve their potential for carbon-stock accumulation without harvest. Proforestation would remove more CO_2 from the atmosphere than would reforestation or afforestation (the practice of planting trees where none grew previously)[16].

The sixth assessment report from the IPCC finds that protecting natural-forest ecosystems is a priority for reducing greenhouse-gas emissions[17]. Peng *et al.* would no doubt agree, but they are correct in surmising that this strategy remains underappreciated. There is hope, however, that the authors' impressive study will turn this trend around and increase awareness of the enormous potential for reducing emissions by limiting forest harvests.

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Using ecosystem integrity to maximize climate mitigation and minimize risk in international forest policy

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Several key international policy frameworks involve forests, including the Paris Agreement on Climate Change and the Convention on Biological Diversity (CBD). However, rules and guidelines that treat forest types equally regardless of their ecosystem integrity and risk profiles in terms of forest and carbon loss limit policy effectiveness and can facilitate forest degradation. Here we assess the potential for using a framework of ecosystem integrity to guide policy goals. We review the theory and present a conceptual framework, compare elements of integrity between primary and human-modified forests, and discuss the policy and management implications. We find that primary forests consistently have higher levels of ecosystem integrity and lower risk profiles than human-modified forests. This underscores the need to protect primary forests, develop consistent large-scale data products to identify high-integrity forests, and operationalize a framework of ecosystem integrity. Doing so will optimize long-term carbon storage and the provision of other ecosystem services, and can help guide evolving forest policy at the nexus of the biodiversity and climate crises.

KEYWORDS

Paris Agreement, primary forest, carbon, forest degradation, deforestation

Introduction

Forest ecosystems are central to international agreements and frameworks that support and set policy agendas, including the United Nations (UN) Framework Convention on Climate Change (UNFCCC), Convention on Biological Diversity (CBD), Sustainable Development Goals (SDGs), and Convention to Combat Desertification (UNCCD). Forests and their ecosystem services provide critical data to inform global environmental assessments such as the Global Forest Resource Assessments (FRAs) of the UN Food and Agriculture Organization (FAO), the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), the System of Environmental Economic Accounting–Ecosystem Accounting (SEEA-EA), and the World Bank's reports on the Changing Wealth of Nations (Lange et al., 2018). The mitigation significance of forests is recognized in Article 5 of the Paris Agreement. Given their mitigation value, updating forest management practices to reduce emissions and increase withdrawals from the atmosphere should be included in many countries' Nationally Determined Contributions (NDCs; Forsell et al., 2016; Grassi et al., 2017; Roe et al., 2019). Forestry practices have the potential to provide a majority fraction of the Agriculture, Forestry, and Other Land Use (AFOLU) sector's contributions to climate mitigation, which may represent up to one-third of net emission reductions needed to limit warming below 1.5–2°C above pre-industrial levels (Federici et al., 2017; Grassi et al., 2017; Griscom et al., 2017; Roe et al., 2019). The current emissions gap between NDCs and what is required to limit warming to 1.5 or 2°C (UNEP, 2019) means that the role of forests may be even greater; for example, forests are referenced heavily in the Intergovernmental Panel on Climate Change (IPCC) special report on 1.5°C in the context of negative emissions (Dooley et al., 2018; IPCC, 2018).

However, given the finite area of available land and the many ecosystem services they provide, there are often conflicting goals for the management of forests in national and international policy contexts, resulting in incoherent policies and policy objectives (Kalaba et al., 2014; Koff et al., 2016; Tegegne et al., 2018; Timko et al., 2018). For example, many of the UN SDGs focused on promoting economic development are at odds with conserving forests and biodiversity (Ibisch et al., 2016). Unclear and inconsistent definitions and accounting rules mean that forest mitigation measures can have a range of results from large-scale protection that preserves carbon storage, sequestration, and ecosystem services, to perverse outcomes with net carbon loss, degraded ecosystems, and negative impacts on other policy goals (Mackey et al., 2013). For example, bioenergy with carbon capture and storage (BECCS) is used in the majority of current global socioeconomic model scenarios to stay below 1.5–2°C of warming (Roe et al., 2019). At these scales, BECCS will require the conversion of vast quantities of native forests into tree plantations or short-rotation forests (Fuss et al., 2014; Creutzig et al., 2015; Smith et al., 2016; IPCC, 2018). Increased bioenergy use is currently resulting in forest degradation and deforestation that will generate net carbon emissions for decades or longer (Birdsey et al., 2018; Booth, 2018; Sterman et al., 2022). Part of the problem is that forest cover and types are largely seen as fungible within the UNFCCC guidelines (UNFCCC, 2002), with no criteria for forest condition or carbon longevity (Ajani et al., 2013; Hansen A. J. et al., 2020; Keith et al., 2021).

From a carbon perspective, "risk of loss" of the stock is of central importance. The risk of loss from disturbances means that some land-based carbon activities will not provide long-term protection of carbon from release into the atmosphere (e.g., Anderegg et al., 2020). This risk is a primary reason that forest-based solutions are often not considered as reliable ways to reduce net emissions and hence are not prioritized as mitigation activities (Grassi et al., 2017). Yet little consideration has been given to differentiating forest types and management schemes based on their "risk of loss" profiles. The Paris Agreement mentions criteria for mitigation that speak to risk, such as equity, sustainability, and integrity, but as of yet there is little guidance on implementation.

The concept of "ecosystem integrity," or related "ecological integrity," has a long history in theoretical and applied ecology (e.g., Kay, 1991; Tierney et al., 2009; Wurtzebach and Schultz, 2016) and is explicitly referenced [e.g., Paris Agreement, CBD post-2020 Global Biodiversity Framework (Convention on Biological Diversity [CBD], 2021), IPCC Working Group II (IPCC, 2022)] or implied in international agreements and national-level legislation and agency directives (e.g., Australian Government, 1999). By providing a holistic view of ecosystem structure, function, composition, and adaptive capacity, the objective of maximizing ecosystem integrity may have the potential to minimize risk of carbon loss and maximize the ecosystem services provided by forests, thereby facilitating greater policy coherence across sectors (Koff et al., 2016; Dooley et al., 2018; Barber et al., 2020). However, the concept is not prioritized in international policy nor operationalized in most national forest policies, thus falling well short of its potential. There are no specific actions or supporting mechanisms for ecosystem integrity in the Paris Agreement, and parties have not articulated how they will identify and protect high-integrity ecosystems. Instead of representing a guiding framework, ecosystem integrity is largely viewed as a potential co-benefit (Bryan et al., 2016; Funk et al., 2019). Particularly important is providing a definition and framework for ecosystem integrity that the CBD (though the Global Biodiversity Framework) and the UNFCCC (through the Global Stocktake) can utilize to achieve their biodiversity and climate mitigation objectives.

Here we review the potential for a framework of ecosystem integrity to minimize risk in forest-based mitigation policies and maximize ecosystem service co-benefits. We first discuss the theory of ecosystem integrity and provide a working conceptual framework. We then compare important elements of ecosystem integrity between primary and human-modified forests, with a focus on elements most relevant for carbon mitigation including risk profiles. Finally, we discuss the policy and management implications of this comparative analysis. By drawing on ecological theory and several sub-disciplines within ecology, we integrate knowledge into a coherent framework of ecosystem integrity (**Figure 1**) that can be used to guide both forest policy at the international level as well as implementation in the form of land use decisions, metrics, and priorities at the national and jurisdictional levels. Our review draws upon decades of evolving forest policy and published literature, including but not limited to peer-reviewed articles, as well as engagement with stakeholders, practitioners, policy makers, and forest ecologists.

Framework for forest ecosystem integrity

Definition

Many definitions of ecosystem integrity exist because ecosystem integrity is not a simple absolute physical property but rather a multidimensional and scale-dependent emergent phenomenon that encompasses important system components and their interactions. The concept has received considerable attention over the past several decades because of the human benefits derived from natural processes and ecosystem states. As noted by Muller et al. (2000), "ecosystem integrity turns out to be the ecological branch of sustainability."

Here we adopt and build upon the general framework originally provided by Kay (1991), whereby ecosystem integrity *integrates different characteristics of an ecosystem that collectively describe its ability to achieve and maintain its optimum operating state, given the prevailing environmental drivers and perturbations, and continue its processes of self-organization and regeneration (i.e., autopoiesis)*. One of the main theoretical divides about ecosystem integrity relates to differentiating compositional (e.g., species richness, genetic diversity, or presence of threatened species), structural (e.g., vegetation density, biomass, food chains, and trophic levels) or functional (e.g., productivity, energy flows, and nutrient cycling) aspects of integrity (De Leo and Levin, 1997; Pimentel et al., 2013; Roche and Campagne, 2017). We suggest these are largely inseparable given the fundamental importance of structural and compositional elements in supporting functional forest ecosystem integrity and the many interdependencies among composition, structure, and function. In practice, available data and resources will determine what can be measured at a particular spatial and temporal scale. Because ecosystem integrity includes the provision of ecosystem services for human benefit, its evaluation typically includes a human dimension (Kay, 1991; De Leo and Levin, 1997; Kay and Regier, 2000; Dorren et al., 2004; Roche and Campagne, 2017).

Components of ecosystem integrity

Based on decades of theoretical and applied studies, we provide a framework for understanding the components of forest ecosystem integrity, their drivers, and their inter-linkages (**Figure 1**). It is important to note that all elements of ecosystem integrity are affected by the prevailing environmental and site characteristics of a given forested location, which must be accounted for when comparing specific locations in space and/or time.

Foundational elements

Forest ecosystem integrity is based on physiological structures that efficiently use and dissipate energy (**Figure 1**). These dissipative structures, or "ecological orientors" (Muller et al., 2000), generate a gradient of energy degradation *via* metabolic reactions that create and maintain themselves (i.e., self-organization). Progressively accumulated exergy (i.e., available energy) becomes stored emergy (i.e., all the energy used to generate a product or service) (Campbell, 2000; Kay and Regier, 2000; Muller et al., 2000). Over the course of evolution, community assembly, and forest succession, this process generates optimized (generally high but not too high; Hengeveld, 1989; May, 2001) ecosystem complexity and distance from thermodynamic equilibrium (Odum, 1969; Kay, 1991; Holling, 1992; Campbell, 2000; Muller et al., 2000), with associated levels of structural complexity, functional diversity, and niche complementarity (Tilman, 1996; Tilman and Lehman, 2001; Thompson et al., 2009). Ecosystem processes that sustain and regulate this self-organizing system, such as productivity, evapotranspiration, reproduction cycles, and nutrient cycling and retention, are optimized in the process (Muller et al., 2000; Dorren et al., 2004; Migliavacca et al., 2021). The resulting forest is a non-linear, self-organizing, holarchic and open system, with reciprocal power relationships between levels (Kay and Regier, 2000).

A critical property of ecosystem integrity that is difficult to assess from structural or compositional elements alone is stability. Following Grimm and Wissel (1997), stability is comprised of resistance (or constancy), resilience, and persistence, which collectively represent an ecosystem's ability to resist or be resilient to change at both short and long time scales (Kay, 1991, 1993; Regier, 1993; Muller, 1998; Kay and Regier, 2000; Andreasen et al., 2001; Parrish et al., 2003). In the case of forest ecosystem integrity, primary drivers of change (exposure) include human land use and other human pressures, and climate change including extreme weather events and increasing disturbances. Resistance indicates a forest's ability to maintain stability *via* dynamic equilibrium within defined ecosystem

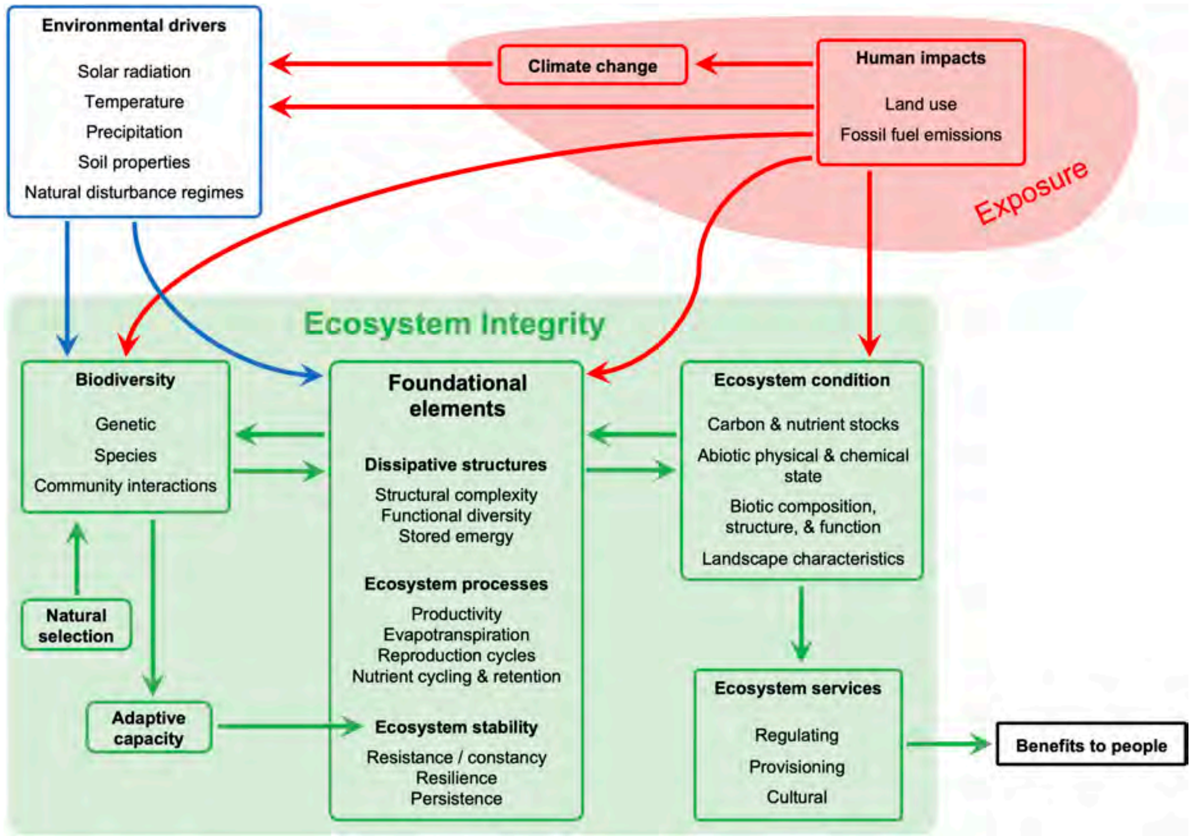

FIGURE 1

Conceptual framework of ecosystem integrity. Integrity is based on foundational elements including dissipative structures, ecosystem processes, and ecosystem stability. These are underpinned by biodiversity, natural selection, and adaptive capacity, and in turn generate a given ecosystem condition and benefits to people. Ecosystem integrity is impacted by environmental drivers and human impacts, including land use and climate change.

bounds (Hughes et al., 2002; Loreau et al., 2002) in response to these drivers. Forest resistance is conferred by negative feedbacks and buffers, for example stable microhabitats in forest interiors and functional redundancy across species. Resilience indicates the ability to return to optimal operating conditions after a state-altering perturbation (Holling, 1973; Kay, 1991; Kay and Regier, 2000; Muller et al., 2000; Thompson et al., 2009). The resulting ecosystem state can be somewhat altered (i.e., "ecological resilience" as opposed to "engineering resilience"), but when viewed over an appropriate time span, a resilient forest is able to maintain its "identity" in terms of taxonomic composition, structure, ecological functions, and process rates–and hence exhibit persistence (Thompson et al., 2009). Forest resilience is generally conferred by regenerative capacity *via* biological legacies (Franklin et al., 2000; Lindenmayer et al., 2019). These components of stability are supported by an ecosystem's adaptive capacity, or the capacity for adaptive change in response to new conditions (Angeler et al., 2019). For example, genetic diversity, species diversity, and phenotypic plasticity allow for varied and time-evolving expression of adaptive traits and species within an ecosystem in response to changing environmental conditions, disturbances, or other pressures (Savolainen et al., 2007; Reed et al., 2011; Rogers et al., 2017). Hence, adaptive capacity is supported by biodiversity (**Figure 1**).

Biodiversity

These foundational elements of integrity are derivatives of the underlying biodiversity of a forest ecosystem, including diversity at the genetic, species, and community levels (**Figure 1**). A wealth of literature provides evidence that biodiversity supports net primary productivity (Chapin et al., 1997; Diaz and Cabido, 2001; Hooper et al., 2005; Thompson et al., 2009; Tilman et al., 2014; Liang et al., 2016; Duffy et al., 2017; de Souza et al., 2019; Matos et al., 2020), adaptation (Steffen et al., 2015; King et al., 2019), resistance (Pimm, 1984; Walker, 1995; Ives et al., 1999; Lehman and Tilman, 2000; McCann, 2000; Loreau et al., 2002; Dorren et al., 2004; Hooper et al., 2005; Thompson et al., 2009; Hautier et al., 2015), resilience (Peterson et al., 1998; Loreau et al., 2001;

Hooper et al., 2005; Drever et al., 2006; Thompson et al., 2009; Ajani et al., 2013; Oliver et al., 2015; King et al., 2019), functional diversity (Cadotte et al., 2011; Levin, 2013; Karadimou et al., 2016), and overall ecosystem functioning (e.g., Lawton, 1997; Tilman, 1997; Hooper et al., 2005; Cardinale et al., 2012; Watson et al., 2018; King et al., 2019). These relationships exist because natural selection yields the characteristic biodiversity and phenotypic plasticity best suited to prevailing environmental conditions, including fluctuating resource inputs, extreme events, periods of stress, and natural disturbances. Specific mechanisms include biotic control of grazing, population density, and nutrient cycling; niche selection and complementarity; biotic and abiotic facilitation; and functional redundancy (i.e., the “insurance hypothesis”) (e.g., Naeem et al., 1995; Tilman, 1996; Tilman et al., 1997; Yachi and Loreau, 1999; Loreau, 2000; Tilman and Lehman, 2001; Pretzsch, 2005; Scherer-Lorenzen and Schulze, 2005; Jactel and Brockerhoff, 2007; Thompson et al., 2009; Hantsch et al., 2014; Wright et al., 2017; Liu et al., 2018).

Ecosystem condition

The foundational elements of ecosystem integrity form the basis for assessing ecosystem condition (Keith et al., 2020), specifically in the context of the System of Environmental-Economic Accounting (Committee of Experts on Environmental-Economic Accounting, 2021). Ecosystem condition is defined as “the quality of an ecosystem that may reflect multiple values, measured in terms of its abiotic and biotic characteristics across a range of temporal and spatial scales” (Keith et al., 2020). Ecosystem condition is measured in terms of variables that reflect the state, processes, and changes in the ecosystem, including (i) carbon and nutrient stocks, (ii) abiotic physical and chemical states such as water quantity and quality; (iii) biotic composition, structure, and function; and (iv) landscape diversity and connectivity. Indicators of condition are derived when variables are transformed by assessment against a reference condition. For a given biome and prevailing environmental conditions, these state variables are optimized by the foundational elements of ecosystem integrity and biodiversity (Phillips et al., 1994; Thompson et al., 2009; Roche and Campagne, 2017; Di Marco et al., 2018; Liu et al., 2018).

Ecosystem services

Characteristics of ecosystem condition that relate to the supply of ecosystem services represent an instrumental anthropocentric dimension. Specific ecosystem services can be linked to characteristics of ecosystem condition, and condition indicators can be associated with multiple services (Keith et al., 2020). Ecosystem services can be broadly categorized as regulating, provisioning, and cultural services (Millennium Ecosystem Assessment, 2005; Kandziora et al., 2013; IPBES, 2019; Committee of Experts on Environmental-Economic Accounting, 2021). Regulating services include clean and regulated water flow, air quality, pest and pathogen containment, erosion control, nutrient regulation, resistance and resilience to natural hazards, waste regulation, carbon sequestration and storage, and climate regulation from local to global scales. Provisioning services include the animals, plants, and minerals used for food, medicine, energy, and infrastructure. Cultural services include customary values, ecotourism and nature-based recreation, scientific research, and education.

The concept of ecosystem integrity is useful because it integrates across many properties of forest ecosystems, and thereby optimizes values useful to humans and other organisms. In the words of Koff et al. (2016), “ecosystem integrity is a scientific paradigm that fits the political needs of the present global development agenda focused on complex human-environmental interactions.” The concept is holistic and can be adapted to local, national, or international contexts. At jurisdictional levels, the related concepts of “ecological integrity” and “biological integrity” have been used operationally to provide benchmarks for natural resource management (Karr, 1996; Harwell et al., 1999; Campbell, 2000; Muller et al., 2000; Parrish et al., 2003; Tierney et al., 2009; Wurtzebach and Schultz, 2016; Roche and Campagne, 2017). However, as noted above, the international policy community has yet to implement these terms. This is important because ecosystem integrity may be directly linked to forest and carbon risk profiles that, if understood and prioritized, could greatly aid our ability to utilize forests for mitigation and adaptation.

Comparison of ecosystem integrity between forest types

Here, we compare components of ecosystem integrity most relevant for international policy across commonly recognized broad categories of forest types, focusing on primary forests and forests with significant levels of human modification and pressure. We focus on components of ecosystem integrity most pertinent to forest-based climate mitigation, including forest risk profiles as governed by exposure and stability as well as carbon stocks and fluxes. As noted previously, direct comparisons between forest types must account for environmental and site drivers, including the prevailing biome (e.g., tropical, temperate, or boreal) and heterogeneity within as determined by climate, soils, hydrology, and natural disturbance regimes.

Following Kormos et al. (2018), Food and Agriculture Organization of the United Nations [FAO] (2020), and IUCN (2020), primary forests are defined as: (i) largely undisturbed by industrial-scale land uses such as logging, mining, hydroelectric development, and road construction; (ii) established and regenerated by natural biological, ecological, and evolutionary processes; (iii) including the full range of successional stages at a landscape level from pioneer, secondary growth, and old-growth forest stands; and (iv) with the vegetation structure, community networks, and taxonomic composition principally reflecting natural processes including natural disturbance regimes. Primary forests can therefore be distinguished from naturally regenerating forests that are subject to conventional forestry management for commodity production (Puettmann et al., 2015), as well as planted forests, including plantations. For our purposes, primary forest therefore encompasses a range of commonly recognized forest descriptors including intact, virgin, ecologically mature, and old growth forests (Buchwald, 2005; Mackey et al., 2013; DellaSala et al., 2022b).

Foundational elements of ecosystem integrity

Comparison of dissipative structures

In this section we focus on structural complexity because of its importance for carbon stocks. Other components of dissipative structures (**Figure 1**) will be highlighted for their role in supporting ecosystem integrity in following sections (including functional diversity as it relates to biodiversity in the section "Biodiversity," and stored emergy as manifested in biomass and carbon stocks in section "Ecosystem condition"). High-integrity forests that have been allowed time to respond to their emergy signature develop a set of relatively complex ecosystem structures (Campbell, 2000). Canopy structure is particularly influential for other elements of ecosystem integrity such as microclimate, runoff, nutrient cycling, and biodiversity (Hobbie, 1992; Parker, 1995; Didham and Lawton, 1999; Siitonen, 2001; Asner et al., 2010; Goetz et al., 2010; Hansen et al., 2014). Primary tropical forests in particular develop tall, multi-story dense canopies with large variations in plant size and emergent canopy dominants (Kricher, 2011; Hansen A. J. et al., 2020). Temperate forests also develop complex forest canopies as they age, which is associated with high levels of biodiversity and carbon storage (DellaSala et al., 2022b).

Canopy height, in turn, is positively related to aboveground biomass and carbon storage. For example, in Brazil, Democratic Republic of the Congo, and Indonesia, primary forests were 38–59% taller and contained 70–148% more aboveground biomass than other dense tree cover types, including degraded forests, secondary regrowth, and tree plantations (Turubanova et al., 2018). When felling the largest trees or clear-cutting entire stands, logging decreases canopy height, homogenizes forest canopies, and reduces structural complexity (Pfeifer et al., 2016; Rappaport et al., 2018; Bourgoin et al., 2020), which can take centuries to recover. Structural complexity also relates to non-living forest structures, such as dead wood, that provide supporting functions including nutrient cycling, soil formation, and habitat for myriad species (Janisch and Harmon, 2002; Millennium Ecosystem Assessment, 2005; Gamfeldt et al., 2013). When directly compared, primary forests consistently contain a greater volume and diversity of dead wood than forests managed for commodity production (e.g., Guby and Dobbertin, 1996; Siitonen et al., 2000; Siitonen, 2001; Debeljak, 2006).

Comparison of ecosystem processes

Here we focus on ecosystem productivity given its importance for climate mitigation, but note that other ecosystem processes will be highlighted in following sections (evapotranspiration as it relates to drought risk in section "Comparison of risks from drought," reproduction cycles as they relate to regeneration in section "Comparison of regenerative capacity," and nutrient cycling and retention as it relates to nutrient stocks in section "Comparison of ecosystem condition"). Differences in ecosystem productivity and carbon fluxes among forest seral stages have been the subject of much debate. One viewpoint is that forests containing younger trees are more productive, with both higher net primary productivity (NPP, including photosynthesis and autotrophic respiration) and net ecosystem productivity (NEP, also including heterotrophic respiration) than ecologically mature forests (e.g., Ryan et al., 1997; Simard et al., 2007; Goulden et al., 2010). This view has often justified the conversion of primary forests into regrowth forests. While it is true that secondary forests often have higher rates of photosynthesis, this is not always the case, particularly when accounting for the impacts of higher species richness in older primary forests (Liu et al., 2018) and the entire age profile of timber rotations, including times with bare soil and young trees. A wealth of evidence clearly shows that old-growth forests continue to sequester carbon in significant quantities in aboveground biomass, dead wood, litter, and soil organic matter (Phillips et al., 1998; Zhao and Zhou, 2006; Luyssaert et al., 2008; Lewis et al., 2009; Thompson et al., 2013; Gatti et al., 2014; Grace et al., 2014; McGarvey et al., 2015; Schimel et al., 2015; Lacroix et al., 2016; Baccini et al., 2017; Phillips and Brienen, 2017; Qie et al., 2017; Lafleur et al., 2018; Mitchard, 2018). This is why Pugh et al. (2019) found that old-growth forests (defined in that study as > 140 years) cover roughly 39% of global forest area and contribute 40% of the current global forest carbon sink, which in turn represents roughly two-thirds of the terrestrial carbon sink (Friedlingstein et al., 2019).

More importantly, when comparing these CO_2 fluxes in the context of mitigation actions, the entire life cycle of management and disturbance must be taken into account. From a carbon balance perspective, converting primary forests into young forests logged for biomass energy, wood supply, or other uses does not offset the original conversion emissions for many decades to centuries (Cherubini et al., 2011; Holtsmark, 2012; Mitchell et al., 2012; Keith et al., 2015; Birdsey et al., 2018; Hudiburg et al., 2019; Malcolm et al., 2020), creating a large carbon debt on policy-relevant timescales (generally years to 1–3 decades). Hence the size, longevity, and stability of accumulated forest carbon stocks, including in the soils, are important mitigation metrics in addition to the rate of annual sequestration (Mackey et al., 2013; Keith et al., 2021).

Stability and risk profiles

Ecosystem stability is comprised of resistance, resilience, and longer-term persistence (**Figure 1**). Combined with exposure to external perturbations, properties of ecosystem stability provide critical information for risk assessments. Risk assessments are undertaken and utilized in a wide variety of scientific and operational contexts (Fussel and Klein, 2006; Glick et al., 2011; Oppenheimer et al., 2014; Rogers et al., 2017), and are critically important to ensure mitigation actions result in long-term carbon storage. Nevertheless, risk assessments are currently either not undertaken or done so in mostly rudimentary and incomplete ways for forest-based carbon mitigation (Mignone et al., 2009; Ajani et al., 2013; Anderegg et al., 2020). Here we focus on the risk of a forest ecosystem experiencing a state-altering disturbance that results in carbon loss to the atmosphere.

Comparison of risks from wildfire

Wildfires are major natural disturbances in temperate and boreal forest ecosystems, although historically rare in tropical wet forests unless caused by humans (Randerson et al., 2012; Archibald et al., 2013; Giglio et al., 2013; Andela et al., 2017). The area burned by wildfire has been increasing in high-canopy cover forests globally over the past 20 years (Andela et al., 2017), and human-caused fires are a major driver of the loss of intact forest landscapes (Potapov et al., 2017). Extreme fire weather conditions have increased in most forests globally over the last half-century (Jolly et al., 2015; Jain et al., 2017; Dowdy, 2018), and wildfires are projected to become more widespread and intense due to climate change (Ward et al., 2012; Flannigan et al., 2013; Abatzoglou et al., 2019; Dowdy et al., 2019; Rogers et al., 2020). Humans have increased forest fire risk by augmenting forest fuels through active management (DellaSala et al., 2022a) and by increasing the number and sources of ignition (Balch et al., 2017). The majority of documented megafires globally have been started by humans under extreme fire weather conditions (Ferreira-Leite et al., 2015; Bowman et al., 2017).

A large body of literature shows that forests managed for commodity production, degraded, or disturbed forests are generally more susceptible to fires because of drier microclimates and fuels, higher land surface temperatures that promote air movement between forests and neighboring open areas, and human ignitions due to access and proximity, particularly in the tropics (e.g., Uhl and Kauffman, 1990; Holdsworth and Uhl, 1997; Cochrane et al., 1999; Laurance and Williamson, 2001; Siegert et al., 2001; Donato et al., 2006; Lindenmayer et al., 2009, 2011; Brando et al., 2014; DellaSala et al., 2022a). Although fires are a natural disturbance agent throughout most boreal forests (Viereck, 1973; Payette, 1992; Gromtsev, 2002; Soja et al., 2007; Rogers et al., 2015), fire frequency in boreal forests increases in proximity to human land use due to fuel drying, human access, and forestry practices such as leaving slash on site, particularly in Siberia (Kovacs et al., 2004; Achard et al., 2008; Ponomarev, 2008; Laflamme, 2020; Terrail et al., 2020; Shvetsov et al., 2021).

In many forest systems, fires in previously logged or managed landscapes can be more intense/severe, emit more carbon to the atmosphere, and take longer to recover than fires in ecologically mature or primary forests due to increased fuel availability, lower fuel moisture, and dense secondary forests that carry crown fires and are susceptible to extensive tree mortality (Odion et al., 2004; Stone et al., 2004; Thompson et al., 2007; Lindenmayer et al., 2009, 2011; Price and Bradstock, 2012; Kukavskaya et al., 2013; Taylor et al., 2014; Bradley et al., 2016; Dieleman et al., 2020; De Faria et al., 2021; Landi et al., 2021). In general, larger and older trees have a greater chance of surviving fires due to thicker bark and lower relative scorch height (Laurance and Williamson, 2001; Lindenmayer et al., 2019). Increased fuel availability in secondary forests can also facilitate fire spread (Lindenmayer et al., 2011). Positive feedbacks between fires and secondary vegetation can lead to permanent forest loss, i.e. "landscape traps," at the warm / dry edge of forest ranges (Payette and Delwaide, 2003; Hirota et al., 2011; Lindenmayer et al., 2011; Staver et al., 2011; Brando et al., 2014; Kukavskaya et al., 2016; Lindenmayer and Sato, 2018). Primary forests are generally more resistant to fire because of higher humidity and fuel moisture, the presence of understory species such as ferns and mosses that limit light penetration to the forest floor and increase water retention, and much less human access (Ough, 2001; Lindenmayer et al., 2009; Taylor et al., 2014; Zylstra, 2018; Funk et al., 2019).

Comparison of risks from drought

Severe droughts represent 60–90% of climate extremes impacting gross primary productivity in the past 30 years (Zscheischler et al., 2014), are a major driver of tree mortality and forest die-off (Allen et al., 2010, 2015; Anderegg et al., 2013; McDowell and Allen, 2015; McDowell et al., 2016; Rogers et al., 2018), and are expected to increase with future climate change (Cook et al., 2014; Trenberth et al., 2014; Yi et al., 2014; Xu et al., 2019; Zhou et al., 2019; De Faria et al., 2021). A large body of literature indicates closed canopy forests are more resistant to drought, particularly in the tropics, due to shading, biophysical microclimate buffering, thicker litter layers, deeper roots, and increased water use efficiency as trees develop (e.g., Briant et al., 2010; von Arx et al., 2013; Frey et al., 2016; Brienen et al., 2017; Qie et al., 2017; Giardina et al., 2018; Caioni et al., 2020; Elias et al., 2020). For a given level of realized drought, some evidence points to larger older trees being more susceptible to drought impacts (Phillips et al., 2010; Girardin et al., 2012; Bennett et al., 2015; McDowell and Allen, 2015; McIntyre et al., 2015; Chen et al., 2016; Clark et al., 2016). Yet there is also contrasting evidence. For example, younger boreal forests can be more susceptible to drought compared to mature forests (Luo and Chen, 2013; Hember et al., 2017) due to competition for space and nutrients and less extensive and shallower root systems. Tree diversity, which is generally higher in primary compared to human-modified forests (see section "Biodiversity"), may increase resistance and resilience to drought *via* adaptive responses and functional redundancy (Jump et al., 2009; Sthultz et al., 2009; Dale et al., 2010; Harter et al., 2015), and intact forest canopies can be relatively resistant and resilient to short-term climate anomalies including drought (Williamson et al., 2000; Saleska et al., 2007). Evidence also suggests that mechanical "thinning," which is frequently proposed and implemented to combat drought, decreases stand-level water use in the short-term but actually increases individual tree water demand *via* higher leaf-to-sapwood ratios and hence drought vulnerability in the long-term (McDowell et al., 2006; Kolb et al., 2007; D'Amato et al., 2013; Clark et al., 2016).

Mature forests transpire large quantities of water from relatively deep in the soil profile, increasing regional cloud cover and precipitation. This acts to increase the proportion of "recycled" water within a given region and thereby decreases the prevalence of regional droughts (Foley et al., 2007; Spracklen et al., 2012; Ellison et al., 2017). For example, air passing over intact tropical forest landscapes can contain twice the moisture content as air over degraded forests or non-forest landscapes (Sheil and Murdiyarso, 2009). Degradation and the loss of intact forest landscapes increases dry and hot days, decreases daily rainfall intensity and levels, and exacerbates regional droughts (Deo et al., 2009; Alkama and Cescatti, 2016).

Comparison of risks from pests and pathogens

Pests and pathogens are an increasing threat to many forests globally, particularly as climate change alters life cycles, potential ranges, and host-pest interactions (Carnicer et al., 2011; Kautz et al., 2017; Seidl et al., 2017; Simler-Williamson et al., 2019). Mature boreal and temperate forests can be more susceptible to pests and pathogens compared to younger forests, in part due to decreases in the resin flow of defense compounds (Christiansen and Horntvedt, 1983; Hansen and Goheen, 2000; Baier et al., 2002; Dymond et al., 2010). Prominent examples include bark beetle and defoliator susceptibility (Kurz et al., 2008; Raffa et al., 2008; Taylor and MacLean, 2009; Krivets et al., 2015; Kautz et al., 2017). Nevertheless, ecologically mature forests tend to be resilient to biotic infestations, as these cyclical events initiate succession and lead to stand- and landscape-level heterogeneity (Holsten et al., 2008; Thompson et al., 2009). Moreover, tree diversity (measured in terms of genetic, species, and age) tends to limit pest and pathogen spread and damage because of resource dilution, host concealment, phenological mismatches, increased predators and parasitoids, alternative hosts, and metapopulation dynamics (Root, 1973; Karieva, 1983; Pimm, 1991; Watt, 1992; Zhang et al., 2001; Jactel et al., 2005; Pautasso et al., 2005; Scherer-Lorenzen and Schulze, 2005; Thompson et al., 2009; Guyot et al., 2016).

In terms of human influence, anthropogenic disturbances such as selective logging can introduce forest pests and diseases (Gilbert and Hubbell, 1996), including non-native, and evidence suggests forest edges and logged forests are more susceptible to beetle attacks due to increases in available host niches and altered moisture conditions (Sakai et al., 2001). Many pests, particularly in temperate and boreal forests, take advantage of weakened tree defenses during drought (Raffa et al., 2008; McDowell et al., 2011; Anderegg and Callaway, 2012; Hicke et al., 2012; Keith et al., 2012; Poyatos et al., 2013; Anderegg et al., 2015). Monocultures, or tree plantations, have been shown to be particularly vulnerable due to a lack of tree diversity, high tree density, and the associated host-pest interactions (Jactel et al., 2005; Macpherson et al., 2017; Lee, 2018).

Comparison of risks from windthrow

Windthrow events can lead to forest mortality and are expected to increase in some regions with climate change (Klaus et al., 2011; Saad et al., 2017). Although these events are somewhat stochastic, they are also influenced by soils, orography, regional climate regimes, and forest composition and structure. Similar to the risks of pests and pathogens, within a given stand there is evidence that older and taller trees are more susceptible to windthrow due to the physics of taller trees and root rot (Lohmander and Helles, 1987; Ruel, 1995). Nevertheless, fragmented or thinned forests experience elevated mortality and collapse of trees from windthrow because of increased exposure (Laurance and Curran, 2008; Reinhardt et al., 2008; Schwartz et al., 2017).

Comparison of risks from species range shifts

Climate regimes have strong influences on the potential and realized ranges of forest tree species, evidenced by the paleoecological record (Overpeck et al., 1991; DeHayes et al., 2000; Davis and Shaw, 2001) and current assemblages (e.g., Neilson, 1995; Foley et al., 2000), and considerable scientific effort is focused on projecting future responses to climate change (e.g., Sitch et al., 2003; Elith and Leathwick, 2009; Rogers et al., 2011, 2017; Ehrlen and Morris, 2015; Prasad et al., 2020). How trees and forest ecosystems will respond is uncertain due to complex interactions between the pace of climate change, physiological tolerances, dispersal and migration rates, phenotypic plasticity and adaptation, the presence of climate refugia, migration of associated species / symbionts, and forest fragmentation, among others (Davis and Shaw, 2001; Iverson et al., 2004; Jump and Penuelas, 2005; Mackey et al., 2008; Nicotra et al., 2010; Prasad, 2015; Rogers et al., 2017). In general, current and projected climate change is expected to degrade biodiversity due to species extinctions and the contraction of realized ranges (Miles et al., 2004; Campbell et al., 2009). Forest and landscape fragmentation in particular is known to hinder resilience and species migration because of the loss of suitable areas for dispersal and limitations on gene flow (Collingham and Huntley, 2000; Loreau et al., 2002; Scheller and Mladenoff, 2008; Thompson et al., 2009). Large areas of primary forests are expected to have higher adaptive capacity and stability compared to forests under human pressure because of their connectivity, biodiversity, and microclimate buffering (Mackey et al., 2015; Watson et al., 2018; Thom et al., 2019; see section "Biodiversity").

Comparison of risks from land use degradation

Human land use pressures on forests generally result in both direct environmental impacts as well as further, often unplanned, degradation or deforestation that accumulates spatially and temporally. This is exemplified by the fact that smaller fragments of primary forest have an elevated likelihood of loss (Hansen M. C. et al., 2020). New roads are the primary driver of further degradation as a result of their construction, use, and continued access (e.g., Trombulak and Frissell, 2000; Wilkie et al., 2000; Laurance et al., 2009; Laurance and Balmford, 2013; Ibisch et al., 2016; Alamgir et al., 2017; Venier et al., 2018; Maxwell et al., 2019). Roads render the surrounding forests much more susceptible to agricultural conversion (Asner et al., 2006; Boakes et al., 2010; Gibbs et al., 2010; Laurance et al., 2014; Kormos et al., 2018), logging (Laurance et al., 2009; Barber et al., 2014), and expanded networks of secondary and tertiary roads (Arima et al., 2008, 2016; Ahmed et al., 2014). Logging and transportation can also lead to severe erosion and nutrient runoff, impacting downstream water quality and quantity (Carignan et al., 2000; Hartanto et al., 2003; Foley et al., 2007), and damage the surrounding forest. For example, in the Amazon, it has been estimated that for every commercial tree removed *via* selective logging, roughly 40 m of roads are created, nearly 30 other trees greater than 10 cm in diameter are damaged, and between 600 and 8,000 m^2 of canopy is opened (Holloway, 1993; Asner et al., 2004). Furthermore, roads reduce animal habitat, are barriers to animal movement and lead to increased animal mortality, including from unregulated hunting, all of which decrease connectivity and genetic exchange (Dyer et al., 2002; Frair et al., 2008; Laurance et al., 2009; Taylor and Goldingay, 2010; Clements et al., 2014). One consequence is a decline in carbon-dense tree species due to overhunting of seed-dispersing animals (Osuri et al., 2016; Maxwell et al., 2019). It is important to note that roughly 95% of deforestation in the Amazon occurs within 5.5 km of a road (Barber et al., 2014), and that illegal logging represents 85–90% of all logging in the tropics (Lawson and MacFaul, 2010; Lawson, 2014; Hoare, 2015) and still roughly one-quarter of logging in Russia (Food and Agriculture Organization of the United Nations [FAO], 2012; Kabanets et al., 2013), which contains the largest areal forest coverage of any country (Food and Agriculture Organization of the United Nations [FAO], 2020). Overall, road building and industrial logging are the largest drivers of initial forest degradation and fragmentation (Hosonuma et al., 2012).

In addition to their direct impacts, roads and land use further degrade forests due to edge effects. Forests at or near an edge can have substantially drier microclimates, increased windshear and movement of dry air into forests, invasive species (dispersed *via* roads and more favorable microclimate conditions for competition), weeds and vines, sun exposure, soil erosion, and fuel loads due to drying and previous logging and fire (Laurance and Williamson, 2001; Mortensen et al., 2009; Brando et al., 2014). This leads to a variety of unfavorable impacts and further risks. Carbon densities tend to be significantly lower near forest edges. For example, biomass is reduced by roughly 50% within 100 m, 25% within 500 m, and 10% within 1.5 km of a forest edge (Laurance et al., 1997; Chaplin-Kramer et al., 2015; Maxwell et al., 2019). Aggregated across the tropics, edge effects are estimated to account for up to one quarter of all carbon loss from tropical deforestation (Putz et al., 2014). Primary productivity is also generally lower near forest edges, and fire susceptibility is higher due to elevated and drier fuel loads and increased human access (Laurance et al., 1998; Cochrane et al., 1999; Nepstad et al., 1999; Laurance and Williamson, 2001; Foley et al., 2007; Adeney et al., 2009; Brando et al., 2014). For example, roads are strong predictors of ignition and wildfire frequency in temperate forests (Hawbaker et al., 2013; Faivre et al., 2016; Parisien et al., 2016; Balch et al., 2017; Ricotta et al., 2018), and road expansion in Siberia has been shown to promote logging and human-caused forest fires (Kovacs et al., 2004). A variety of ecosystem services are degraded due to edge effects, including hydrologic regulation, water quality, modulation of regional climate, and amelioration of infectious diseases (Laurance and Williamson, 2001; Foley et al., 2007). Although the impacts are strongest at a forest edge, the effects can generally be detected up to 2 km from the edge, with higher tree mortality up to 1 km and wind disturbance up to 500 m (Broadbent et al., 2008). Globally, fragmentation is thought to be at a critical threshold, with roughly 70% of the world's forest within 1 km of a human-created forest edge (Haddad et al., 2015; Taubert et al., 2018).

Comparison of regenerative capacity

Ecosystem resilience is underpinned by the natural regenerative capacity of a forest ecosystem, and hence represents a major component of ecosystem stability and integrity (**Figure 1**). Regeneration from major disturbance events requires biological legacies, which are broadly defined as the remaining living and dead structures and organisms that can influence recovery (Franklin et al., 2000; Jogiste et al., 2017). These include living and dead trees, shrubs and other plants, seeds, spores, fungi, eggs, soil communities, and living animals (Franklin et al., 2000; Stahlheber et al., 2015; Lindenmayer et al., 2019). Compared to secondary or human-modified forests, primary forests tend to have the biological legacies (Catterall, 2016; Chazdon and Uriarte, 2016; Lu et al., 2016; Poorter et al., 2016; Lindenmayer et al., 2019) and favorable microclimates (von Arx et al., 2013) required for optimal regeneration. This is evidenced by the fact that secondary forest regeneration is aided by proximity to primary forests (Schwartz et al., 2015; Kukavskaya et al., 2016). Clearcut logging also generates low levels of biological legacies and higher regeneration failures after subsequent fires compared to forests not previously logged (Perrault-Hebert et al., 2017), which is exacerbated by post-fire "salvage" logging (Donato et al., 2006; Lindenmayer et al., 2019). Successive disturbances continue to decrease regenerative capacity, and can lead to permanent forest loss and emergence of non-forest ecosystems (Payette and Delwaide, 2003; Johnstone et al., 2016; Kukavskaya et al., 2016). Compared to degraded or human-modified forests, primary forests with large extents also host a much larger array of seed dispersers and pollinators (Muller-Landau, 2007; Wright et al., 2007; Abernethy et al., 2013; Harrison et al., 2013; Peres et al., 2016).

Comparison of biodiversity

Biodiversity underpins and is affected by the foundational elements of ecosystem integrity (**Figure 1**), but is also a metric of ecosystem condition and can be considered an ecosystem service in its own right. Globally, trees are among the most genetically diverse of all organisms, and forests collectively support the majority (roughly 80%) of terrestrial biodiversity (Hamrick and Godt, 1990; Barlow et al., 2007; Pimm et al., 2014; Federici et al., 2017). There is a substantial body of literature on the effects of disturbance and stand age on biodiversity, with some disagreement among studies depending on context (e.g., Paillet et al., 2010; Edwards et al., 2011; Moreno-Mateos et al., 2017; Kuuluvainen and Gauthier, 2018; Matos et al., 2020). Nevertheless, there are clear and definitive negative impacts of human disturbance and land use on biodiversity (Cairns and Meganck, 1994; Ellison et al., 2005; Barlow et al., 2007, 2016; Gibson et al., 2011; Alroy, 2017; Giam, 2017). Primary and ecologically mature forests typically harbor higher biodiversity than human-modified forests (Lesica et al., 1991; Herbeck and Larsen, 1999; Rey Benayas et al., 2009; Zlonis and Niemi, 2014; Miller et al., 2018; Watson et al., 2018; Lindenmayer et al., 2019; Thom et al., 2019), especially in the understory (e.g., Lafleur et al., 2018). Disturbance generally results in a change in species composition toward early pioneer species (e.g., Bawa and Seidler, 1998; Liebsch et al., 2008; Venier et al., 2014). The effect of human activities on the provision of ecosystem services is evident even if there is little change in the overall forest cover. Degradation in logged forests can be in the form of structural changes such as reduction in old age classes of trees that can cause loss in breeding habitat, particularly for birds (Rosenberg et al., 2019; Betts et al., 2022), and compositional changes such as shifts in tree species abundance that differ in foliar nutrient concentrations that support arboreal folivores (Au et al., 2019). Under less intensive agriculture management, agroforestry can maintain a significant fraction of biodiversity, but it is still considerably lower than in native forests (De Beenhouwer et al., 2013; Vallejo-Ramos et al., 2016).

Biodiversity analyses are also strongly dependent on spatial scale, whereby higher levels of management and disturbance homogenize forest composition and age structure across the landscape, and consequently the biota it supports (e.g., Devictor et al., 2008; de Castro Solar et al., 2015; Tomas Ibarra and Martin, 2015). What can be concluded is that (i) degraded and intensively managed forests tend to harbor lower biological and functional diversity compared to primary forests, which support many as yet unidentified species and act as repositories for species that cannot survive in secondary or degraded forests (Barlow et al., 2007; Gibson et al., 2011), and (ii) natural disturbances are effective at maintaining landscape heterogeneity and the species that depend on disturbed and young forests (Lindenmayer et al., 2019). Global biodiversity loss is currently orders of magnitude higher than background rates and is driven primarily by deforestation and forest degradation (Newbold et al., 2016; Giam, 2017). It is worth noting that although natural tree diversity in boreal forests is typically much lower than in temperate or tropical forests (Thompson et al., 2009; Hill et al., 2019), the biodiversity of other species groups such as bryophytes and lichens can be very high (DellaSala, 2011; Kuuluvainen and Gauthier, 2018), functional diversity in boreal forests is generally high (Esseen et al., 1997; Wirth, 2005), and the broad genetic variability and phenotypic plasticity of boreal trees allows them to tolerate a wide range of environmental conditions (Gordon, 1996; Howe et al., 2003).

Comparison of ecosystem condition

Given our focus on climate mitigation, the primary metric of concern for ecosystem condition is carbon stocks. Primary and ecologically older forests have been consistently found to have the highest carbon stocks compared to secondary, degraded, intensively managed, or plantation forests (e.g., Harmon et al., 1990; Cairns and Meganck, 1994; Nunery and Keeton, 2010; Burrascano et al., 2013; Mackey et al., 2013; Keith et al., 2015, 2017; Federici et al., 2017; Lafleur et al., 2018; Watson et al., 2018). For example, a recent meta-analysis shows that primary tropical forests store on average 35% more carbon than forests affected by conventional management for commodity production (Mackey et al., 2020). Across the tropics, intact forest landscapes cover approximately 20% of total area but store 40% of total aboveground biomass (Potapov et al., 2017; Maxwell et al., 2019). This is fundamentally a function of where carbon is stored in these forests. In wet tropical and some temperate primary forests, roughly half the biomass carbon is stored in the largest 1–3% diameter trees (Stephenson et al., 2014; Lutz et al., 2018; Mildrexler et al., 2020), which have long residence times (Koerner, 2017; van der Sande et al., 2017), and are typically the first to be felled (Cannon et al., 1998; Sist et al., 2014; Gatti et al., 2015; Rutishauser et al., 2016). Agricultural landscapes store comparatively less carbon, but the addition of trees *via* agroforestry has the potential to add up to 9 Pg C globally (Chapman et al., 2020). In boreal forests, especially those that are poorly drained, the majority of forest ecosystem carbon is stored in dead biomass, peat, and soil organic layers that accumulate over the course of forest succession, often protected by permafrost (Deluca and Boisvenue, 2012; Bradshaw and Warkentin, 2015; Lafleur et al., 2018; Walker X J et al., 2020). Boreal forests managed for timber are kept at younger ages, with soils that store significantly less carbon due to mechanical disturbance, tree species conversion, and impacts on litter composition, nutrient cycling, and bryophyte communities (Liski et al., 1998; Jiang et al., 2002; Seedre et al., 2014; Lafleur et al., 2018). Even outside the boreal zone, soil carbon can be a significant fraction of total ecosystem carbon (e.g., Keith et al., 2009), and logging activities generally deplete forest soil carbon due to soil compaction and disturbance, erosion, changes in microclimate that increase respiration rates, reduced leaf litter and root exudates, loss of micorrhizal network carbon, and post-logging "slash" burning (Rab, 2004; Zummo and Friedland, 2011; Buchholz et al., 2014; James and Harrison, 2016; Hume et al., 2018; Mayer et al., 2020). Globally, forests are thought to store only half of their potential carbon stock, with 42–47% of the reduction due to forest management and modification (the remainder being deforestation and land cover changes; Erb et al., 2018). Natural regeneration of forests could in turn restore 123 Pg C, or 27% of the total biomass carbon that has been lost (Erb et al., 2018).

Forest management, degradation, and conversion can also result in the loss of key nutrients such as nitrogen and phosphorous, among others, which are otherwise retained efficiently in undisturbed forests (Likens et al., 1970; Markewitz et al., 2004; Olander et al., 2005; Liu et al., 2019). Nutrients can be artificially added, but heavily managed systems require large inputs to maintain their state and productivity capacity (Noss, 1995; Merino et al., 2005; Pandey et al., 2007). Other elements of ecosystem condition are affected similarly and highlighted elsewhere (landscape connectivity / fragmentation in section "Comparison of risks from land use degradation," biodiversity in section "Comparison of biodiversity," and water quality and quantity in section "Comparison of ecosystem services").

Comparison of ecosystem services

A large body of literature indicates the higher number, quality, and value of ecosystem services provided by primary forests compared to human-modified forests and landscapes. These include regulating services such as water quality and quantity (DellaSala, 2011; Brandt et al., 2014; Keith et al., 2017; Kormos et al., 2018; Taylor et al., 2019; Vardon et al., 2019); carbon storage and sequestration as an ecosystem service of global climate regulation (United Nations [UN], 2021) [discussed above, but see Keith et al. (2019) and Uganda Bureau of Statistics [UBOS] (2020) for examples using Ecosystem Accounts]; local to regional biophysical cooling (Spracklen et al., 2012; Lawrence and Vandecar, 2015); regulation of runoff, sediment retention, erosion control, and flood mitigation (Hornbeck and Federer, 1975; Jayasuriya et al., 1993; Dudley and Stolton, 2003; Furniss et al., 2010; van Haaren et al., 2021); provisioning services such as abundance of game and fish (Gamfeldt et al., 2013; Brandt et al., 2014); cultural services such as landscape aesthetics, recreation, and tourism (Brandt et al., 2014; Brockerhoff et al., 2017); cultural practices and knowledge (Normyle et al., 2022); contributions to physical and psychological health (Stier-Jarmer et al., 2021); and general assessments across a suite of services (e.g., Myers, 1997; Harrison et al., 2014; Shimamoto et al., 2018; Maes et al., 2020).

For example, a detailed assessment of the differences between primary forests and post-logging regrowth forests in terms of their ecosystem condition, the physical supply of a suite of ecosystem services, and their monetary valuation showed the superior aggregated value of the primary forest (Keith et al., 2017). The impacts of mechanical disturbance due to logging, roading, and mining on soil properties reduce the ecosystem services of soil nutrient availability, water holding capacity and erosion prevention (Hamburg et al., 2019). A general assessment of the total economic value of ecosystem services provided by forest ecosystem types showed that primary forests had a higher median value (USD 139 ha^{-1} year^{-1}) compared with secondary forests (USD 128 ha^{-1} year^{-1}) (Taye et al., 2021). These aggregated values include only the market values for services when known and could not account for non-market values, for example that would be needed to assess biodiversity habitat or many cultural services. The highest reported values for specific ecosystem services were for airflow regulation, water cycle regulation and food for freshwater plants and animals. These services would all have their highest provision from natural ecosystems. In contrast, the value of timber and fiber products is significantly lower.

Lessons from comparative analysis

Taken as a whole and for a given set of environmental conditions, our comparative analysis shows that primary forests have the highest levels of ecosystem integrity compared to human-modified forests, including naturally regenerating forests managed for commodity production, plantations, and previously forested landscapes. One primary set of mechanisms are positive feedbacks whereby forest disturbance tends to beget more disturbance (e.g., Seidl et al., 2017), and degradation begets more degradation (e.g., Venier et al., 2018; Watson et al., 2018). In terms of variables most relevant for mitigation, adaptation, and other international forest policy goals, primary forests store the highest carbon stocks, present the lowest risks of forest and carbon loss reversal, have the highest biodiversity, and provide the largest stocks of ecosystem assets and highest quality flows of ecosystem services, including benefits to the global community, local communities (Vickerman and Kagan, 2014), and Indigenous peoples.

Based on our review, and because human-modified forests can encompass a wide range of management strategies and intensities, we provide further summaries of ecosystem integrity for five main categories of forest types: (A) primary forests; (B) secondary forests; (C) production forests; (D) agro-forests; and (E) plantations (**Figure 2** and **Table 1**). Primary forests have the most developed dissipative structures, the highest levels of ecosystem processes, greater stability and recovery, and thus greater resilience and the lowest risk of loss and damage. As defined here, secondary forests are in recovery from past human impacts especially logging. Although they can transition to primary forests over time, these forests lack some old growth characteristics, are more vulnerable to wildfire and other natural disturbances, and have missing elements of biodiversity. Production forests are a result of conventional forest management for commodity production, and tend to be kept at relatively young ages with associated reductions in dissipative structures, carbon stocks, and resilience. An example of commercial agro-forests is shade coffee where retaining some natural canopy tree cover provides some additional ecosystem service benefits. Subsistence agro-forests are common in many tropical development countries such as Vanuatu where these household and community gardens were, and in many cases still are, the main source of food. Commercial plantations include monocultures of trees species that are essentially tree farms for commodity production (wood, palm oil). Note that there are gradients of human modification, stand age, and ecosystem integrity within these broad categories. For example, mature forests recovering from past human disturbances may not have the full suite of structural, functional, and compositional benefits as primary forests, but they can gain these over time, and generally have higher ecosystem integrity than forests

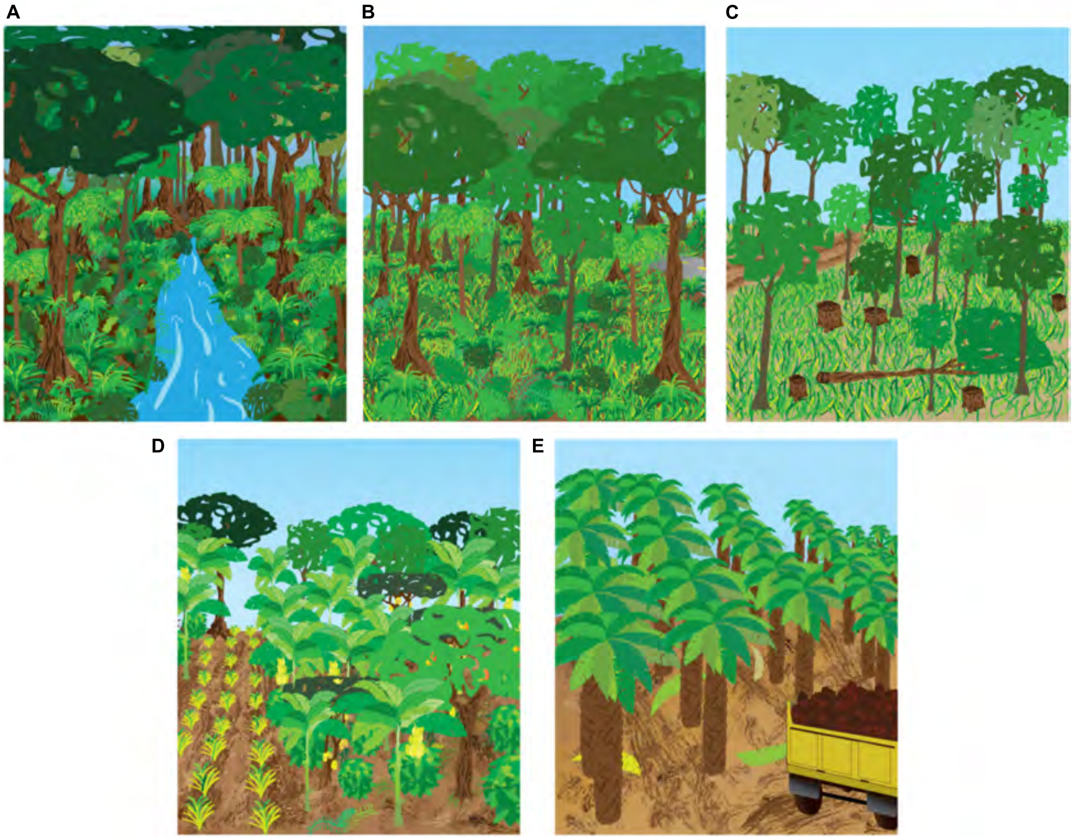

FIGURE 2
Graphical illustrations of five main forest types considered for ecosystem integrity comparisons, including **(A)** primary forests, **(B)** secondary forests, **(C)** production forests, **(D)** agro-forests, and **(E)** plantations. Note this illustration focuses on tropical forests, but the same general differences apply across forest biomes.

TABLE 1 Comparison of ecosystem integrity foundational elements between five main forest types.

Primary forest

- Naturally regenerated forest of native tree species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed
- Likely to have never been commercially logged or intensely managed
- At a landscape level, can comprise early successional (seral) stage following natural disturbances
- More likely to contain full complement of evolved natural biodiversity
- Often the customary territories of Indigenous Peoples

Dissipative structures	*● Ecosystem processes*	*● Stability and risk profiles*	*● Ecosystem integrity level*
● Canopy trees dominated by large, old trees ● In wet tropics, closed canopies ● Dense soil organic stocks ● Typically significant quantities of dead biomass	● Fully self-generating (autopoiesis) ● In temperate and boreal forests, includes seral stages following natural disturbances ● Tight nutrient cycling with minimal leakage and/or erosion ● Clean water supply	● Highly resistant and/or resilient to extreme weather events ● In boreal and temperate biomes, fire-adapted plant species ● Rich biodiversity provides functional and phenotypic adaptive capacity	● High levels for all three factors

Secondary forest

- Natural forests recovering from prior human land use impacts
- Canopies dominated by pioneer and secondary growth tree species
- If not subsequently disturbed by human land use, can continue to develop additional primary forest attributes over time

● Dissipative structures	*● Ecosystem processes*	*● Stability and risk profiles*	*Ecosystem integrity level*
● In wet tropics, canopy closure can occur within 1–2 decades ● Aboveground living significantly less than primary forests ● Some dead biomass may remain	● Fully self-regenerating so long as primary propagules/seed stock are available ● Soil carbon and nutrients stocks can be depleted due to past erosion and biomass removal	● In temperate and boreal forests, increased exposure to wildfire and drought impacts due to more open canopy and drier forest interior ● Reduced biodiversity impairs some key processes (e.g., pollination, top-down tropic control)	● Moderate depending on time since disturbance

Production forest

- The consequence of conventional forest management for commodity production (e.g., timber, pulp)
- Forest predominantly composed of trees established through natural regeneration, but management favors commercially valuable canopy tree species

● Dissipative structures	*● Ecosystem processes*	*● Stability and risk profiles*	*Ecosystem integrity level*
● Logging regimes maintain a predominantly even-aged, younger age structure (∼20–60 years) ● Simplified vertical vegetation structure	● Canopy tree species natural regenerated but some level of assisted regeneration common ● Ongoing soil loss	● More flammable forest conditions ● Greater exposure to invasive species	● Low to moderate depending on intensity of logging regimes and biodiversity loss

Agro-forestry (commercial, subsistence)

- Some level of natural tree species is maintained with subsistence food or commercial crops grown (e.g., shade coffee).
- Swidden subsistence farming commonly used by traditional communities
- Utilizes a mix of natural and assisted regeneration

Dissipative structures	*Ecosystem processes*	*Stability and risk profiles*	*Ecosystem integrity level*
● A curated canopy of trees, often remnant from primary forest or planted from local stock ● Little if any understory ● Ground cover are food crops	● In tradition swidden system, closed nutrient cycle through use of natural regeneration ● Canopy trees buffer food crops from extreme weather and help maintain soil moisture	● Intensive small-scale management and modest level of biodiversity provides assisted resilience and adaptive capacity	● Low to moderate given sufficient management inputs

(Continued)

TABLE 1 (Continued)

Commercial plantation

- Forest predominantly composed of trees established through planting and/or seeding and intensely managed for commodity production (timber, pulp, plant oil)

Dissipative structures	*Ecosystem processes*	*Stability and risk profiles*	*Ecosystem integrity level*
• Typically mono-cultures that are harvested at around a young age (∼10–20 years)	• Soil water and nutrient retention • Can utilize natural pollinators from neighboring or remnant natural forests	• Exposed to extreme weather events, invasives, pests, and disease • Intensive large-scale management needed	• Low

recovering from more recent human disturbance (DellaSala et al., 2022b).

Implications for policy, management, and future research

Evaluating ecosystem integrity

We have shown that the risk of forest carbon loss can be minimized by prioritizing actions that maintain and enhance forest ecosystem integrity. Ecosystem integrity therefore has the potential to be used as an integrating framework for evaluating forest-based mitigation and adaptation actions. Because ecosystem integrity is an inherently complex concept, the scientific, management, and policy communities need approaches and tools to measure and interpret gradients of integrity consistently across forest types and jurisdictional boundaries (Karr, 1996; Grantham et al., 2020). The metrics and their interpretation should ideally account for the range of spatial and temporal scales involved: small patches of high-integrity forests are valuable, but landscape context is required; snapshots in time are useful, but longer-term dynamics are needed to fully understand integrity.

A complete and exhaustive global representation of forest ecosystem integrity may currently be beyond our reach. Nevertheless, several existing data products represent important elements of ecosystem integrity, each with their own advantages and limitations, and can be used to guide decision making. In the humid tropics, natural and hinterland forests (primary forests and mature secondary growth) have been mapped using multispectral satellite imagery (Turubanova et al., 2018) and spatial statistics (Tyukavina et al., 2016). Canopy structural integrity has recently been mapped using space-based lidar, multispectral imagery, and human pressure indices (Hansen et al., 2019; Hansen A. J. et al., 2020), representing an important step in delineating gradients of integrity. These mapping approaches are inherently more challenging outside the humid tropics where environmental gradients generate a range of potential forest cover and types. Global products therefore tend to rely more on metrics based on the relationships between forest loss/degradation and proximity to human activities, including roadless areas, forest fragmentation, loss of tree cover, and measures of the "human ecological footprint" (Hansen et al., 2013; Haddad et al., 2015; Ibisch et al., 2016; Venter et al., 2016b,a; Beyer et al., 2020; Grantham et al., 2020; Williams et al., 2020). Global Intact Forest Landscapes (Potapov et al., 2008, 2017) have been widely used, but these include patches of non-forest ecosystems and exclude areas of high-integrity forests in patches <50,000 ha. The Food and Agriculture Organization of the United Nations (FAO) has reported on primary forests since 2005 in their global forest assessment reports (Food and Agriculture Organization of the United Nations [FAO], 2020), but a lack of consistency in national-level reporting makes comparisons and trend detection difficult.

Similar to Grantham et al. (2020), we stress the importance of using local data and field observations to further identify and refine estimates of forest ecosystem integrity derived from coarser-scale global mapping products. These may include landscape-level metrics such as frequency distributions of stand age, biomass, coarse woody debris, biodiversity, forest patch sizes and shapes, and forest types and species composition. Individual countries have data archives, collection programs, and often agency directives that either include ecosystem integrity metrics or those with high relevance for integrity assessments (e.g., Muller et al., 2000; Tierney et al., 2009; Wurtzebach and Schultz, 2016). Applying the internationally endorsed SEEA-EA system should also enable a consistent framework for comparisons across spatial and temporal scales. The SEEA-EA standard provides guidance for classifications, definitions, spatially explicit analysis, and temporal consistency. Technical guidance on ecosystem integrity indicators was recently provided by Hansen et al. (2021). Although criteria were provided in the context of CBD's post-2020 Global Biodiversity Framework, many would apply outside this context, including a need for biome to global scale products with spatial resolution sufficient for management ($\leq$ 1 km), temporal re-assessment at intervals of 1–5 years, ability for indicators to be spatially aggregated without bias, credibility through validation and peer review, and accounting for reference states within a given climate, geomorphology, and ecology. Finally, we note the importance of understanding how any given metric of ecosystem integrity connects to the conceptual framework of ecosystem integrity (**Figure 1**).

Implementing ecosystem integrity

Protecting primary forests

Given the superior benefits of primary forests, follows that protecting them would significantly contribute to meeting international climate, biodiversity, and SDGs. Primary forests are disappearing at a rapid rate (e.g., Potapov et al., 2017; Food and Agriculture Organization of the United Nations [FAO], 2020; Hansen M. C. et al., 2020; Silva Junior et al., 2021) and urgently need higher levels of protection to ensure their conservation; only roughly one-fifth of remaining primary forests are found in the International Union for Conservation of Nature (IUCN) Protected Areas Categories I-VI (Mackey et al., 2015). Proven effective mechanisms to protect primary forests include enforcing existing and establishing new reserves and protected area networks, limiting new road construction, payments for ecosystem services, effective governance, and protecting the rights and livelihoods of indigenous peoples and local communities (Mackey et al., 2015; Kormos et al., 2018; Walker W. S et al., 2020). Complementary measures and enabling conditions include supporting legislation and enforcement of protection status, industry re-adjustment to source alternative fuel, food and wood products, and management of weeds, pests, feral animals, and livestock grazing (Mackey et al., 2020).

Protecting primary forests will also be facilitated by changes to current international forest and carbon accounting rules. Existing "net" forest cover accounting rules, such as the IPCC good practice guidelines for national greenhouse gas inventories and the land sector, are problematic because they report net changes and treat all forests equally, regardless of their integrity, thereby incentivizing the conversion of primary forests into commodity production (Mackey et al., 2013, 2015; Peterson and Varela, 2016; Moreno-Mateos et al., 2017; Funk et al., 2019; Skene, 2020). Such changes in forest management can have the perverse effect of accelerating emissions and degrading ecosystems. Similarly, flux-based carbon accounting effectively hides the emissions or lost sequestration potential from logging primary forests (e.g., Skene, 2020) and does not account for the risk profiles of different forest types. Reporting "gross" forest cover changes as well as adopting stock-based accounting (Ajani et al., 2013; Keith et al., 2019, 2021) could more fully leverage an ecosystem integrity framework, and ultimately ensure the maximum mitigation benefits and ecosystem services are secured from Earth's remaining forests.

Management of other forest types

Management of secondary forests for commodity production, along with tree plantations and agroforestry, can contribute to climate mitigation and other SDGs and reduce pressure on primary forests and other natural forests with high levels of ecosystem integrity (Watson et al., 2018; Roe et al., 2019; Chapman et al., 2020). However, the key is to direct these management activities to previously deforested or degraded lands and accompany them with systematic landscape planning and effective governance (Dooley et al., 2018; Kormos et al., 2018; Martin et al., 2020; Morgan et al., 2020). For example, much of the overall timber demand could be harvested from secondary forests, but these are often overlooked as resources by land owners, the timber industry, and governments (Bawa and Seidler, 1998). Globally, intensively managed tree plantations or planted forests supply over 50% of global wood supply (Warman, 2014) yet occupy only 7% of global forest cover (Food and Agriculture Organization of the United Nations [FAO], 2020). It is therefore feasible to meet global wood supply with existing plantations and additional ones established on previously cleared or degraded land. These land uses, however, are decidedly not beneficial for carbon budgets or ecosystem services when undertaken at the cost of clearing or degrading primary forests.

Governments and forest managers can aim to optimize the ecosystem integrity of secondary forests (for example in terms of yield, regenerative capacity, and biodiversity) within the confines of their intended uses (Thompson et al., 2009; Grantham et al., 2020). In tandem with alternative fibers, this will help alleviate pressures on primary forests. A similar argument exists for agricultural productivity (Laurance et al., 2001; Hawbaker et al., 2006; Sabatini et al., 2018). All of these activities can be done with appropriate landscape planning in ways that collectively increase economic yield and ecosystem services, and serve local communities (Bawa and Seidler, 1998; Burton et al., 2006; Mathey et al., 2008; Food and Agriculture Organization of the United Nations [FAO], 2012; Naumov et al., 2016).

Afforestation, forest restoration, and proforestation (i.e., allowing secondary forests to naturally regrow and restore their ecosystem carbon stocks) are also important components of forest-based mitigation and conservation activities (Giam et al., 2011; Griscom et al., 2017; Verdone and Seidl, 2017; Moomaw et al., 2019; Roe et al., 2019; Cook-Patton et al., 2020). Proforestation holds promise for near-term mitigation because the established trees are already on the steepest part of their growth curve (Moomaw et al., 2019; Mackey et al., 2020). However, none of these forest management activities can replace the carbon stocks and ecosystem services of high-integrity primary forests on decadal to century timeframes. It is also generally less expensive to protect primary forests than to reforest or restore forests (Possingham et al., 2015; Griscom et al., 2017). Furthermore, potential "overcrediting" for offset and restoration schemes can result in net harm and carbon emissions, whereas "overcrediting" for primary forest protection only reduces the benefits, but does not lead to net societal and climate damages (Anderegg et al., 2020). We therefore urge that forest restoration should be conducted in concert with protection of primary forests, and not instead.

Finally, we note that selective logging, or so called "reduced impact logging" in tropical forests has been shown many times to be unsustainable (Zimmerman and Kormos, 2012; Kormos et al., 2018), as it results in significant damage to the target forests as well as collateral damages to surrounding forests due to road building, transportation, and further clearing for land uses such as agriculture (Kormos and Zimmerman, 2014; Mackey et al., 2020). Generally, as timber extraction becomes less intensive, the per-tree collateral damages increase exponentially (Gullison and Hardner, 1993; Boot and Gullison, 1995; Bawa and Seidler, 1998; Umunay et al., 2019; Zalman et al., 2019). After the first cut, selective logging is much less economically viable compared to plantations and intensive forestry (Bawa and Seidler, 1998; Naumov et al., 2016). Even measures aimed at reducing emissions *via* collateral damages from selective logging may not generate benefits and merely serve to justify and subsidize the degradation of high-integrity primary forests (Macintosh, 2013; Watkins, 2014; Gatti et al., 2015). Overall, selective logging and its associated degradation may be as much or more harmful than outright deforestation for pan-tropical forests and their carbon stocks (Nepstad et al., 1999; Foley et al., 2007; Baccini et al., 2017; Erb et al., 2018; Bullock et al., 2020; Matricardi et al., 2020).

Relevance for international policy

There has been a recent uptick in the recognition of the importance of ecosystem integrity and primary forests for multiple climate, biodiversity, and SDGs. For example, the preamble to the Paris Agreement notes the importance of ensuring the integrity of all ecosystems, and recent international policy developments point to the importance of maintaining and restoring ecosystem integrity for achieving the goals of the Rio Conventions and all of the SDGs, but in particular SDG 15 (Life on Land). The importance of primary forests for achieving synergistic climate and biodiversity outcomes was also reflected in Working Group II (IPCC, 2022) and III (Nabuurs et al., 2022) of the IPCC's Sixth Assessment Report, as well as key decisions from the CBD 14th Conference of the Parties (14/5 and 14/30) (Convention on Biological Diversity [CBD], 2018).

We strongly recommend an increased focus on integrating climate and biodiversity action, which provides an opportunity to deliver multiple societal goals through ensuring the integrity of ecosystems (Barber et al., 2020). The importance of the nexus between effective action on climate change and biodiversity is reflected in the findings of the first ever joint workshop of the IPCCC and IPBES held in 2021 (Pörtner et al., 2021), which encouraged synergistic climate and biodiversity action and identified priorities for action, in particular the protection and restoration of carbon and species rich natural ecosystems such as forests.

The integrity of ecosystems is also being promoted by civil society as an important factor to consider in the UNFCCC Global Stocktake, a central pillar of the Paris Agreement against which its success or failure will be judged (Climate Action Network, 2022). We suggest that utilizing the UN SEEA-EA to benchmark protection and restoration actions would provide critical information on ecosystem integrity elements for the Global Stocktake to inform high-benefit / low-risk nature-based solutions in evolving NDCs. Successful implementation of the ecosystem provisions of the UNFCCC and the Paris Agreement, including decisions made at COP 25 (1.CP 25 para. 15) calling for integrated action to prevent biodiversity loss and climate change; and COP 26 (CMA/3 para. 21 and 1.CP/26 para. 38) emphasizing "...the importance of protecting, conserving and restoring nature and ecosystems, including forests ...," depends upon understanding the significance of ecosystem integrity for stable long term carbon storage and the overall health of the biosphere.

Other recent policies and guiding documents include the Glasgow Leaders' Declaration on Forests and Land Use (United Nations Climate Change, 2021), CBD post-2020 Global Biodiversity Framework (Convention on Biological Diversity [CBD], 2021), IUCN Policy Statement on Primary Forests Including Intact Forest Landscapes (IUCN, 2020), IPBES Global Assessment Report (IPBES, 2019), the New York Declaration on Forests 5-Year Assessment Report (NYDF Assessment Partners, 2019), the European Parliament resolution to protect and restore forests (European Parliament, 2020), and Indonesia's moratorium on converting primary forests and peatlands (Austin et al., 2019).

Nevertheless, there is still much work to be done at national and international levels, with the evolving Paris Rulebook and country NDC's arguably representing the largest opportunity. Translating all these international declarations into coherent national and jurisdictional policies will require an agreed-upon framework of ecosystem integrity, such as provided here, and applicable data products tools for implementation.

Future research directions

Because ecosystem integrity is such an integrative and multidisciplinary concept, research gaps are relatively extensive. We therefore do not offer an exhaustive list, but rather a prioritized assessment of future research directions to improve the understanding, valuation, and operationalization of ecosystem integrity. First and foremost, operationalizing forest ecosystem integrity at scales relevant to policy and planning that span from landscape planning (Morgan et al., 2022) to national strategies (Center for Biological Diversity [CBD], 2022) and international agreements (United Nations [UN], 2021) requires accurate and updated maps of ecosystem integrity and its components. Existing products (described in section "Evaluating ecosystem integrity") touch on aspects of canopy structural integrity, can be used to identify areas of remaining natural forests, and, using time series data, can locate where they have been lost (**Figure 3**). However, their ability to differentiate levels of integrity between forests is limited, and they do not account for the longer-term ecosystem dynamics that comprise functional integrity. It will therefore be helpful to leverage the time series of now decades-long satellite records such as Landsat and the Moderate Resolution Imaging Spectroradiometer (MODIS) to incorporate metrics of stability / resistance, and to capture smaller patches of high-integrity forests, such as in Shestakova et al. (2022). In boreal and temperate forests with naturally occurring stand-replacing disturbances, for example wildfire, it will be critical to accurately separate these from human disturbances, for example by using spatial pattern recognition techniques (e.g., Curtis et al., 2018).

For the purpose of primary forest protection, accurate maps of regularly updated primary forests are needed at sufficient spatial scales and accuracy to support both country-level assessments as well as local decision making. Spatial assessments of forest ecosystem integrity and components, as opposed to categorical maps of forest/no-forest or broad forest types, are particularly needed. In addition to developing countries, this information is needed in the United States, Europe, and other developed countries with little remaining primary forests. In these cases, the most ecologically mature forests for a given ecosystem type (e.g., DellaSala et al., 2022b) likely represent the highest integrity levels rather than primary forests per se (**Table 1** and **Figure 2**) and similarly require both field and remote sensing analysis to be defined and identified (e.g., Federal Register, 2022). Aside from mapping methodologies and data products, we stress the need for continued and new field monitoring programs that evaluate and track ecosystem integrity components as they are impacted by climate and human land use at various scales.

More focused scientific studies on the components of ecosystem integrity as described here (**Figure 1**) are needed to better define, quantify, and monitor integrity in different ecoregions. For example, we know relatively little about how biodiversity and ecosystem composition in many forested regions globally is responding to the combined impacts of climate change, landscape fragmentation, and land use, nor how these will continue to evolve in the future. Such understanding would facilitate management decisions to increase ecosystem integrity or limit its decline, which is particularly important for managing future risks and vulnerability of carbon stocks in the context of carbon markets and offsets (Anderegg et al., 2020). Developing methods for comprehensive yet transferable ecosystem service valuations are particularly important for both scientific understanding as well as conservation mechanisms such as Payments for Ecosystem Services and the UN System of Environmental Ecosystem Accounting.

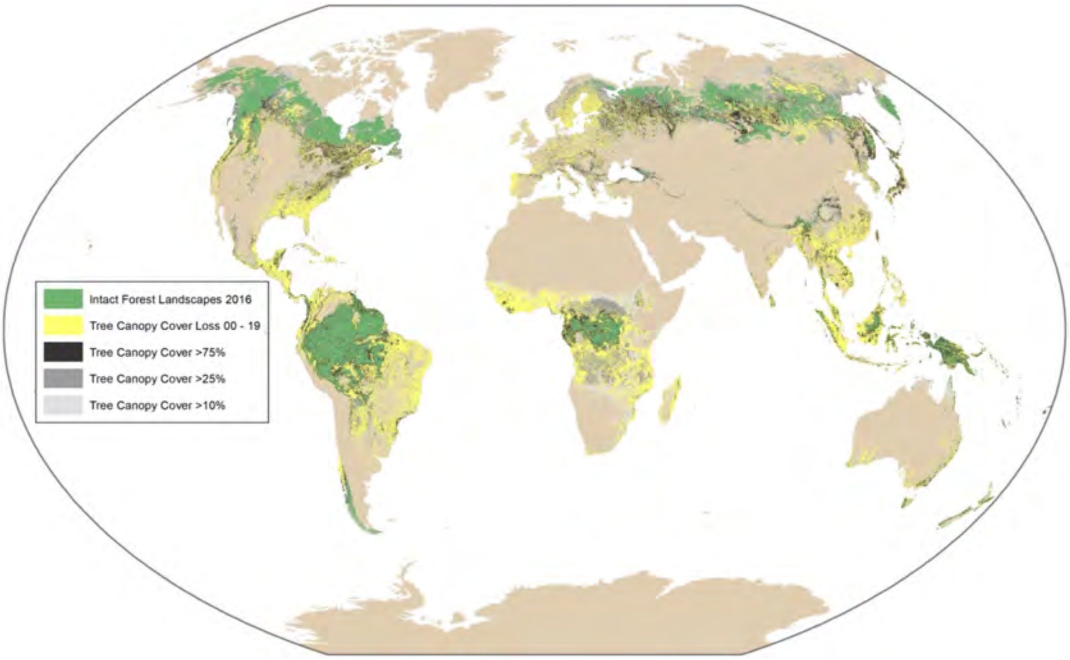

FIGURE 3
Global forest condition as indicated by metrics of Intact Forest Landscapes (IFLs), tree canopy cover, and tree canopy cover loss (from 2000 to 2019). IFLs for the year 2016 are taken from Potapov et al. (2017), and tree cover and tree cover loss outside of IFLs are from Hansen et al. (2013).

Finally, we suggest prioritizing research that optimizes the distribution of secondary forest management, including intensive plantations, to alleviate the pressure on primary and high integrity natural forests worldwide, as well as policy mechanisms needed for incentivization. Such research needs to account for regionally varying economic and equity issues in order to be effective.

Conclusion

In this paper we reviewed the components, importance, and potential for ecosystem integrity to help guide international forest policy and foster greater policy coherence across the climate, biodiversity, and sustainable development sectors. Our operating framework for forest ecosystem integrity encompasses biodiversity, dissipative structures, ecosystem processes, ecosystem stability, and the resulting ecosystem condition and services. A comparative analysis showed that, compared to forests with significant human modification, primary forests generally have higher ecosystem integrity and thus lower risk profiles for climate mitigation.

The scientific and management communities need better tools to accurately forecast the risks associated with different forest ecosystems, particularly those being managed for natural climate solutions and mitigation (Anderegg et al., 2020). Given these tools may be years or more away, we suggest focusing on ecosystem integrity is an optimal solution for categorizing forest-based risks and protecting ecosystem services. Doing so would (i) optimize investment in land carbon stocks and mitigation potential, (ii) identify stocks that provide the best insurance against risk of loss, and (iii) ensure the highest levels of benefits from ecosystem services, thereby optimizing compatibility and synergy between mitigation, adaptation, and SDGs. A number of large-scale data products exist to guide this focus. Nevertheless, there are substantial remaining gaps in terms of understanding, mapping, monitoring, and forecasting forest ecosystem integrity and its components in the midst of increasing human pressure and climate changes. Because primary forests have a higher level of ecosystem integrity than forests managed for commodity production, plantations, or degraded forests, we stress the continuing and increased need for their protection. An effective strategy is to create high carbon density strategic carbon and biodiversity reserves that include primary forests and recovering secondary forests that are quickly accumulating carbon (Law et al., 2022).

Author contributions

BR, BM, VY, and HK conceived the study. BR, BM, and HK led the writing, with contributions from CK, DD, GB, JD, RH, RB, TS, VY, and WM. All authors contributed to the article and approved the submitted version.

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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

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Adapt to more wildfire in western North American forests as climate changes

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Wildfires across western North America have increased in number and size over the past three decades, and this trend will continue in response to further warming. As a consequence, the wildland–urban interface is projected to experience substantially higher risk of climate-driven fires in the coming decades. Although many plants, animals, and ecosystem services benefit from fire, it is unknown how ecosystems will respond to increased burning and warming. Policy and management have focused primarily on specified resilience approaches aimed at resistance to wildfire and restoration of areas burned by wildfire through fire suppression and fuels management. These strategies are inadequate to address a new era of western wildfires. In contrast, policies that promote adaptive resilience to wildfire, by which people and ecosystems adjust and reorganize in response to changing fire regimes to reduce future vulnerability, are needed. Key aspects of an adaptive resilience approach are (*i*) recognizing that fuels reduction cannot alter regional wildfire trends; (*ii*) targeting fuels reduction to increase adaptation by some ecosystems and residential communities to more frequent fire; (*iii*) actively managing more wild and prescribed fires with a range of severities; and (*iv*) incentivizing and planning residential development to withstand inevitable wildfire. These strategies represent 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. We propose an approach that accepts wildfire as an inevitable catalyst of change and that promotes adaptive responses by ecosystems and residential communities to more warming and wildfire.

wildfire | resilience | forests | wildland–urban interface | policy

Wildfire is a key driver of ecosystem change that increasingly poses a significant threat and cost to society. In western North America (hereafter, the West), warming, frequent droughts, and legacies of past management combined with expansion of residential development have made social–ecological systems (SESs) more vulnerable to wildfire. As the annual area burned has increased over the past three decades, we are confronting longer fire seasons (1, 2), more large fires (3, 4), a tripling of homes burned (5), and more frequent large evacuations. In 2016, the Fort McMurray Fire in Alberta, Canada and the Blue Cut Fire in southern California prompted evacuation orders for a combined total of more than 160,000 people. The costs of wildfire have also risen substantially since the 1990s. The US Congress appropriated $13 billion for fire suppression and $5 billion for fuels management in fiscal years 2006–2015 (6). Other societal costs, including real estate devaluation, emergency services, and postfire rehabilitation, total up to 30 times the direct cost of firefighting (7).

Notwithstanding these costs, many plants, animals, and ecosystem services benefit from fire, and those dependent on frequent fire have been negatively affected by the significantly reduced burning resulting from fire suppression, as compared with the period before European settlement

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(8). However the response of ecosystems to increases in wildfire activity and warming in the coming decades is not well understood. Broad heterogeneity among western forest landscapes in terms of biophysical environment, past management, human footprint, and the role of fire and future warming creates a complicated playing field. Managing ecosystems, people, and wildfire in a changing climate is a complex but critical challenge that requires effective and innovative policy strategies (9, 10).

Our key message is that wildfire policy and management require a new paradigm that hinges on the critical need to adapt to inevitably more fire in the West in the coming decades. Policy and management approaches to wildfire have focused primarily on resisting wildfire through fire suppression and on protecting forests through fuels reduction on federal lands. However, these approaches alone are inadequate to rectify past management practices or to address a new era of heightened wildfire activity in the West (11–14).

In delivering this message, we focus specifically on the distinction between specified, adaptive, and transformative resilience (15, 16). Rigorous definition and critical assessment of resilience to wildfire are needed to develop effective policy and management approaches in the context of climate change. We suggest an approach based on the concept of adaptive resilience, or adjusting to changing fire regimes (e.g., shifts in prevailing fire frequency, severity, and size) to reduce vulnerability and build resilience into SESs. Adaptive resilience to wildfire means recognizing the limited impact of past fuels management, acknowledging the important role of wildfire in maintaining many ecosystems and ecosystem services, and embracing new strategies to help human communities live with fire. Our discussion focuses on western North American forests but is relevant to fire-influenced ecosystems across the globe. We emphasize that long-term solutions must integrate relevant natural and social science into policies that successfully foster adaptation to future wildfire.

Why Has Coping with Wildfire Become Such a Challenge?

Three primary factors have produced gradual but significant change across western North American landscapes in recent decades: the warming and drying climate, the build-up of fuels, and the expansion of the wildland–urban interface (WUI; the zone where houses meet or intermingle with undeveloped wildland vegetation).

In terms of climate, wildfire activity is closely tied to temperature and drought over time scales of years to millennia (2, 17–19). Globally, the length of the fire season increased by 19% from 1979 to 2013, with significantly longer seasons in the western United States (1). Since 1985, more than 50% of the increase in the area burned by wildfire in the forests of the western United States has been attributed to anthropogenic climate change (20). Increases in the number of wildfires and area burned in most forested ecoregions of the West are a result of rising temperatures, increased drought, longer fire seasons, and earlier snowmelt (1–4, 21). Specifically, since the 1970s the frequency of large fires has increased most dramatically in the forests of the Northwest (1,000%) and Northern Rocky Mountains (889%), followed by forests in the Southwest (462%), Southern Rockies (274%), and Sierra Nevada (256%), in response to earlier snowmelt and a longer fire season (21). Based on spatial overlays in western United States forests of large wildfires since 1984 (Monitoring Trends in Burn Severity, available at www.mtbs.gov/dataaccess.html and Existing Vegetation Types, available at https://www.landfire.gov/vegetation.php), we found that in northern regions with dramatic increases in fire activity (the Canadian Rockies, Middle Rockies, and Idaho Batholith ecoregions) cold/wet subalpine forests predominantly burned. These forests characteristically burn at high severity and have not experienced a significant build-up of fuels. Overall, cold/wet forests account for about a quarter of total forest burning in the US West since 1984.

Fire suppression, in addition to past logging and grazing and invasive species, has led to a build-up of fuels in some ecosystems, increasing their vulnerability to wildfire. For example, drier, historically open coniferous forests in the West ("dry forests") have experienced gradual fuels build-up in response to decades of fire suppression and other land-use practices (8, 22, 23). Historically, predominantly frequent, low-severity fires killed smaller, less fire-resistant trees and maintained low-density dry forests of larger, fire-resistant trees. Large, high-severity fires now threaten to convert denser, more structurally homogeneous dry forests to nonforest ecosystems, with attendant loss of ecosystem services (24). However, only forests in the Southwest show a clear trend of increasing fire severity over the last three decades, and only a quarter to a third of the area burned in the western United States experienced high severity during that time (25, 26). Although fuels build-up in dry forests can increase the area burned because of higher contagion, the 462% increase in the frequency of large fires in southwestern forests since the 1970s is also a result of an extension of the fire season by 3.6 mo [the average for the western United States is 2.8 mo (21)]. Overall, dry forests account for about half of the total forest burning in the western United States since 1984.

Alongside these increases in warming and fuels, the WUI has expanded tremendously in the past few decades, augmenting wildfire threats to people, homes, and infrastructure. Between 1990 and 2010, almost 2 million homes were added in the 11 states of the western United States, increasing the WUI area by 24% (27). Currently, most homes in the WUI are in California (4.5 million), Arizona (1.4 million), and Washington (1 million) (27). Since 1990, the average annual number of structures lost to wildfire has increased by 300%, with a significant step-up since 2000 (28). About 15% of the area burned in the western United States since 2000 was within the WUI, including a 2.4-km community protection zone, with the largest proportion of wildfires burning in the WUI zone in California (35%), Colorado (30%), and Washington (24%) (Fig. 1) (27). Additionally, almost 900,000 residential properties in the western United States, representing a total property value more than $237 billion, are currently at high risk of wildfire damage (29). Because of the people and property values at risk, WUI fires fundamentally change the tactics and cost of fire suppression as compared with fighting remote fires and account for as much as 95% of suppression costs (28). Together, these gradually changing variables—climate change, fuels build-up, and residential development—interact with rapid combustion to increase wildfire risks and costs to society and some ecosystems substantially.

Potential Consequences of Future Wildfire

Wildfire activity is predicted to increase in the West over the next century (20, 30, 31). This anticipated ramp-up in burning and possible directional changes in fire regimes (e.g., increases in fire frequency, severity, and/or size) could transform the composition, structure, and function of many forest (8, 32, 33), shrubland, and grassland ecosystems (34). Changes in temperature and precipitation in semiarid shrublands and grasslands may reduce fuel availability subsequently, to the extent that fire occurrence, size, and severity in such areas will eventually decline (35). Thus, although fire activity is projected to increase in the West in the near term (i.e., in the next few decades), longer regional trends will depend on feedbacks between vegetation and fire as well as on anthropogenic alterations in vegetation and land use (36, 37).

Increased exposure of communities to wildfire is also expected with additional warming. More than 3.6 million ha, or almost 40% of the current WUI in the western United States, is predicted to experience moderate to large increases in the probability of wildfire in the next 20 y (Fig. 2). This increase is in addition to the growing wildfire risk to developed nonurban areas (e.g., energy production) and infrastructure (e.g., power lines, pipelines) that define a broader wildland–development

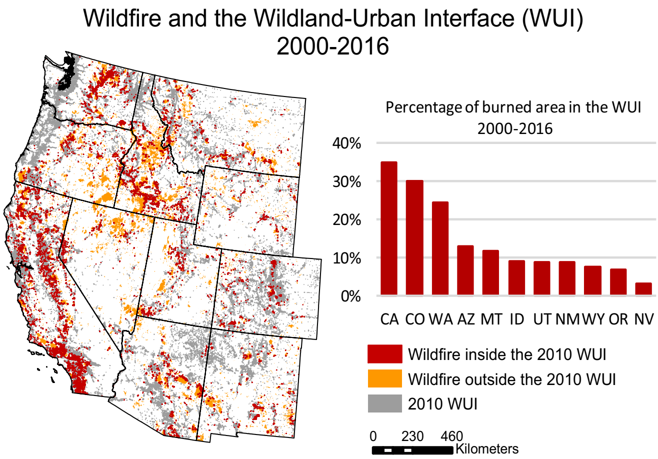


Fig. 1. (*Left*) Area burned by wildfires between 2000 and 2016 across the western United States inside and outside the 2010 WUI including a 2.5-km community protection zone (27). (*Right*) About 15% of the WUI burned during this period, with largest proportions of the WUI burning in California, Colorado, and Washington.

interface. Continued WUI growth will further increase human exposure to wildfires (38) and anthropogenic ignitions (37, 39). By midcentury, 82 million people in the western United States are likely to experience more and longer "smoke waves," defined as consecutive days of high, unhealthy particulate levels from wildfires (40). Climate change and increasing exposure of existing and future development to wildfire and smoke present a dangerous and vexing problem for residents, local officials, fire fighters, and managers.

Gradual but significant changes in climate, fuels, and the WUI affect wildfire impacts on ecosystems and society but are difficult to recognize and are challenging to alter meaningfully. There often is a lack of political will to implement policies that incur short-term costs despite their long-term value or to change long-standing policies that are ineffective. For example, few jurisdictions have the will or means to restrict further residential development in the WUI, although modifying and curtailing residential growth in fire-prone lands now would reduce the costs and risks from wildfire in the long term. Furthermore, although the impacts of fire suppression on fuels build-up are now well understood, fire-suppression policies still dominate current fire management (13). Projected global warming of at least 1.1–3.1 °C in the coming century offers a unique opportunity to change policy and the course of our response to wildfires (41). A paradigm shift now in approaches to WUI development and management of fire and fuels can yield tremendous benefits to society later.

Specified, Adaptive, and Transformative Resilience to Wildfire

Resilience is increasingly invoked as a guiding principle in strategies that address the social and ecological dimensions of wildfire. The US Forest Service's National Cohesive Wildland Fire Management Strategy (42) specifically addresses the need to bolster social and ecological resilience to increasing wildfires. Although often invoked in wildfire management and policy, resilience is defined inconsistently or neglects social or ecological contexts, despite the need for uniformity and specification in setting goals and evaluating progress (43, 44).

Defining resilience to wildfire in an SES is especially challenging in the WUI, where people, ecosystems, and wildfire interact over multiple spatial and temporal scales (12). An SES is the intersection and interdependence of biophysical units and associated people and institutions. Resilience in an SES generally has been defined as the capacity to absorb disturbance so as to retain essential structures, processes, and feedbacks and to adapt to and reorganize following disturbance (45). These perspectives of resilience, absorbing versus adapting to disturbance, offer different guiding principles for policy and management in responding to wildfire and measuring success over different planning timelines (44). Here we outline a consistent framework that defines resilience to wildfire in coupled SESs based on the concepts of specified resilience and general resilience, the latter of which includes adaptive and transformative approaches (Table S1) (15, 16, 44).

When climate trends or disturbance regimes are relatively stable and well-characterized and planning horizons are short (years), specified resilience or restoration is an appropriate guiding principle. "Specified resilience" refers to the buffer capacity of a system to retain its identity after a well-specified disturbance (16). Specified resilience reflects the concept of ecological resilience, which refers to the capacity of a system to absorb or tolerate disturbance without shifting to a qualitatively different state controlled by a different set of processes (46). In terms of wildfire, specified resilience applies when fire characteristics are within the bounds of historical range of variability (HRV) of disturbance regimes and a burned forest recovers without converting to another state, e.g., to a nonforest state such as a persistent grassland. In a social context, specified resilience is evident when a community recovers economically and rebuilds similar structures in similar locations following a wildfire (44, 47). Management guided by specified resilience often values recent ecological and social dynamics, particularly when the goal is the conservation of particular species or landscapes. Such management is often informed by short temporal windows of HRV, or "recent HRV" (rHRV) (Fig. 3). This approach can be useful for responding to fires in the short term. However, when social and environmental conditions change rapidly, this approach may foster management goals that are unrealistic or unsustainable in the long run (48, 49).

When climate and wildfire trends are changing and planning horizons are intermediate (decades), general resilience is a more appropriate and desirable guiding principle. "General resilience" refers to the capacity of an SES to adapt or transform in response to unknown shocks or disturbances outside the rHRV (16). Adaptive resilience incorporates aspects of change, reorganization, learning, and adaptability in response to changing climate and disturbance regimes and is an on-going process achieved by harnessing adaptive capacity. In an ecological context, adaptive resilience refers to actively or passively supporting species compositions and fuel structures that are better adapted to a warming, drying climate with more wildfire. Management of specified resilience maintains ecosystems within the rHRV,

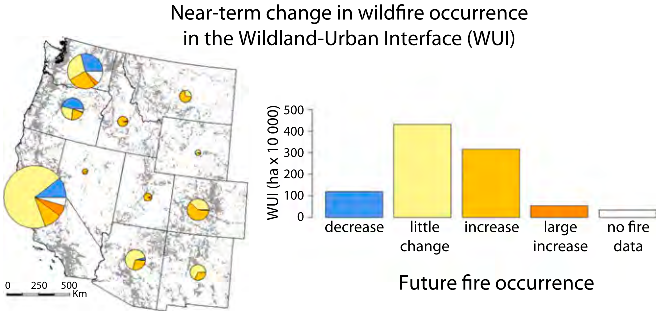


Fig. 2. (*Left*) Area of the WUI in the conterminous western United States, classified according to projected near-term changes in fire occurrence. The size of each pie is scaled relative to the area of the WUI (both intermix and interface) in each state, based on data from Martinuzzi, et al. (27). Within each pie, slices represent the proportion of WUI area overlapping the five categories of projected fire occurrence for the period 2010–2039, based on data from Moritz, et al. (30). (*Right*) The bar chart summarizes the area of the WUI projected to experience each level of change in fire occurrence in the western United States.

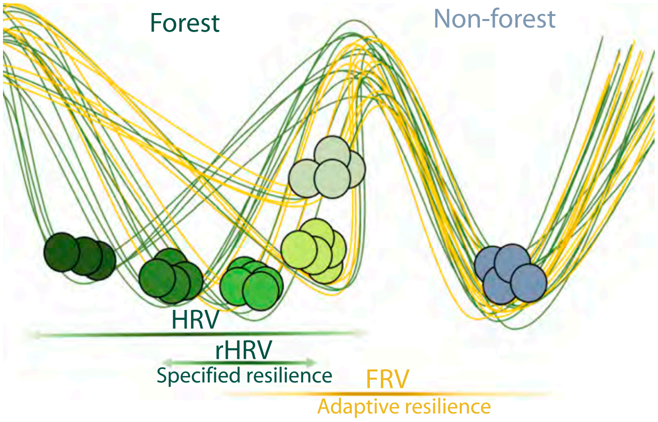


Fig. 3. **Conceptual ball-and-basin representation of specified and adaptive resilience across a forested landscape. Lines defining basins depict the ranges of variation in fire regimes across forest types. Sets of green balls reflect the variation in abundance and composition within different forest types, and the set of blue balls represents nonforest ecosystems. Specified resilience of forests to wildfire is maintained within basins that fall within an rHRV of fire regimes over recent decades to centuries, typically derived from historical documents, remotely sensed data, and tree-ring data. Longer definitions of HRV reflect variation in fire regimes over the last 4,000–5,000 y, when present-day forest types were established in most regions; these data are derived from paleoecological reconstructions. Adaptive resilience to changing fire regimes is reflected within basins that fall within the FRV (yellow). Under the FRV, shifts to nonforest ecosystems remain unlikely in some cases (lower green balls) and more likely in other cases with easier transition to nonforest basin (higher green balls). Changes in the severity, frequency, and size of fire regimes and long-term regeneration following fire events reflect adaptive responses to changing fire regimes and climate conditions across broad scales.**

whereas managing for adaptive resilience considers how changing disturbance regimes may favor suites of traits that are better adapted to a future range of variability (FRV) (Fig. 3) (22). Alignment of fire regimes with adaptive regeneration traits of native vegetation defines a safe operating space (50). The HRV can still play a role by providing insight into how adaptive traits align with changing disturbance regimes to confer adaptive resilience, but under the FRV the safe operating space is shifting (Fig. 3) (50, 51, 52). In a social context, communities exhibiting adaptive resilience engage in ecological, psychological, social, and policy processes that set the community on a trajectory of change to reduce future vulnerability (Fig. 4) (53). Strategies may include changing building codes to make structures more fire-resistant, planning communities to avoid or withstand future wildfire, or providing incentives, education, and resources to reduce vulnerability to future wildfire (47). Adaptive resilience also involves institutional learning, where past management approaches to wildfire evolve.

When climate and wildfire trends are significantly altered from historical trends and/or variability, and planning horizons are long (century), transformative resilience may be necessary. "Transformative resilience" refers to planned fundamental change in response to drastically altered disturbances that have the potential to create broad-scale, systemic shifts in ecological states or radical shifts in values, beliefs, social behavior, and multilevel governance. Examples might include significant regional changes in ecosystem states and associated loss of ecosystem services and/or the relocation of communities of people away from wildfire-prone areas (44, 54). Rapid, planned social–ecological transformation is rare and difficult to implement because of uncertainties about future risk, inflexible institutions and behaviors, and the high cost of transformative action (55).

Although distinct, these approaches to resilience may be nested. Promoting specified resilience may make some forests better poised for adaptive resilience as climate changes, but in some forests or conditions specified resilience may not be effective as climate changes (e.g., refs. 56, 57). Allowing postfire shifts from forest to grassland or shrubland may increase adaptive resilience to changing wildfire and climate conditions. Approaches to adaptive resilience could reduce the need for transformation if efforts keep pace with climate and wildfire trends or may help pave the way toward inevitable social–ecological change. Embracing specified resilience may be the easiest, most familiar path with the least uncertainty, but this approach is short-sighted and could come at the cost of adaptation to future wildfire as climate change continues.

Taking an adaptive resilience approach now is critical, because specified resilience, although useful in some contexts, will become a less useful guiding principle as we exceed HRVs. Adaptive resilience means adjusting to changing fire regimes and climate—in both social and ecological systems—by taking advantage of opportunities to moderate potential impacts and cope better with the consequences. Adapting to wildfire sooner rather than later provides the widest benefits to society at the least cost. If we do not adapt to wildfire now, disruptive and unintended transformations of SESs in the West may ensue.

How Policy and Management Can Promote Adaptive Resilience to Wildfire

Current approaches to managing wildfire focus primarily on controlling fire through suppression and secondarily focusing on managing fuels build-up in forests. Within the context of current and future trends in wildfire, we evaluate the following three approaches in terms of their promise for fostering adaptive resilience in ecosystems and residential communities living with more wildfire: (*i*) managing fire, (*ii*), managing fuels, and (*iii*) promoting adaptive capacity (Fig. 5).

Fig. 4. **Wildfires are catalysts of change that promote adaptive resilience by communities and ecosystems to future wildfires. (*A* and *B*) Example of adaptation in communities. (*A*) A home burned in the 2010 Fourmile fire, Boulder County, CO, which at the time was the most destructive fire in Colorado history in terms of home loss. (*B*) A home that survived the 2016 Cold Springs fire, where many residents managed structural and vegetative fuels around their home to reduce fire hazard after the Fourmile fire through Boulder County's Wildfire Partners program. (*C* and *D*) Heterogeneity in wildfire severity promotes diversity in postfire regeneration and fuels in the 2002 Rodeo-Chediski fire, Coconino and Navajo counties, AZ (*C*) and the 2016 Canyon Creek fire, Grant County, OR (*D*). Photographs courtesy of REUTERS/Alamy Stock Photo (*A*), Wildfire Partners (*B*), Tom Bean/Alamy Stock Photo (*C*), and M.A.K. (*D*).**

Managing Wildfire

Suppressing Fewer Fires and Prescribing More Burning. Increasing the use of prescribed fires and managing rather than aggressively suppressing wildland fires can promote adaptive resilience as the climate continues to warm. Many dry forests currently experience significantly less burning than in the period just before European settlement (8, 35, 58). In recognition of the fire-dependence of many ecosystems, the 1995 Federal Wildland Fire Management policy ushered in the first federal policy aimed at reintroducing more wildfire on public lands; that policy remains in effect today. US federal agencies actively managed an average of 75,000 ha of lightning-caused fires per year under the Wildland Fire Use policy from 1998–2008 and currently burn about 1 million hectares per year with prescribed fires (58). However, prescribed fires still constitute only about 10% of the treatments implemented by the US Forest Service in the West and burn about one-third of the area burned by wildfires (National Interagency Fire Center, https://www.nifc.gov/). In the United States and Canada, suppression remains the primary approach to wildfire, with more than 95% of all wildfires suppressed (28). Continued aggressive fire suppression is counterproductive to building adaptive resilience to increasing wildfire in the long term (13, 14).

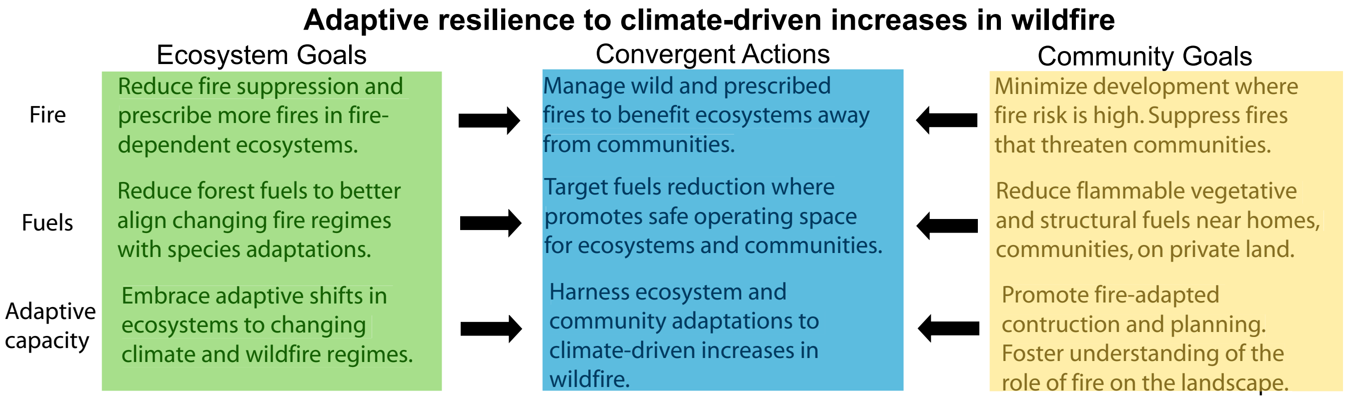
Using Fire to Foster Adaptive Resilience to Climate Change. In some systems, fire today attenuates future fire effects, because flames that burn dead and live fuel limit where and how severely subsequent fires burn, at least for a time (59–61). Fires often create complex patterns of burn severity that create variation in postfire regeneration and fuels (62–67). As fire regimes shift over time, individual fire events filter for species adapted to changing fire and climate conditions (68). Strategic planning for more managed and uncontrolled wild fires on the landscape today (69) may help decrease the proportion of large and severe wildfires in the coming decades and may enhance adaptive resilience to changing climate. Prescribed fires, ignited under cooler and moister conditions than are typical of most wildfires, can reduce fuels and minimize the risk of uncontrolled forest wildfire near communities. In contrast to wildfires, prescribed fire risks are relatively low, and more than 99% of prescribed fires are held within planned perimeters successfully (58).

Challenges to increasing use of managed and prescribed fires vary from the public's limited experience with smoke and wildfire to significant direct health impacts of smoke on vulnerable populations, including children, the elderly, and low-income communities (40, 70, 71). Some smoke hazards can be reduced through careful planning and management of fire, public health monitoring, and provisioning of health services for vulnerable populations. Public perceptions of fire are also an important hurdle, given the success of Smokey Bear's fire-prevention campaign and because most urban and suburban residents have very limited experience with wildfire compared with rural residents of the early 20th century. Therefore, public education programs that demonstrate the inevitability of wildfire will be a key aspect of living with increasing fire in the West. We need to develop a new fire culture. Despite these and various legal and operational challenges (58), the benefits of prescribed fire and managed wildfires to ecosystems and communities are high (72). Promoting more wildfire away from people and prescribed fires near people and the WUI are important steps toward augmenting the adaptive resilience of ecosystems and society to increasing wildfire.

Managing Fuels

Limiting Reliance on Fuels Treatments to Alter Regional Fire Trends. Managing forest fuels is often invoked in policy discussions as a means of minimizing the growing threat of wildfire to ecosystems and WUI communities across the West. However, the effectiveness of this approach at broad scales is limited. Mechanical fuels treatments on US federal lands over the last 15 y (2001–2015) totaled almost 7 million ha (Forests and Rangelands, https://www.forestsandrangelands.gov/), but the annual area burned has continued to set records. Regionally, the area treated has little relationship to trends in the area burned, which is influenced primarily by patterns of drought and warming (2, 3, 20). Forested areas considerably exceed the area treated, so it is relatively rare that treatments encounter wildfire (73). For example, in agreement with other analyses (74), 10% of the total number of US Forest Service forest fuels treatments completed 2004–2013 in the western United States subsequently burned in the 2005–2014 period (Fig. 6). Therefore, roughly 1% of US Forest Service forest treatments experience wildfire each year, on average. The effectiveness of forest treatments lasts about 10–20 y (75), suggesting that most treatments have little influence on wildfire. Implementing fuels treatments is challenging and costly (7, 13, 76, 77); funding for US Forest Service hazardous fuels treatments totaled $3.2 billion over the 2006–2015 period (6). Furthermore, forests account for only 40% of the area burned since 1984, with the majority of burning in grasslands and shrublands. As a consequence of these factors, the prospects for forest fuels treatments to promote adaptive resilience to wildfire at broad scales, by regionally reducing trends in area burned or burn severity, are fairly limited.

Targeting Fuels Treatments in Ecosystems with Fuel Build-Up and on Private Lands. Strategically targeting treatments in areas where fuels build-up has increased the expected burn severity may augment the adaptive resilience of those ecosystems to increasing wildfire. For example, treating drier forests, where the likelihood of fire is



	Ecosystem Goals		Convergent Actions		Community Goals
Fire	Reduce fire suppression and prescribe more fires in fire-dependent ecosystems.	→	Manage wild and prescribed fires to benefit ecosystems away from communities.	←	Minimize development where fire risk is high. Suppress fires that threaten communities.
Fuels	Reduce forest fuels to better align changing fire regimes with species adaptations.	→	Target fuels reduction where promotes safe operating space for ecosystems and communities.	←	Reduce flammable vegetative and structural fuels near homes, communities, on private land.
Adaptive capacity	Embrace adaptive shifts in ecosystems to changing climate and wildfire regimes.	→	Harness ecosystem and community adaptations to climate-driven increases in wildfire.	←	Promote fire-adapted contruction and planning. Foster understanding of the role of fire on the landscape.

Fig. 5. **Convergent actions that promote adaptive resilience to climate-driven increases in wildfire in the West by ecosystems and communities, based on goals related to management of fire, fuels, and adaptive capacity.**

high, may also increase opportunities to modify wildfire behavior and postfire recovery. Burn severity has increased because of past fire suppression and fuels build-up in low-elevation dry forests adapted to predominantly frequent, low-severity surface fires (8, 11, 22, 25, 78, 79). In these forests, fuels treatments that remove midstory and understory fuels through thinning and prescribed fire can reduce fire intensity, severity, and rate of spread and may promote adaptive resilience to more frequent fire. Such forests were preferentially treated under the National Fire Plan in 2004–2008 (80). Thinning may effectively restore more frequent, low-severity fire in some dry forests, but when thinning is combined with the expected warming, unintended consequences may ensue, whereby regeneration is compromised and forested areas convert to nonforest (56, 57, 81). Strategic placement of treatments to promote low-severity fire at ecotones between dry and mesic forest distributions may help facilitate postfire migration of species better adapted to warmer, drier conditions.

Midelevation mixed conifer forests, or mesic forests, which typically experienced broad variance in fire frequency and severity, may also benefit from fuels treatments that reduce the likelihood of large patches of high-severity fire and facilitate the migration of species adapted to drier, warmer conditions (77). In contrast, cold/wet forests, such as high-elevation subalpine forests, are adapted to high-severity fire that historically recurred at relatively long (∼100–300 y) intervals (19, 82, 83) and have not experienced unprecedented fuels build-up in recent decades. Severe wildfires have occurred for millennia across a broad range of forests and shrublands, and in many ecosystems species are adapted to severe fire (17, 19, 84, 85), although postfire regeneration may be comprised by drier, warmer conditions (86).

Fuel-reduction treatments also hold promise for locally reducing wildfire hazard around WUI communities if treatments are strategically located to protect homes and the surrounding vegetation. Fuel reduction on federal lands and in municipal watersheds is a primary management tool that has limited application in the WUI, where the majority of land is privately owned (87). Home loss to wildfire is a local event, dependent on structural fuels (e.g., building material) and nearby vegetative fuels (88, 89). Therefore, fuels management for home and community protection will be most effective closest to homes, which usually are on private land in the WUI where ignition probabilities are likely to be high (37). Programs that facilitate the targeted removal of fuels from private land, such as community chipping programs, have been highly successful in some areas, at relatively low cost. The Wyden and Good Neighbor authorities and federal programs, such as the US Forest Service Collaborative Forest Landscape Restoration Program, take an "all-lands" approach to forest management through collaboration with landowners and communities. These policies and programs are roadmaps for augmenting fuel-management efforts across land ownerships. These and other more ambitious policies that facilitate significant fuels management on private land, on a par with fuel-reduction efforts on federal lands, are needed. New policies that facilitate private-land fuels management are critical to augment significantly the adaptive resilience of communities to increasing wildfire.

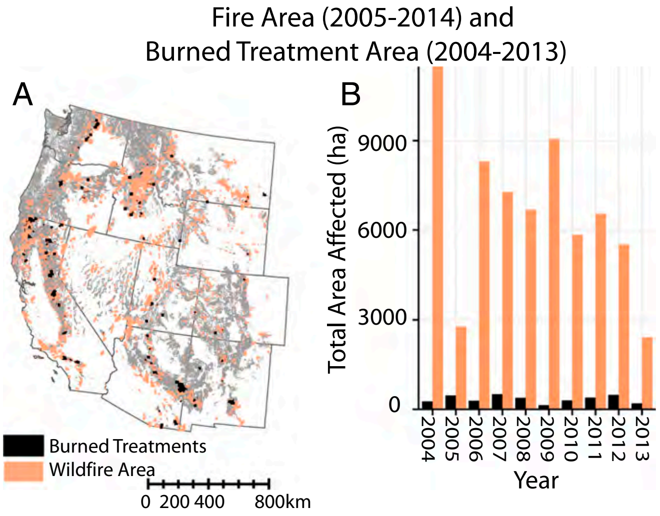


Fig. 6. (*A*) Spatial distribution and area of US Forest Service fuels treatments from 2004–2013 and wildfire from 2005–2014 across forests and woodlands in the western United States. About 3% of the total treated area and 10% of the total number of treatments burned in the period 2005–2014. (*B*) Annual total wildfire area and total burned treatment area. Data are from the following: (1) US Forest Service fuels treatments: Hazardous Fuel Treatment Reduction Polygon (https://data.fs.usda.gov/geodata/edw/datasets.php), (2) Wildfires >1000 ac: Monitoring Trends in Burn Severity Burned Areas Boundaries (www.mtbs.gov/dataaccess.html), (3) Wildfires ≤1000 ac: GeoMAC Historic Fire Perimeters (https://rmgsc.cr.usgs.gov/outgoing/GeoMAC/historic_fire_data/).

Promoting Adaptive Capacity

Fostering and Embracing Adaptive Shifts in Ecosystems. Management of fire and fuels will help some ecosystems withstand more frequent fires and possibly may reduce the risk of larger, more severe fires that may compromise forest recovery. Such efforts will be significant in high-value ecosystems or locations, in helping slow the pace of change and providing a chance for ecosystems and species to adapt to changing fire regimes. The HRV concept can guide management in identifying ecological vulnerabilities and adaptation strategies to changing disturbance regimes (Fig. 3) (50, 51, 52). However, quantifying ecological objectives outside the HRV will be increasingly important in guiding management as fire regimes and climate continue to change (90, 91). Given such uncertainties, management must be adaptive and iterative, and monitoring will be critical to assessing progress. Given the vast area of fire-prone forests in the West, management can directly affect only a small portion of forests. In the majority of forested ecosystems beyond our effective reach, we will have to accept and even embrace changing ecological conditions. While some forests may be entering decades of significant change with high tree mortality in response to drought, wildfire, insect outbreaks, and legacies of past management (86, 92), they also are in the process of adjusting to new conditions to which they will be better adapted and that may challenge our existing philosophies of and approaches to conservation.

Creating Fire-Adapted Communities. The majority of home building on fire-prone lands occurs in large part because incentives are misaligned, where risks are taken by homeowners and communities but others bear much of the cost if things go wrong. Therefore, getting incentives right is essential, with negative financial consequences for land-management decisions that increase risk and positive financial rewards for decisions that reduce risk. For example, shifting more of the wildfire protection cost and responsibility from federal to state, local, and private jurisdictions would better align wildfire risk with responsibility and provide meaningful incentives to reduce fire hazards and vulnerability before wildfires occur. Currently, much of the responsibility and financial burden for community protection from wildfire falls on public land-management agencies. This arrangement developed at a time when few residential communities were embedded in fire-prone areas. Land-management agencies cannot continue to protect vulnerable residential communities in a densifying and expanding WUI that faces more wildfire (12). The US Government Accountability Office questioned the US Forest Service's prioritizing protection of WUI communities that lie under private and state jurisdictions and has argued for increased financial responsibility for WUI wildfire risk by state and local governments (93). This shift in obligation would enhance adaptive governance and could increase the motivation to pursue adaptive resilience of WUI communities to increasing wildfire (94).

Another promising approach for increasing adaptive resilience of WUI residents to wildfire is the promotion of fire-adapted planning in communities. Providing incentives for counties, communities, and homeowners to plan fire-safe residential development for both existing and new homes and discouraging new development on fire-prone lands will make communities safer (89, 94–96). Communities can use land-use and development codes that encourage developers to set aside open space and recreational trails as fuel breaks and require ignition-resistant construction materials in fire-prone settings. For example, San Diego, California enforces strict brush management regulations; the Flagstaff, Arizona fire department uses a WUI development code to protect properties; and Santa Fe, New Mexico applies stringent fire-safe regulations on new developments to protect its watershed (97). Programs such as the Community Planning Assistance for Wildfire (CPAW; planningforwildfire.org), funded by the US Forest Service and private foundations, offer assistance to communities in the form of advice on land-use planning and detailed mapping of wildfire risk. Another example is California, which employs a statewide Fire Hazard Severity Zone map to guide development plans and building codes that reduce wildfire risk. With 84% of potential WUI lands in the West still undeveloped (98), land-use planning now has high potential to reduce the vulnerability of communities to future wildfire. Furthermore, fire-adapted planning may increase management options in terms of how, where, and when fire can be used as a tool for reducing the spread of wildfires into communities and rejuvenating fire-dependent ecosystems, thus increasing the adaptive resilience of communities and ecosystems to more wildfire.

Strengthening and expanding programs such as Fire Adapted Communities, Fire Adapted Communities Learning Network, Firewise Communities USA, and FireSmart Canada will also help communities become more fire-adapted. Capacities to assume these responsibilities will vary significantly among homeowners, communities, and local jurisdictions with markedly different risks and resources (99–101). For example, home hazard mitigation programs and community planning tools are more successful in communities at the fringe of urban areas that have more financial resources and often have a greater trust in government than in more isolated, resource-dependent WUI communities, immigrant non–English-speaking communities, or tribal and First Nations communities (101). Although some tax incentives and rebates are available for wildfire risk mitigation on and around homes, more comprehensive programs that include broader incentives and support are needed for meaningful and widespread impacts. Efforts that combine wildfire-specific efforts with other community capacity-building efforts may leverage the networks that enable communities to act on shared notions of risk (102).

Overall, a shift in resources from the defense of the WUI from wildfire to the mitigation of wildfire hazards and risks in advance of events will build a safe operating space for fire-prone communities that increases adaptive resilience to wildfire. Encouraging development away from fire-prone areas, reducing fuels on private lands in and near communities, and retrofitting and building homes to withstand ignition will increase the adaptive capacity for managing more wildfire (89), similar to adaptive approaches for other natural hazards such as flooding and earthquakes (12). Communities and institutions are long-lived, and disruptive events such as wildfires create windows of opportunity that can shift rules, norms, and expectations to increase adaptive resilience to future wildfires.

Conclusions

Policies that foster adaptive resilience enable WUI communities and fire-prone ecosystems to adjust to increased wildfire risk and reduce future vulnerability. Adaptive resilience provides a realistic framework as the climate warms and wildfires increase, but how will we know if we are achieving adaptive resilience to future fires? On the societal front, minimizing the costs of suppression in the WUI, the number of homes lost to wildfire, the area burned in the WUI, and the number of smoke-related health problems are some metrics. Developing state- or county-wide maps of fire hazard, home survivability rating, and the adaptive capacity of communities would be useful tools in developing this framework.

Some ecosystems will survive and thrive as they adapt to novel future conditions, but not all will. Embracing rather than resisting ecological change will require a significant paradigm shift by individuals, communities, and institutions and will challenge our conservation philosophies. Wildfire is an important catalyst of responses to climate change by communities and ecosystems. Patterns of wildfire are changing with rising global temperatures, and will accelerate in the future. What we can do now is focus management efforts on the places where intervention is needed to slow the pace of change and thereby give particular species and ecosystems a chance to adapt. We also can change how we build, live, and work in fire-prone landscapes to keep our communities safe, healthy, and vibrant.

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Review

Management for Mountain Pine Beetle Outbreak Suppression: Does Relevant Science Support Current Policy?

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Abstract: While the use of timber harvests is generally accepted as an effective approach to controlling bark beetles during outbreaks, in reality there has been a dearth of monitoring to assess outcomes, and failures are often not reported. Additionally, few studies have focused on how these treatments affect forest structure and function over the long term, or our forests' ability to adapt to climate change. Despite this, there is a widespread belief in the policy arena that timber harvesting is an effective and necessary tool to address beetle infestations. That belief has led to numerous proposals for, and enactment of, significant changes in federal environmental laws to encourage more timber harvests for beetle control. In this review, we use mountain pine beetle as an exemplar to critically evaluate the state of science behind the use of timber harvest treatments for bark beetle suppression during outbreaks. It is our hope that this review will stimulate research to fill important gaps and to help guide the development of policy and management firmly based in science, and thus, more likely to aid in forest conservation, reduce financial waste, and bolster public trust in public agency decision-making and practice.

Keywords: bark beetle; clearcut; climate change; climate change adaptation; daylighting; *Dendroctonus ponderosae*; forest pest management; monitoring; sanitation; thinning

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1. Introduction

Insect outbreaks are increasing in size and severity on a global scale [1]. In North America alone, three massive insect outbreaks occurred within the last two decades, all involving native bark beetles in conifers [2]. Of these, the mountain pine beetle (*Dendroctonus ponderosae*) outbreak is an order of magnitude larger than any previously recorded. A variety of factors, natural and anthropogenic, converged to result in these dramatic events [2]. Each outbreak has not only had severe ecological effects, but each has also triggered human responses that, for better or for worse, have resulted in additional impacts along with massive expense [3]. Predictions are that outbreaks of bark beetles will become more frequent and severe in the future [4,5] indicating an imperative need to critically assess the efficacy and impacts of our approaches to their management.

Outbreaks of bark beetles are not new. They have been occurring for millennia and have played a major role in shaping coniferous forest ecosystems of the world. While considerable research has been conducted on controlling bark beetles, massive gaps in knowledge remain. In particular, there is a disturbing dearth of rigorous replicated empirical studies assessing the effects of various management strategies, particularly timber harvest treatments, for bark beetle outbreak suppression. Even fewer studies have focused on how such treatments meet explicit goals or affect forest structure, function and future outbreak dynamics [6]. Particularly pertinent at this time, there is a lack of information to address forest adaptation to climate change in light of increasingly “out of historic norm” behavior of bark beetles. Despite this, there is a widespread belief in the policy arena that timber harvesting is an effective and necessary tool to address beetle infestations. That belief has led to proposals for, and enactment of, significant changes in federal environmental laws to encourage more timber harvests. Our question is, does that belief have a sound grounding in current science?

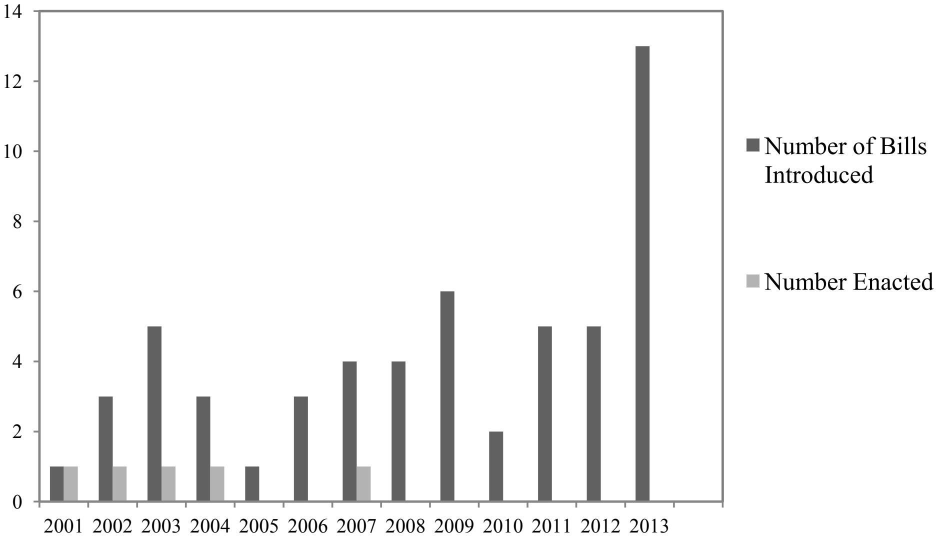
In this review, we focus on mountain pine beetle as an exemplar to critically evaluate the state of science behind the use of timber harvest treatments for bark beetle suppression during outbreaks. The mountain pine beetle was chosen because it is the most studied, most intensively managed, and most aggressive of the irruptive bark beetles. It has also responded strongly to climate change, resulting in a recent massive outbreak of unprecedented size that, in turn, has initiated numerous human responses, mostly involving implementation of timber harvests. It has also initiated many policy changes with many more currently in the pipeline.

We begin with an overview of the current policy situation. We then briefly review the biology of mountain pine beetle to form a foundation for understanding the factors that initiate and maintain outbreaks and how anthropogenic factors are contributing to current problems. We then describe the primary timber harvest treatments used to suppress bark beetle outbreaks and examine how well relevant science and ecological principles support their use. We conclude with a discussion on how well policy reflects the actual state of current science and identify where significant gaps between science and practice occur particularly in light of climate change. We also discuss the need to use advanced tools, including genetics and remote sensing, to adapt old practices to new situations-particularly in the realm of climate change adaptation. It is our hope that this review will stimulate research to fill important gaps and to help guide the development of policy and management firmly based in science, and thus, more likely to aid in forest conservation, reduce financial waste, and bolster public trust in public agency decision-making and practice.

2. The Current Policy Situation

There have been many recent proposals to streamline, reduce, or eliminate perceived legal obstacles to implementing timber harvests to address beetle epidemics on federal public lands (Figure 1). Between the 107th Congress (January 2001) and the 113th Congress (present), we found 55 bills that were introduced where at least one goal of the legislation was to increase timber harvests in order to respond to beetle infestations (Figure 1). Most of these proposals focused on the US Forest Service, which manages the majority of forests on federal public lands.

Figure 1. Number of bills involving timber sales that included bark beetle control that were introduced and/or enacted from 2001 to 10 July 2013.



Some of these proposals have been enacted. By far, the most important legal change has been the Healthy Forest Restoration Act of 2003 (HFRA). HFRA reduced the level of environmental analysis required for certain timber projects under the National Environmental Policy Act (NEPA), specifically by limiting the number of alternatives that the Forest Service was required to analyze. It also significantly restricted the ability of members of the public to challenge certain timber projects in court (by making participation in the agency's administrative process a precondition for filing suit). Further, it sought to streamline the Forest Service's internal administrative process for considering citizen challenges to certain timber projects. HFRA applies nationally to all National Forest System and Bureau of Land Management lands, and has resulted in forest treatment projects on an average of 220,000 acres of federal land per year since its enactment [7]

HFRA authorizes this streamlined process for timber projects on "Federal land on which…the existence of an epidemic of disease or insects, or the presence of such an epidemic on immediately adjacent land and the imminent risk it will spread, poses a significant threat to an ecosystem component, or forest or rangeland resource, on the Federal land or adjacent non-Federal land" [8,9].Moreover, while other types of HFRA projects in old growth forests are subject to limitations intended to protect old growth structure and large trees, timber projects to address insect epidemics can occur in old growth forests without those limitations [10,11].

HFRA also sets up a special experimental management process to develop better management methods for beetle infestations. After a long list of findings by Congress about the risks of beetle infestations in US forests, Congress authorized up to 250,000 acres of "applied silvicultural assessment and research treatments" on National Forests that would be categorically excluded from NEPA; these treatments could include timber harvesting [12,13]. HFRA section 401(b)(3) [14] requires that these applied silvicultural assessments and treatments must be peer reviewed by non-agency scientists.

HFRA is not alone. Another enacted bill created exemptions from environmental laws to allow timber harvest projects in a geographically limited area. As part of a massive supplemental appropriations act to address recovery from the September 11, 2001 terrorist attacks, Congress exempted a series of timber harvest projects in the Black Hills of South Dakota from any and all environmental laws; the law specifically stated that the projects were intended to reduce both fire risk and beetle infestations [15].

Other recent enactments create additional incentives for timber harvests intended to address beetle infestations. Congress permitted state forestry agencies to perform beetle control timber harvest projects on federal lands in Colorado and Utah under what is called "Good Neighbor Authority" [16]. These state forestry agencies must also implement "similar and complementary" services on state land adjacent to federal land in order to use the authority. Additionally, in the 2008 Farm Bill, Congress expanded subsidies for the production of "renewable biomass" energy to include timber produced from projects intended to reduce or contain disease or insect infestation [17].

There have been many more recent proposals for additional changes. Congress has considered multiple bills to expand the scope of HFRA. One proposal would require the Forest Service to implement at least one insect and disease control pilot project in at least one subwatershed in every national forest in a state that is "subject" to an insect or disease epidemic [18–24].Congress has also considered many other changes to encourage timber harvesting to control beetle infestations besides expanding HFRA. Some proposals would expand the exemptions to the Forest Service's Roadless Rule (which prohibits commercial timber projects and road construction in unroaded areas of National Forests) in order to allow more timber projects that are intended to address beetle infestations; some of these projects would be exempt from judicial review [25–27].

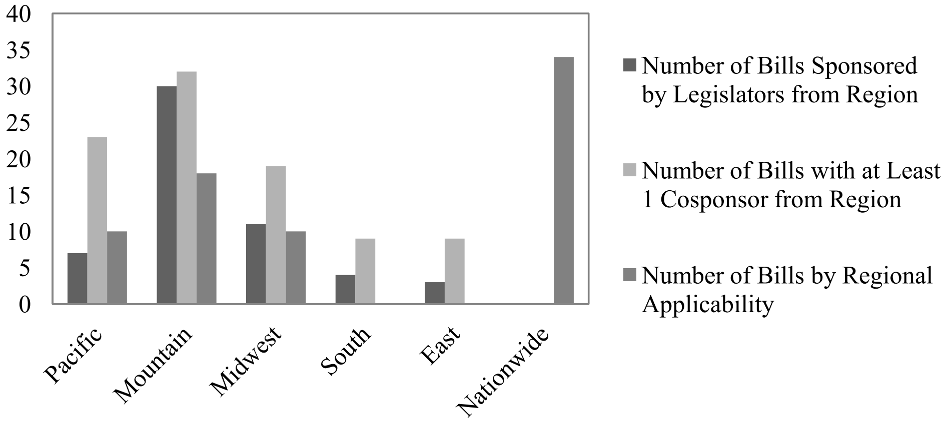
Congress has considered giving additional benefits under the Clean Air Act for "renewable biomass" produced from timber projects on federal lands, including projects intended to control beetle infestations [28,29], giving grants and other subsidies for beetle control timber projects [30], extending the Good Neighbor Authority to more states [31–33], and reducing or eliminating the fee that private timber contractors pay for timber contracts in exchange for agreements to implement restoration work, such as culvert removals, road improvements, or invasive weed removal, if the project provides insect control and other forest management benefits [26]. Finally, two bills have proposed that designation of additional federal lands as protected wilderness be paired with exemptions of beetle-related timber projects from environmental laws [34,35].

Throughout this policy debate, members of Congress and major stakeholders have regularly stated that timber harvest on federal lands is a necessary component of efforts to fight beetle infestations and control outbreaks and that additional flexibility under environmental laws is necessary for agencies to pursue these timber harvest projects [36–41].

Likewise, the U.S. Forest Service and other U.S. federal land management agencies have prescribed timber harvests as a necessary component of beetle control. For example, the Forest Service's Western Bark Beetle Strategy calls for the agency to "reduce the number of trees per acre and create more diverse stand structures to minimize extensive epidemic bark beetle areas" by using thinning and other harvest treatments [42]. While the Forest Service has applauded HFRA as "very helpful" in addressing beetle outbreaks (U.S. Forest Service, Review of the Forest Service Response: The Bark Beetle Outbreak in Northern Colorado and Southern Wyoming, September 2011), available at [43], agency leaders do not look favorably upon all legislative proposals to weaken environmental laws to facilitate timber harvest for beetle control. For example, Tom Tidwell, Chief of the Forest Service, criticized recent bipartisan legislation [25] because it would "shortchange the environmental review process, cut out public engagement and collaboration…and override roadless protections." (Testimony from House Subcommittee on Public Lands and Environmental Regulation Legislative Hearing on H.R. __, H.R. 1294, H.R. 818, H.R. 1345, H.R. __, and H.R. 1442 available at [44].

Given the geographic concentration of federal public lands in the West, most of the bills have a specific focus on western states, and were introduced or supported by westerners (Figure 2). But that is not universally the case. Two of the proposals to expand the scope of HFRA were sponsored by Representative Markey, a Democrat from Massachusetts [19,23]. Moreover, support for these bills is bipartisan, showing that the belief that timber harvest can address beetle infestations crosses the political spectrum. Of the 55 total bills, 17 were sponsored by Democrats alone, 21 sponsored by Republicans alone, and 17 had bipartisan sponsors. Markey himself has received very high ratings from the League of Conservation Voters, with a 94% lifetime score from the group.

Figure 2. Bill sponsorship, co-sponsorship, and applicability by region. (Pacific = CA, OR, W, AK, HI; mountain states = MT, ID, NV, WY, UT, CO, AZ, NM; Midwest = ND, SD, NE, KS, MN, IA, MO, WI, IL, IN, MI, OH; SOUTH = TX, OK, AR, LA, KY, TN, MS, AL, GA, FL, SC, NC, VA, WV; east = ME, NH, VT, MA, NY, RI, CT, NJ, DE, MD, PA).



The 55 bills introduced since 2001 show that many legislators, particularly those from western states, believe that timber harvests are a necessary tool to address beetle infestations. This belief has led to the enactment of laws that reduce compliance burdens under NEPA and other federal environmental laws. There are many more proposals for additional significant changes to federal environmental laws to encourage more timber harvests for beetle control. While “there is certainly a tremendous amount of social and political pressure to ‘do something’ about beetles,” there is also growing concern by many that timber harvests for beetle control are expensive and ineffective and that long-term impacts on forests are unknown [42 citing Ann Merwin, director of policy and government affairs for the Wilderness Society]. The policy debate demonstrates the need to critically examine how well these treatments work and place policy in the context of the best available science.

3. A Mountain Pine Beetle Primer

The mountain pine beetle is native to pine forests in western North America [45]. During outbreaks, it can kill millions of trees across extensive areas. The ability to cause such widespread mortality has led it to be described as the most destructive forest pest on the continent [46]. Indeed, economic and aesthetic impacts of outbreaks can be severe. From a manager’s perspective, outbreaks are often perceived as a symptom of poor “forest health”, while ecologists more often view outbreaks as natural ecological processes integral to the maintenance and resilience of the forest. These differing human perceptions have led to conflicting and ambiguous management goals as well as scientific, social, and political conflict.

The mountain pine beetle is polyphagous on pines (*Pinus*) [45]. It attacks not only native pines but also exotic pines used in ornamental landscaping. Within the natural range of the beetle, only *P. jeffreyi* appears to be avoided, likely due to its unusual chemistry [45]. Pines are well defended and are not easy targets for the beetle. They produce constitutive defenses consisting of resin that can flush the tiny beetles from trees, often drowning them [47–49]. Pines also produce induced defenses in the phloem comprised of resin containing elevated concentrations of toxic monoterpenes [49,50]. Induced defenses develop in response to attack, and thus, involve a lag time of one or more days to develop and can last for a month or more even when trees are killed [51].

To contend with a defensive host, the mountain pine beetle has evolved a complex chemical communication system it uses to coordinate a mass attack on a tree [52]. A female beetle will land, begin to tunnel, and release an aggregation pheromone that attracts conspecifics of both sexes to the tree. Subsequent arrivals release additional pheromone increasing attraction to the tree [53]. If enough beetles respond, the tree can be overwhelmed in just a few days. As defenses are depleted, the beetles release an anti-aggregation pheromone which repels late arriving beetles and acts to reduce intra-specific competition among brood [53]. At this point, the tree has reached “a point of no return” [54]. It will not recover and will slowly die, although it may remain green for nine months or more due to translocation of water to needles by capillary action in the xylem.

The number of beetles needed to kill a tree varies and depends, in part, on the strength of its defenses [55]. In general, as the strength of defenses increase so does the number of beetles needed. Several factors influence the strength of tree defenses. Trees weakened by drought, disease or damage can be overwhelmed by only a few hundred beetles while very vigorous trees may require many hundreds or even thousands [56]. Genetics of the host tree also play an important role. Within a tree species, different genotypes result in differing levels of resistance and susceptibility [57,58]. Genetic differences are even more pronounced when considering differences in defenses among *Pinus* species [59,60].

The ability of tree defenses to affect mountain pine beetle success varies by whether the beetle is in endemic (non-outbreak), incipient (building) and eruptive (outbreak) phases. During the endemic phase, when beetle populations are low, host tree defenses are the major constraint in the ability of beetles to kill trees. However, tree defenses become inconsequential once the threshold to the incipient stage has been surpassed [61]. When numbers are low, beetles attack smaller diameter trees with low defenses. However, once populations rise to the incipient stage, beetles choose larger, healthier, resource-rich trees, despite their superior defenses [61]. Because larger trees have thicker phloem resources to support larval development, they support greater beetle productivity which results in positive feedback that helps fuel the expansion of the outbreak. Thus, host tree traits (primarily host defenses and diameter class) that determine which trees are killed when populations are low, may be unimportant or even have an opposing effect on beetle success when populations are high [61].

It is often reported in the press that mountain pine beetle populations are cyclical. This is not the case. The population dynamics of insects that develop cyclical outbreaks are typically dominated by *delayed* negative density dependent feedback involving regulation by natural enemies and induced resistance mechanisms [62]. This type of feedback results in predictable intervals (cycles) between outbreaks although the amplitude of population peaks can vary due to spatiotemporal variation in abiotic conditions. Bark beetle dynamics, instead, are driven by alternations of negative density dependent and positive density dependent feedbacks resulting in sporadic unpredictable population eruptions primarily driven by threshold effects and typically triggered by abiotic factors, particularly climate [61–63]. It is critical to distinguish between cyclical and eruptive population dynamics as insects exhibiting these two types of dynamics demand different management and monitoring approaches. In particular, eruptive dynamics are triggered by abiotic factors typically outside the realm of human manipulation.

Mountain pine beetle can remain in non-outbreak phase for very long periods of time, even when forests are composed of suitable age classes of host trees and in a condition often considered to be highly susceptible and "unhealthy". Outbreaks occur *only* when multiple thresholds involving temperature, tree defenses, and brood productivity are surpassed that allow positive feedbacks to amplify across several scales [2,64]. While outbreak development is complex, the primary elements that must exist are an abundance of suitable hosts *and* a trigger [63]. Triggers for mountain pine beetle that allow population amplification and subsequent widespread outbreak initiation are warm temperatures and drought, conditions that often co-occur [65]. There can also be a substantial lag period, even several years, from the initiation of the abiotic factors that trigger an outbreak to when populations actually amplify [65,66]. However, once a threshold number of beetles is surpassed, the outbreak becomes self-perpetuating.

While forest conditions alone do not cause outbreaks, certain forest conditions can support larger and more severe outbreaks once they are initiated. Mountain pine beetle attacks only pines (except in rare instances where it "bleeds over" into spruce) [67], and typically only those larger than ca. 15 cm in diameter [68]. Therefore, forests comprised mainly of large diameter pine can be at higher risk of widespread mortality when a trigger occurs than are forests comprised of young, small diameter pine or composed of a mix of tree species including non-pines [68]. Processes that homogenize forest structure and composition such as abnormally widespread stand replacement events (e.g., fires of 1910, Yellowstone 1988) or particular types of forest management (e.g., some timber harvest practices, fire suppression) that alter forest composition and structure over large areas, can contribute substantially to the extent and severity of an outbreak once it is initiated. Processes that result in heterogeneity, such as "normative" wildfires and bark beetle outbreaks, and some land management practices (e.g., restoration treatments focused on restoring a mosaic structure of forest stands of different age classes) tend to reduce outbreak severity and extent by reducing the amount of contiguous susceptible hosts [68].

Climate acts as a trigger for mountain pine beetle outbreaks for a very good reason. Like all insects, mountain pine beetle is poikilothermic-it cannot regulate its body temperature, and thus, all its metabolic rates and vital functions are dependent upon the temperature of its environment [69]. As temperatures rise, feeding, activity, development and reproductive rates increase. Importantly, this also means that the length of the mountain pine beetle life cycle is determined by temperature [69]. Under optimal thermal conditions, development is univoltine (one year). A univoltine cycle allows synchronized emergence of brood adults in mid-late summer, supporting not only mass attacks, but also attacks at a time that allows subsequent offspring to enter winter as cold-hardened larvae [70,71]. Cold hardening is a gradual process that occurs as temperatures fall in autumn. Once larvae are cold hardy it can take temperatures as low as −40 °C to kill significant numbers [72]. However, cold air incursions in fall when beetles are not yet cold hardened or in spring when larvae have lost cold hardening in preparation for transitioning to the adult stage can result in widespread mortality. This can halt an outbreak if subsequent conditions are no longer favorable for the beetle. However, if favorable conditions return, beetle populations rebuild. Importantly, outbreaks require a univoltine life cycle combined with moderate winter temperatures [73].

In areas where temperatures are too cool to support a univoltine life cycle, a semivoltine (longer than one year) life cycle occurs [73]. A semivoltine life cycle is maladaptive for the beetle in several ways. First, adaptive seasonality is disrupted, increasing the percentage of brood that enter winter in stages vulnerable to freezing (eggs, pupae and adults). Additionally, mortality increases when beetles must pass through two winters and feed on a food source increasingly depleted in moisture, nutrients, and symbiotic fungi [74]. Warm periods support not only greater brood production and survival in areas typically suitable for the beetle, but also allow a transition from a semivoltine to a univoltine life cycle in areas otherwise too cool. This increases the spatial extent of suitable habitat and tree mortality. Thus, abnormally warm periods can vastly increase the total area suitable for the beetle and play a major contribution to the synchronicity and coalescence of outbreaks across regions [2,65].

Drought can also play an important role in outbreak initiation. Host tree defense mechanisms are compromised during drought allowing beetles to more easily attack trees [2,75]. Tree defenses are major constraints when beetles are in non-outbreak phase. However, drought-weakened trees can support population amplification until a point where stand level densities surpass a critical threshold. Once this threshold is passed, tree defenses lose their importance in regulating beetle populations [61]. Very importantly, drought stresses large numbers of trees at a regional scale. This results in large numbers of trees that are easier for the beetles to kill, further supporting outbreak intensification [65,76].

Recent studies have found that drought occurring years or even decades before the outbreak can influence outbreak initiation. Furthermore, prolonged drought stress appears to pre-condition trees to be more susceptible, an effect that can continue for years after normal precipitation has returned [58,65,77]. There also appears to be a genetic component to tree sensitivity to drought, and subsequently, susceptibility to beetles. In two studies, one conducted in whitebark pine and the other in ponderosa pine, differences in growth of surviving trees and trees killed by beetles over the last century suggest that adaptive differences to changes in climate exist. In the whitebark pine study, the trees studied were co-dominants and not significantly different in diameter age or mean growth over their lifetimes [58]. However, trees that were killed exhibited faster rates of growth in the first half of the century suggesting they were better adapted to the cooler wetter conditions of that period. The surviving trees had greater growth in the latter half of the century when conditions were warmer and drier. Millar *et al.* [58]) suggested that the beetle-caused tree mortality in the stands they studied resulted in a strong natural selection event that removed trees less fit under our current climate while leaving those more well-suited.

Likewise, Knapp *et al.* [77] found genotypes of ponderosa pine that were slow-growing in the two to three decades prior to the outbreak were much more vulnerable to beetle infestation than those that were fast-growing, again suggesting the beetle may act as a selective agent shifting genetic structures in stands over time to those most suited to prevailing climatic conditions. In lodgepole pine, trees of similar age and diameter growing intermixed in the same stand and under the same conditions exhibited different levels of sapwood moisture that were highly correlated with susceptibility to beetle attack [74] hinting at genetic differences in water efficiency. Those with lower sapwood moisture were attacked and killed by the beetle while those with higher sapwood moisture were not [74].

While mountain pine beetle has developed outbreaks for millennia, the current outbreak is far outside the historic norm [2,78]. The unprecedented size and severity of this outbreak is due to a combination of increasingly favorable climate for the beetle and forest conditions. Warming trends have supported the development of a univoltine cycle in many areas that previously were too cool and have resulted in greater beetle productivity and survival [79]. This has led to massive tree mortality, not only in areas previously favorable for the beetle, but also in areas previously suboptimal or unusable. Warmer temperatures and high population levels have also supported expansions of the beetle's range hundreds of kilometers further north in British Columbia and eastward across Alberta [80–82]. In these new locations, the beetle is infesting naïve hosts including (in the eastern expansion) a novel species, jack pine [80,82]. These naïve hosts exhibit lower defenses to beetle attack [83] as well as similar chemical compositions to natural hosts [84] promoting establishment. Predictions are that the beetle will continue to move across the continent through the boreal forest and finally into eastern pine forests [78].

Warming has also allowed the beetle to move higher in elevation where it is devastating whitebark pine, a tree that is foundational to the western North American subalpine ecosystem and that was previously protected from the beetle by cold [73,85]. Movement into the subalpine has been supported by overall warmer temperatures and milder winters allowing the beetle to switch from a semivoltine to a univoltine life cycle while simultaneously reducing winter mortality [85–87]. The resulting mortality to whitebark pine in many areas, particularly the greater Yellowstone Ecosystem, has been so severe the tree is now proposed for listing as an endangered species [88]. The tree is already listed as an endangered species in Canada due to the combined effects of mountain pine beetle and white pine blister rust [89].

4. Mountain Pine Beetle Outbreak Suppression

Treatments used to mitigate the effects of mountain pine beetle are grouped into three broad categories. Treatments that strive to reduce or eliminate beetle populations are termed direct controls [90]. Treatments aimed at increasing tree vigor and altering stand conditions to be less favorable for beetles are called indirect controls [90,91]. Prophylactic treatments aim to protect high value individual trees or stands of trees from infestation. Salvage, while often included in beetle management programs does not actually reduce or impact beetle populations-it is the removal of dead trees for economic or other reasons and often involves removal of trees that are already ‘empty’ of beetles and thus has no impact on beetle population size. Because our focus is on how well science supports the use of timber harvests (including tree felling and destruction of trees in place) to reduce or suppress bark beetle outbreaks, we will focus primarily on direct and indirect controls concentrating on these treatments.

Direct control includes sanitation treatments such as removing single trees or small patches of trees that are infested with the insect, clearcutting (also called block harvesting) and prescribed burning of infested trees, as well as fell and burn, trap trees, debarking, and application of insecticides or toxins such as MSMA (monosodium methanearsonate). Sanitation cuts attempt to remove most or all beetles in an area by removing infested trees before the beetles developing within them can emerge and disperse [90,92]. Prescribed burns, fell and burn, debarking, and toxin applications attempt to destroy beetles in infested trees on-site. Trap trees are trees that are baited with attractant pheromone baits in an attempt to draw beetles into specific areas where they are concentrated into the baited trees which are subsequently taken to the mill or destroyed. Each of these methods relies on killing as many beetles as possible in order to lower beetle population thresholds below which they can maintain outbreak dynamics.

Indirect controls are primarily silvicultural in nature. The main treatment used for mountain pine beetle is thinning. Thinning is thought to act by reducing inter-tree competition for water, nutrients, and light, enhancing greater tree vigor, and thus defenses against the beetle [93]. Thinning treatments are also thought to reduce successful beetle attacks by altering microsite conditions by increasing temperatures on bark surfaces on bark in summer and decreasing them in winter, as well as disrupting beetle communication by increasing wind flow [94,95]. A new treatment recommended for reducing bark beetle infestation is “daylighting” which involves removing trees and shrubs from around trees that are to be protected to increase light on the tree’s stems to disrupt beetle colonization. Other silvicultural treatments include removal of beetle-suitable hosts (mature trees and old growth) and conversion of stands from species preferred by beetles (pines) to species that are not hosts or converting stands that are primarily pine to a mixed species composition [91,92]. Most of these approaches involve, completely or partially, the use of timber harvests.

4.1. Efficacy of Direct Controls

Direct control treatments are extremely expensive in time, effort and resources. They address only one aspect of an outbreak which is the amount of beetles present in a stand or area. Because they do not address the underlying conditions that support an outbreak (climate, tree condition/stress) their effects are considered a holding action until conditions shift to being less favorable for the beetle [92].

Direct control efforts must be maintained at a high level on an annual basis until the outbreak ceases [3,90,96]. It is highly controversial whether direct controls are effective in reducing tree mortality in the short-term, and if they can be effective in halting or suppressing outbreaks in the long-term.

One of the biggest problems in assessing the utility of direct controls is a general lack of monitoring or *post hoc* assessments of the outcomes of implementing these practices. Despite decades of direct control and large-scale implementation of these practices, few rigorous studies on its efficacy have been done and there remains no agreement among scientists or foresters regarding its ability to reduce beetle populations or losses of trees. Studies conducted prior to the current outbreak have variously concluded that direct treatments may merely act to delay infestation of susceptible stands [97], or that if used correctly, can be effective [98,99]. Many studies found that while some treatments slowed the rate of infestation, overall, they had little to no impact on mountain pine beetle populations [97,100–104].

The US and Canadian governments have spent hundreds of millions of dollars in direct control efforts to address the current outbreak. However, assessments of the efficacy of these efforts are nearly non-existent and only a few studies on assessments have been published. The few that have been published are reviewed here. Although much of our review addresses how well science supports US policy, we use primarily studies conducted in Canada as few studies have been published on direct control measures during the current outbreak in the US.

Nelson *et al.* [3] evaluated the efficacy of five direct control treatments in British Columbia roughly midpoint in the portion of the current outbreak as it progressed in that province. The assessment was extremely short-term and looked only at the response of beetles in the year immediately post-treatment. However, it provides one of the very few broadscale assessments ever conducted of the efficacy of direct controls during an outbreak. The treatments assessed were applications of MSMA, trap trees, fell and burn, and clearcutting. The study was split into three geographic regions to account for potential sources of variability due to location and different background levels of beetles. The northern-most region was at the margin of the beetles range (expansion zone) and possessed relatively low beetle populations, while the central and southern regions had higher beetle populations and were known to have supported high beetle populations historically. The study found that, overall, sites receiving MSMA treatments exhibited higher infestation intensities (a metric based on kernel density estimators) than randomly selected untreated sites with similar characteristics. This was particularly pronounced in the southern region. Results for trap tree treatments showed substantial variability within and among regions. A reduced infestation rate in response to treatment was observed more often than not in the northern area where beetle pressure was low. However, in the central and southern regions where beetle pressure was higher, the range of infestation intensities was similar for treated and untreated sites although a larger number of comparisons found higher infestation intensities in the treated sites. The overall conclusion was that MSMA and trap tree treatments may be effective, but not reliably, and only when beetle pressure is low and environmental conditions are not highly favorable for the beetle.

Results for fell and burn were also variable. In the northern region, intensities were lower overall in treated *vs.* untreated sites. However, in the central area, treated areas tended to have greater infestation intensities. In the southern area, no discernible effect of treatment was seen. Therefore, like with trap trees, fell and burn appeared to sometimes be effective, but only when populations of beetles were low, and became increasingly unreliable as beetle pressure increased and the infestation moved into outbreak phase.

Removal of trees in patches was studied only in the central region. No significant effect of treatment was detected. Clearcuts were assessed in the central and southern areas and were found to lead to a significant reduction in infestation intensity. In almost all cases, infestation intensities were lower in treated *vs.* untreated areas. However, this was likely due to the removal of all living trees (potential subsequent hosts) that survived the beetle as well as the infested trees. The overall conclusion of the study was that mitigation treatments are effective when populations are low to moderate and if infested trees can be kept to 2.5 or fewer per hectare. Efficacy was also recognized to be contingent upon a high level of accuracy in detecting infested trees and wide-scale and continuous implementation of treatments. However, with only one year of data, the authors could not predict how long treatments would need to be sustained to remain effective, nor what effect beetle pressure from surrounding areas might have on the subsequent fate of treated stands. No follow up study has been published to report how these treatments fared as the outbreak progressed.

Fell and burn has been a stalwart component of the direct control efforts against mountain pine beetle in Canada during the current outbreak, particularly on the advancing front as the beetle expands its range eastward. Coggins *et al.* [105] examined the efficacy of fell and burn treatments to "stabilize" such infestations (*i.e.*, prevent expansion) using field plot data from sites at the expanding edge of the mountain pine beetle infestation in 2008 in eastern British Columbia and western Alberta. The authors used multiple modeling scenarios along with ground data to demonstrate how infestations may develop with and without mitigation, and to predict how long mitigation may need to be maintained to be effective given different levels of infestation and detection accuracy. They found non-mitigated plots experienced more tree mortality due to the beetle and that infestations in these plots expanded more rapidly. The higher the expansion factor (means rate of increase, e.g., 2 would indicate a doubling of the population each year) the greater the detection accuracy that was required to maintain a static population. When a beetle population had an expansion factor of 5.1 (high), an 80% detection rate was required, whereas with a population with an expansion factor of 1.1 (very low), the minimum detection rate could be as low as 10% and still be effective. The authors also modeled how long it would take to achieve population stability given different levels of infestation. On average, across their stands, with a 70% detection accuracy rate, mitigation would take 11 years, at 80% 6 years, and at 90% 3 years. The actual mean mitigation efficiency at their sites was found to be 43%, a level at which no control could occur. They concluded that the stabilization of mountain pine beetle populations is possible, but only with a much higher detection accuracy than commonly occurs coupled with an intense level of mitigation maintained potentially over a very long timeframe.

Wulder *et al.* [96] looked at the effectiveness of sustained mitigation on slowing the beetle's expansion in western Canada. The results were difficult to assess because of the unevenness of application of mitigation treatments (for example, in one year only 68% of sites slated for mitigation were treated) and differences in background beetle populations. However, such a situation is typical and thus may represent the reality of many on-the-ground direct control efforts. One site where little mitigation was conducted early on, did exhibit a strong increase in tree mortality due to the beetle that declined once extensive mitigation efforts were implemented. However, overall, the conclusion was that mitigation must be extensive and continuous to work and may only be effective when populations are low to moderate.

Trzcinski and Reid [104] studied the trajectory of beetle populations in treated and untreated zones in Banff National Park from 1997–2004. The Park used a combination of pheromone-baited trees and fell and burn to remove as many beetles as possible from treatment zones—they also conducted prescribed burns to reduce beetle numbers and lodgepole pine hosts. The area colonized by the beetle increased rapidly over this time period in both the untreated and treated zones. After four years of treatment, control measures did not reduce the area affected by beetles and infestations continued to expand at a similar rate in both zones. The authors estimated that between 45% and 79% of infested trees had failed to be detected in the treated areas. This equated to *only* 0.7–3.7 infested trees remaining per thousand ha yet still was sufficient to support subsequent rapid beetle population growth.

A general consensus of these studies is that suppression of a beetle outbreak would require massive sustained efforts with extremely high detection rates to succeed. It has been estimated that 97.5% of beetles in an area must be killed to merely stabilize a mountain pine beetle population [90]. Even a small increase in survival above this value can allow a substantial increase in population size. For example, if mortality drops to 95%, this would allow a population to *double* in size annually. If the goal is not just to stabilize a population, but to reduce it, mortality of beetles would need to be higher than 97.5%, a goal that is highly unlikely given the vast areas that would need to be treated on a continual basis when conditions are favorable for outbreak development. Even if 100% removal of infested trees from an area was feasible, the migration of beetles into treated stands from surrounding areas allows reestablishment and subsequent tree mortality further decreasing the potential for effective direct control.

The on-the-ground reality is that direct control efforts typically fall far below the levels needed to stabilize, let alone control, mountain pine beetle populations. In the above cited studies, rates of detection in mitigated stands ranged from 45%–79%. These situations are not unusual. Direct control treatments are laborious, extremely costly and time consuming, and require high levels of training. Logistical difficulties, including proper seasonal timing, access, inclement weather, and lack of trained personnel, increase the odds that they will not be effective. The high financial cost of such efforts coupled with a volatile market for sawtimber, pulp and pellets further complicates the use of direct controls. Importantly, outbreak development is extremely swift and the amount of mitigation required can rapidly outstrip the ability of managers to respond.

During an outbreak the number of trees killed annually is often in the millions and infestations may cover hundreds of thousands of hectares [90]. Carroll *et al.* [90] presents an example of the degree of mitigation that would be required for an outbreak that covers 300,000 hectares with a rate of increase of 2 (the population doubles in one year-a conservative rate for an outbreak). In this case, 150,000 ha of infested trees would need to be removed each year just to maintain a *static* beetle population–this would still allow tree mortality to occur for many years, potentially until most or all mature trees were killed. In reality, such a high level of detection and mitigation is impossible. Given that the goal of direct management is to reduce populations and protect trees, the effort that would be needed to actually reduce such a high beetle population would require an even more unlikely effort.

Studies in other bark beetle systems also have found that a high degree of detection accuracy and intensity of mitigation is required to reduce beetle numbers. Fahse and Heurich [106] found that control of *Ips typographus*, a less aggressive European bark beetle, requires a detection and removal level of around 80% to be effective. They concluded that direct control efforts are useless and should be dropped if survival probabilities of the beetle after treatment are above 20%–30%. This estimate is in line with those developed in studies on mountain pine beetle in North America and highlights the challenge the high reproductive capacity of bark beetles poses when conditions are favorable for outbreak development.

It is not just the difficulty of dealing with the extreme spatial extent of outbreaks and the challenge of detection and treatment that makes the efficacy of direct control measures unlikely, but also the time frame over which direct controls must be maintained. Carroll *et al.* [90] estimated that to control a population involving 10,000 infested trees with expansion factor of 2 (conservative) and with a detection and removal rate of 80% (difficult), it would take at least 10 years of annual treatment to reduce the population to a single tree. If the population was tripling or quadrupling, a more likely scenario during an outbreak, it would take 18 or 41 years, respectively. A costly, intensive detection and treatment program lasting that long, assuming sufficient trees even remained to be infested, would be unlikely [90].

Carroll *et al.* [90] emphasized three requirements for direct controls to be effective in treating *individual* infestations: infestations must be detected early, efforts must be applied quickly and intensively, and control programs must be maintained continuously until the desired population level is achieved. Because of the cost and intensity of treating individual infestations, the US Forest Service recommends that direct control measures only be applied to higher value stands [92]. However, treating individual infestations or stands during outbreaks can fail because of the regional nature of outbreaks. Outbreaks are driven by abiotic factors that affect entire regions (warm temperatures and drought). Thus, they consist of many infestations that occur synchronously across a very large area. These infestations often coalesce to form vast expanses where beetle populations are extremely high. These characteristics mean that many stand level efforts are prone to failure due to high beetle pressure and migration into treated areas by beetles from surrounding areas. Given that treating entire regions is impossible, and that many treatments are not in line with other land use objectives, direct control efforts may in some cases, not be worth their costs. The consensus of studies and retrospectives over the course of several outbreaks is that even after millions of dollars and massive efforts, suppression using direct controls has never been effectively achieved, and at best, the rate of mortality to trees was reduced only marginally [90,101,102,105]

4.2. Efficacy of Indirect Controls

Thinning is the primary indirect control measure used to manage the mountain pine beetle. It is generally considered a preemptive measure to be implemented prior to the initiation of a mountain pine beetle outbreak, although it is increasingly employed to reduce damage by the insect during outbreaks. It is often touted as a global panacea for problems with pest bark beetles. One type of thinning is even termed “beetle-proofing” [107], further reinforcing the view among managers, the public, and policy makers, that this approach is failsafe. While overall, evidence suggests that thinning can reduce mortality of trees due to mountain pine beetle, the outcome is frequently more variable than is often recognized or reported. This is particularly true when outbreak populations are involved.

So how exactly does thinning work, and how well does thinning hold up under outbreak conditions? Surprisingly, the mechanism(s) by which thinning affects beetle activity in forest stands is still not well understood. Two, non-mutually exclusive, lines of thought exist. One hypothesis is that thinning increases tree vigor, and thus tree defenses, by reducing competition among trees for light, nutrients and water [93,108]. Intuitively, this makes sense, and indeed, immediate impacts of thinning on reducing water stress have been seen [109]. Likewise, increases in growth and photosynthetic rates also have been observed post-thinning, albeit after a lag period of one or more years [107,109,110]. Increases in growth and vigor are predicted to increase the amount of energy that trees allocate to defense, leading to greater resistance to beetle attack through increased resin and monoterpene production. In fact, the initial impetus for the use of thinning to manage mountain pine beetle came from an early study that found that ponderosa pines in thinned stands produced more defensive resin [93]. However, subsequent studies have reported a variety of responses in resin production as well as growth in response to thinning. For example, Zausen *et al.* [111] found that ponderosa pines in the thinned stands exhibited lower water stress but also produced less resin. This, along with the thicker phloem (greater food resources) found in trees in thinned stands, indicates they might be not only more susceptible to attack but also a more productive resource for beetles. In contrast, McDowell *et al.* [112] found greater resin flow in thinned stands. Both studies were conducted in southwestern US ponderosa pine forests indicating that the variable responses observed were not due to major regional differences in hosts. Six and Skov [113], in a study conducted in ponderosa pine in the northern Rocky Mountains looking at effects of thinning and burning treatments, found that resin flow was highest in trees in burn treatments, intermediate in controls, and lowest in thinned treatments. Raffa and Berryman [114] tracked the fate of trees over time during an outbreak and found no significant difference between resin flow for lodgepole pines that survived attack vs those killed by the beetle.

A number of studies have noted a reduction in beetle caused-mortality of trees immediately after thinning treatments were applied and before trees had time to respond physiologically to lower stocking densities. This timing suggests that the effects of thinning may have more to do with microsite conditions than to changes in tree vigor or defense. These observations led to the second line of reasoning that thinning affects beetle activity through changes in microsite conditions.

Thinning alters temperature, light intensity and wind speed within a forest stand; factors that can have major effects on insect behavior and success. A number of studies have tried to describe how shifts in microsite conditions due to thinning may influence mountain pine beetle activity. Bartos and Amman [94] investigated how incident solar radiation, wind speed, wind direction and temperature were altered by thinning and whether changes affected beetle responses to stands. They did not conduct statistical analyses on their data; however, there was a trend for south sides of trees in thinned stands to be warmer, and ambient temperatures in thinned stands to be overall warmer during parts of the day. Incident solar radiation was higher in the thinned stand. It is not known if bark temperature affects beetle attack behavior, although higher temperatures on south sides of trees in thinned stands have been suggested to be deleterious to beetle development [94]. However, this speculation does not account for differences in local environmental conditions. For example, at cool sites, increased temperatures and insolation could ostensibly support better beetle development by increasing thermal units sufficiently to support a univoltine life cycle.

Light intensity affects the flight behavior of mountain pine beetles [115]. However, if and how different levels of light in treated and untreated stands affect beetle attack behavior is unclear. It has been hypothesized that a reduced propensity for flight in darker stands might concentrate beetles for mass attack, while beetles may be more likely to disperse in open stands [116].

The hypothesis that light has a strong effect on mountain pine beetle behavior, particularly in reducing attacks, has led to a new treatment called daylighting. This approach is currently being implemented on a broad scale by federal and western state agencies. Daylighting involves removing trees and vegetation from around trees that are targeted for retention and is believed to work by repelling beetles from the boles of trees by increasing light and solar radiation [117]. While widely recommended, the efficacy of this treatment is unknown; there are no published studies on its effects on bark beetles.

Changes in wind speed and direction due to thinning have also been suggested to alter beetle behavior by disrupting beetle communication via disruption of pheromone communication. Schmid *et al.* [118] found no statistically significant differences in horizontal and vertical wind patterns in thinned and unthinned stands. However, disruption of pheromone plumes by greater wind speeds may affect communication and thus the potential for successful attacks [95]. Ultimately, we need to look at actual population dynamics of beetles in treated and untreated stands to understand if microsite effects hold under epidemic conditions. MacQuarrie and Cooke [119] found that, under outbreak conditions, mountain pine beetle populations exhibited density-dependent dynamics and that thinning did not change the epidemic equilibrium. In this study, population growth curves did not exhibit responses that would be expected if microsite conditions played a role in beetle behavior. It is evident that more research is needed to understand how these effects ultimately influence tree mortality due to beetle attack.

While we may not have a complete understanding of how thinning works, it is clear that this practice can have a significant effect on mountain pine beetle infestations. Several studies have reported striking differences in mortality to trees caused by beetles in thinned *vs.* un-thinned forests (reviewed in [120,121]). In contrast, only a small number of studies have reported failures. However, the disparity in numbers of successes and failures must be placed within a broader context. Many studies assessing the efficacy of thinning have been conducted under non-outbreak conditions. Their results do not reflect how stands perform during an outbreak. Additionally, failures are often not reported, dismissed as a result of poor management ‘next door’ or targeted for management without evaluation. This is unfortunate because thinned stands that fail may have particular characteristics that could inform a better understanding and application of this approach.

Studies conducted during outbreaks indicate that thinning can fail to protect stands. In Colorado, thinning treatments in lodgepole pine implemented in response to the outbreak that began in the 90s often only slowed the spread. Klenner and Arsenault [122] reported high levels of mortality due to the mountain pine beetle across a wide range of stands densities in lodgepole pine in British Columbia during the same outbreak. They noted that silvicultural treatments were largely ineffective in reducing damage to the beetle. Preisler and Mitchell [123] found that once beetles invaded a thinned stand the probability of trees being killed there can be greater than in unthinned stands and that larger spacings between trees in thinned stands did not reduce the likelihood of more trees being attacked. Whitehead and Russo [107] reported on the performance of 'beetle-proofed' (stands thinned to an even spacing of about 4–5 m between mature trees) and un-thinned stands in five areas in western Canada during approximately the same time period. These treatments were successful in protecting stands when they were combined with intensive direct control measures (removal of infested trees) in the areas surrounding the thinned units, but failed if units were exposed to beetle pressure from the neighboring area—a situation most thinned stands experience during an outbreak.

Unfortunately, long-term replicated studies monitoring beetle responses to thinned forests from non-outbreak to outbreak to post-outbreak phase are virtually non-existent. One large fully-replicated long-term study was initiated in 1999 under non-outbreak conditions and continues to track beetle activity [113]. In this study, mountain pine beetle was low in all treatments in the period leading up to the outbreak, but increased in some controls and burn treatment replicates as the outbreak developed. Although more trees were killed overall in control units during the outbreak, all controls still retained a greater number of residual mature trees than did thinned stands as they entered the post-outbreak phase [124].

Two factors contribute substantially to our inability to assess how well thinning performs under outbreak conditions. One, very few thinning treatments are monitored after implementation over either the short- or the long-term. Thus, for the vast majority of stands that have been treated, we have no data on how well they perform once an outbreak of the insect initiates (or for that matter, even under non-outbreak conditions). Second, stands that become infested, thinned or otherwise, are often targeted for intensive suppressive management and are cut without assessment or data collection. This even includes studies and sites that are intended to inform management. For example, at the sites studied by Whitehead and Russo [107], infested trees were being removed from the study sites even before data collection for their study could be completed. The long-term study discussed previously [113,124] is under continual pressure to be logged to remove beetle kill even though the site lies within an experimental forest designated specifically for studies assessing the outcomes of forest management.

5. What are the Goals?

When we manage forests, we do so in an attempt to achieve one or more outcomes, preferably with minimal negative effects on non-target resources. To be effective, management must have explicit and appropriate goals as well as clear metrics for success. Ideally, management is monitored to assess how well it meets its goals, where it falls short, and whether and how it can be improved. This approach is called adaptive management and implies an iterative process through time whereby we learn from the outcomes of our actions and base future actions on improving performance [125].

Not only outcomes, but the costs of management must be factored into decision making. These include direct financial costs as well as the less tangible (at least in dollar values) effects on ecosystem services and functions. By considering the full cost of management along with benefits as verified through monitoring and evaluation, we lessen the risk of failure, financial waste, and unnecessary negative environmental impacts.

In assessing how well we meet goals when managing for mountain pine beetle, we must ask several questions. Do our management practices actually control the beetle during outbreaks? Do the outcomes justify the financial and ecological costs? And, what long-term impacts do these treatments have on forests and their ability to adapt to climate change? These questions are difficult to answer. Only limited data are available on the short-term efficacy of direct and indirect controls, and information on long-term effects is virtually nonexistent. The results of short-term assessments can be difficult to interpret. For example, often only the proportion or numbers of trees killed by beetles post-treatment are reported. This does not allow a complete evaluation of outcomes. A study may report that 75% of trees in controls are killed by the beetle, whereas only 10% are killed in thinned stands. At first glance, this appears to be a resounding success in saving trees. However, if we approach this situation from a pretreatment perspective, our interpretation of success may change. In this example, 400 mature trees existed in each plot prior to treatment. After treatment, 100 mature trees remain in the thinned plots (300 trees have been removed by thinning). Doing the math, we find that once the beetles have run their course, more residual living trees (100) actually remain in the control plot than in the thinned plot (90) and, in fact, humans have contributed more to tree mortality than have the beetles. In the case of silvicultural intervention, humans typically must expend considerable effort and expense. They also choose the trees that remain, and thus the structure and composition of the remaining forest. This may result in very different trajectories for residual forests as discussed below.

When we include pre-treatment conditions as well as post-treatment responses we can assess the management efficacy from a more informed position. For instance, in a retrospective study investigating the effects of management on spruce beetle, researchers found that post-infestation, untreated stands had more live spruce trees and greater basal areas. When comparing only residual large spruce, final densities in both stand types were similar [126]. Six [124] found higher numbers of mature living trees remained in control stands of ponderosa pine than in thinned stands post-mountain pine beetle outbreak. In a study in Canada focusing on stocking density of living lodgepole pine post-outbreak, the authors found that, even in hard hit stands, stocking density in post-outbreak unmanaged stands was sufficient to maintain desired levels of productivity [127]. Klutsch *et al.* [128] in a study conducted in lodgepole pine forests in Colorado, found greater mortality of trees due to the beetle in more densely stocked stands. However, while the density and basal area of lodgepole pine in infested plots declined 62% and 71%, respectively, the number of trees that remained and their size distribution post-outbreak indicated that lodgepole pine would remain the dominant overstory tree. In another study in Colorado, the beetle killed 60%–92% of overstory lodgepole pine. However, these stands retained residual overstory trees as well as advance regeneration. Furthermore, untreated stands were predicted to return to pre-outbreak stocking levels approximately 25 years sooner than treated stands [129]. Other studies have found similar results for both lodgepole and ponderosa pine [130–134]. These studies highlight a seldom considered impact of mountain pine beetle- that it can act as a natural thinning agent and seldom removes all mature trees during outbreaks. These effects are an important part of the ecological role that the beetle plays in western pine forests [135].

It is also important to recognize there can be significant differences in long-term forest trajectories for stands thinned by beetles *vs.* those thinned by humans. When humans thin, they select for particular size classes, often favoring the retention of larger, older trees, selecting toward one desired tree species, and often ‘thinning from below’ which removes advanced regeneration (small trees) [123,136]. Thinning prescriptions also typically call for relatively even spacing between residual trees [92,107,121]. Mountain pine beetle, on the other hand, often selects the largest trees during outbreaks (with exceptions; [121,123,131]) which can lower the mean diameter of the stand [128]. However, beetles often leave sufficient numbers of large diameter trees to maintain a dominant overstory of pine. Beetles also leave substantial amounts of advanced regeneration to replace the mature trees that arekilled [121,129]. Spacing among trees after an outbreak is uneven, resulting in a clumpy network of living trees [129]. Patches where all trees are killed are seldom extensive and add to a mosaic structure as forests recover post-outbreak. Heterogeneous stand and mosaic forest structures are more typical of natural conditions and can support greater biodiversity and resilience against fire and subsequent beetle outbreaks [137–139]. In contrast, intensive thinning treatments by humans typically favors the retention of mature pines. Over time, these pine-dominated stands grow, they are predicted to have increased susceptibility and potential for tree mortality from future mountain pine beetle outbreaks [123,136].

Very importantly, the beetle exercises selectivity in the trees it kills. While extremely high numbers may override this selectivity, evidence is accumulating that, even under outbreak conditions, beetles choose trees that have particular qualities. Beetles commonly select trees for attack that exhibit lower growth rates, defenses, and higher water stress [58,74,77]. While these factors can be influenced both locally and regionally by site conditions and climate, much of the variation in these properties within individual stands that affect bark beetle choice likely has a genetic basis. Outbreaks can result in strong natural selection against trees with phenotypes (and likely genotypes) favorable for the beetle and for those that possess unfavorable qualities [58,77]. However, when humans thin forests, trees are removed according to size, species, and density, without consideration of genetics. Thus, trees best adapted to surviving beetle outbreaks are as likely to be removed as those that are not.

When humans thin forests, they typically manage for resistance and resilience, rather than adaptation which involves genetic change. It is very important to distinguish between resistance, resilience, and adaptation, as each have different goals and operate on different temporal scales [140]. Resistance is a short-term holding action where we try to maintain an existing state. Approaches focusing on resistance often require massive interventions and increasing physical and financial investments over time. Such approaches may set forests up for future outbreaks [136] and even catastrophic failure as they surpass thresholds in a warming climate [140]. In contrast, practices that promote resilience attempt to allow forests the ability to adjust to gradual changes related to climate change and to recover after disturbance. However, like resistance, resilience is not a long-term solution. In the long term, forests must be able to adapt to change. Adaptation involves genetic change driven by natural selection. Currently, much of forest management, including bark beetle management, focuses on resistance and resilience, mainly through direct and indirect management, respectively. However, neither approach allows for true adaptation. For long term continuity of our forests, it will be imperative to begin to incorporate this aspect of management into our approaches.

We also need to reassess the ecological role of bark beetles, including the mountain pine beetle, in our forest ecosystems. As has been well demonstrated by a century of fire suppression, the dampening or suppression of natural disturbance can alter forest trajectories in undesirable ways, many of which can be irreversible. Although beetle outbreaks, like fire, can have negative impacts on timber values and aesthetics, their natural role in many forest ecosystems is seldom considered and beetle suppression is often perceived as something that must be conducted at all costs. However, as with fire, suppression of beetles over the long term may alter forests in ways that are not desirable or sustainable. While intensive management for bark beetle suppression is called for in some situations such as in the wildland urban interface, it may not be appropriate in many other areas where natural processes including natural selection are needed to maintain a dynamic and functional forest.

6. What are the Needs in Research and Monitoring?

There is clearly a need to better understand how well management programs aimed at reducing mountain pine beetle work, particularly under outbreak conditions, and what impacts these treatments have on forests in both the short and long term.

Perhaps the biggest area of need is in monitoring. Monitoring is essential to understanding whether mountain pine beetle treatments work, and in which contexts, but as noted above there has been all too little long-term monitoring of the effectiveness of various treatment efforts. This is a failing among both agencies and researchers. Agencies often do not have strong incentives to conduct long-term monitoring: Monitoring is costly; external and internal political pressures focus on short time frames; and monitoring may produce information that conflicts with agency goals or missions. It is also difficult to get strong public pressure to force agencies to conduct the necessary monitoring, particularly when the public has been led to believe that outbreaks are strictly the result of a lack of management. Even for scientists, long-term monitoring projects are not encouraged by short-term funding time frames and professional incentives or norms; monitoring is often not viewed as "real" science, and the long-time frames required for monitoring to result in significant gains in information are often longer than the time frames used for professional advancement (e.g., completion of a dissertation, tenure review) [141].

Addressing the shortage of monitoring for beetle treatments may, therefore, require far more than simply trying to provide additional funds (even assuming additional funding is politically feasible). Scientists can help by encouraging and rewarding projects that involve long-term monitoring. Agencies might try to establish units that are focused specifically on monitoring forest health, insulating monitoring projects from adverse political or bureaucratic pressure [141]. Finally, tools that might reduce the cost of monitoring significantly, such as retrospective studies and remote sensing, should be used to complement traditional monitoring and decrease its costs.

Monitoring is all the more essential if forest health management in general, and beetle treatments in particular, are truly to be guided by adaptive management. The high levels of uncertainty and dynamism associated with beetle infestations and the effectiveness of beetle treatments make adaptive management a very appealing tool to reduce uncertainty and allow us to respond to changes in global climate and forest ecosystems. But adaptive management requires monitoring to be successful [141], monitoring that is currently not occurring even as agencies conduct massive beetle treatments and propose to pursue even more.

There is also a real need to increase research on management efficacy and, in particular, how our approaches affect forest adaptation including genetic responses of trees to climate and the role in bark beetle selectivity and fitness. With a changing climate we will need to develop new approaches rather than trying to force old methods of questionable efficacy onto new conditions.

Unfortunately, most funding for research on bark beetles is very short-term, sometimes even as short as on an annual cycle, and thus cannot hope to address the complexities of beetle responses to treatments. Funding cuts to research personnel, particularly in agencies like the US Forest Service, have exacerbated this problem exactly at the time when the need for rigorous research is increasing at a rapid pace. The US Forest Service has recognized that long-term planning must include explicit goals to increase forest resilience and adaptation to disturbance, including outbreaks of the mountain pine beetle. However, with extreme cuts to budgets and personnel, they are highly constrained to meet these needs at this time. Likewise, cuts in federal funding to agencies such as United States Department of Agriculture and the National Science Foundation concurrently reduce the ability of academic researchers to address these problems.

7. Aligning Policy to Science

Our survey of the relevant literature finds that there is significant uncertainty about whether the most commonly used beetle timber harvest treatments are, indeed, effective. Yet there has been little discussion of this uncertainty in the relevant policy debates. Politicians have instead latched on to beetle timber treatments as a cure-all for beetle infestations and have pushed to weaken or eliminate environmental laws that are perceived to be obstructing these treatments. Agencies such as the US Forest Service, to their credit, have been more nuanced in their support for bills that package beetle timber harvest treatments with weakened environmental laws; they have opposed several proposals to alter environmental laws to allow more treatments, but on the other hand, the agencies have at times also aggressively pushed for the implementation of treatments.

It seems clear that the policy debates–both in the agencies and in Congress–need to be better informed by science. Researchers should be more proactive in communicating their understandings of the current science to policymakers. This does not mean that researchers need to take a position pro or con vis-à-vis beetle treatments, or even vis-à-vis specific legal proposals. In the face of uncertainty, aggressive beetle timber harvest treatments may be warranted in some instances. However, policymakers should be aware of uncertainty when they are making the relevant decisions and should also be more willing to include the voices of scientists in the development of policy.

Given the uncertainty about the effectiveness of many beetle timber harvest treatments, the high financial costs of those treatments, the impacts on other environmental resources and values, and the possibility that in the long-run those treatments may interfere with the ability of North American forests to adapt to climate change, our position is that weakening or eliminating environmental laws to allow more beetle timber harvest treatments is the wrong choice for advancing forest health in the United States. Indeed, given the uncertainty, the costs, and the possibilities of both short-term harm to other resources and long-term ineffectiveness, we believe that the current structure of thoughtful, detailed environmental review for these projects is, in general, appropriate. If agencies believe that they need to be able to react quickly to specific infestations with treatments, and that this quick reaction is incompatible with existing legal procedures, we encourage the agencies to adopt overall programmatic environmental reviews based on the principles of adaptive management. Agencies should be able to build (or tier) on these programmatic reviews to respond quickly to individual events as needed. However, the programmatic reviews should allow the agency to build in the monitoring, replication, and variance of treatments that are essential for successful adaptive management [142].

8. Conclusions

The manner in which policy makers have accepted beetle timber harvest treatments as a panacea for responding to bark beetle outbreaks in North American forests raises a number of red flags. As ecosystems and places that have economic, social, and cultural value to human communities are altered by climate change, there is a risk that people will overreact because of a need to "do something" to respond to change, and to give themselves some sense of control over broader forces that appear to be out of control. That pressure, to "do something", might also interact with the uncertainty about which choices are effective and appropriate (as with beetle timber harvest treatments) to create an opportunity for political pressures to force the adoption of particular choices that benefit specific interest groups [143]. It is perhaps no accident that the beetle treatments that have been most aggressively pushed for in the political landscape allow for logging activities that might provide revenue and jobs for the commercial timber industry. The result is that the push to "do something," uncertainty, and political pressures might lead us to act to respond to climate change before we understand the consequences of what we are doing, in the end producing more harm than good.

Our argument here is not to forgo management, but rather that management should be led by science and informed by monitoring. Both direct and indirect management for bark beetles have their place. However, to manage our forests in a way that best ensures their long-term function while wisely using limited financial resources, policy makers and the public need a clearer understanding of current science and gaps.

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Conflicts of Interest

The authors declare no conflict of interest.

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Are Survivors Different? Genetic-Based Selection of Trees by Mountain Pine Beetle During a Climate Change-Driven Outbreak in a High-Elevation Pine Forest

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Increased mortality of forest trees, driven directly or indirectly by climate change, is occurring around the world. In western North America, whitebark pine, a high elevation keystone species, and lodgepole pine, a widespread ecologically and economically important tree, have experienced extensive mortality in recent climate-driven outbreaks of the mountain pine beetle. However, even in stands experiencing high levels of mortality, some mature trees have survived. We hypothesized that the outbreak acted as a natural selection event, removing trees most susceptible to the beetle and least adapted to warmer drier conditions. If this was the case, genetic change would be expected at loci underlying beetle resistance. Given we did not know the basis for resistance, we used inter-simple sequence repeats to compare the genetic profiles of two sets of trees, survivors (mature, living trees) and general population (trees just under the diameter preferred by the beetles and expected to approximate the genetic structure of each tree species at the site without beetle selection). This method detects high levels of polymorphism and has often been able to detect patterns associated with phenotypic traits. For both whitebark and lodgepole pine, survivors and general population trees mostly segregated independently indicating a genetic basis for survivorship. Exceptions were a few general population trees that segregated with survivors in proportions roughly reflecting the proportion of survivors versus beetle-killed trees. Our results indicate that during outbreaks, beetle choice may result in strong selection for trees with greater resistance to attack. Our findings suggest that survivorship is genetically based and, thus, heritable. Therefore, retaining survivors after outbreaks to act as primary seed sources could act to promote adaptation. Further research will be needed to characterize the actual mechanism(s) of resistance.

Keywords: *Pinus albicaulis*, *Pinus contorta*, *Dendroctonus ponderosae*, whitebark pine, climate adaptation, climate change, natural selection

INTRODUCTION

The capacity of forests to adapt to rapid climate change is not known. Their ability to adapt will vary greatly depending upon tree species, amount and type of genetic variation existing within and among populations, type and degree of change required, strength and type of selection pressure, heritability of desirable traits, and the timeframe over which selection is able to act. Many long-lived sessile organisms, including trees, are unlikely to be able to track shifting conditions through migration (Kremer et al., 2012). This is especially true for those restricted to montane ecosystems where movement higher in elevation ends at the top of the mountain and poleward migration is blocked by competitors, valleys, and development (Jump and Penuelas, 2005; Aitken et al., 2008; Dullinger et al., 2012). For many tree species and forests, adaptation will need to occur in place if they are to persist into the future (Aitken et al., 2008).

Bioclimatic envelope models used to predict range expansions and contractions of forest trees treat species as clones, with all individuals exhibiting identical responses (Mimura and Aitken, 2007). While these models are useful to provide estimates of shifts in habitat suitability, they can mask the high genetic diversity and geographic differentiation of most tree species (Mimura and Aitken, 2007; Thuiller et al., 2008; Reed et al., 2011). Likewise, most management focuses primarily on increasing forest resilience through manipulating stand structure and composition while ignoring genetic diversity, natural selection, and the potential for adaptation (Churchill et al., 2013; O'Hara and Ramage, 2013; DeRose and Long, 2014).

Except for highly fragmented or relictual populations, forest trees possess moderate to high levels of standing genetic variation and often exhibit considerable local adaptation and within and among population diversity (Austerlitz et al., 2000; Hamrick, 2004; Savolainen et al., 2007; Alberto et al., 2013). Adaptation of forests to climate change will depend upon the outcome of interactions between existing genetic diversity, phenotypic plasticity, and selection pressure over a relatively short period of time. However, adaptation in trees can be slow due to long generation times and low mortality of older, well-established, but increasingly maladapted trees that continue to contribute to the gene pool (Savolainen et al., 2007; Kuparinen et al., 2010). Long generation times can result in considerable genetic load with long lags between mean optimal genotype and existing climate (Kuparinen et al., 2010). Additionally, while phenotypic plasticity may allow some genotypes to maintain high fitness over a broad range of environmental conditions and aid in resilience to climate change in the short-term, it may slow down or hinder adaptation and persistence in the longer-term (Valladeres et al., 2014).

Adaptation in trees may be accelerated when new conditions or agents lead to high levels of mortality and directional selection in favor of heritable traits associated higher fitness and survival. For example, Kuparinen et al. (2010) used computer simulations to investigate rates of adaptation to longer thermal growing seasons and found that mortality of established trees was the key factor regulating the speed of adaptation with dispersal ability and maturation age having substantially lesser effects. Disturbances caused by agents that use selective behaviors in choosing individual trees, such as herbivorous insects that respond positively to tree stress, can elicit rapid microevolution even in slow-growing tree species (Petit and Hampe, 2006). Such agents may benefit forests in the long-term by increasing mortality of poorly adapted trees, enhancing the reproductive potential of surviving better-adapted trees, and reducing genetic lag loads in affected populations (Kuparinen et al., 2010; Pedlar and McKenney, 2017).

The mountain pine beetle (MPB) (*Dendroctonus ponderosae*) is a highly selective insect that chooses hosts based on a complex array of chemical cues whose production by the tree is influenced by both tree condition and genotype (Emerick et al., 2008; Blomquist et al., 2010). Secondary metabolic chemicals produced by the tree are used by MPBs to distinguish among tree species as well as to assess the relative strength of defenses of individuals (Blomquist et al., 2010; Raffa et al., 2017). Such chemicals also likely signal adequacy of nutritional content for brood production given that beetles avoid hosts of very poor quality (Taylor et al., 2006; Dooley et al., 2015). Using such cues, a MPB will decide whether or not to enter a particular tree and initiate a mass attack. Once in the tree, the insect converts some terpenes to pheromones important in initiating and sustaining the mass attack required to kill the tree (Blomquist et al., 2010). When MPB populations are low to moderate in size, weakened trees with poor defenses that require fewer beetles to overcome defenses are most often attacked (Boone et al., 2011). However, during outbreaks, MPBs may switch to attacking healthier trees that, although better defended, possess thicker phloem and higher nutritional contents for brood development (Boone et al., 2011). Interestingly, some trees escape attack even when MPB populations are present in high numbers and suitable hosts become increasingly scarce.

In this study, we investigated whether trees that survive MPB outbreaks are genetically different than those that are selected for colonization and killed. Our overarching hypothesis was that surviving trees do not escape by chance, but rather possess genetically based characteristics that confer resistance. The basis for resistance, whether it is the ability to tolerate warmer drier conditions without a reduction in defenses, a chemical profile that negatively affects MPB host location or selection, or some other phenotypic trait, is likely to be under genetic control (González-Martínez et al., 2006; Keeling and Bohlmann, 2006).

MPB outbreaks are triggered by extended periods of warm weather and drought (Meddens et al., 2012). The recent MPB outbreak in western North America was a magnitude larger than any recorded in the past and affected millions of hectares of pine forest (Meddens et al., 2012). The outbreak was primarily driven by climate although its severity was intensified in some areas by past logging practices and fire suppression (Taylor et al., 2006; Creeden et al., 2014; Buotte et al., 2017). Climate change also supported movement of MPB further north in British Columbia and eastward across Alberta into naïve forests (those with no prior history of MPB) of lodgepole pine and jack pine (*P. banksiana*, a novel species for MPB) (Burke et al., 2017). While the size and extent of the recent outbreak was far outside the historic norm, outbreaks of MPB are not unusual and have likely occurred for millennia. Selection by MPB during outbreaks, as well as persistent low-level activity during non-outbreak periods, are believed to have been a major force shaping constitutive and induced defenses in host pines (Raffa and Berryman, 1987; Franceschi et al., 2005). MPB activity in naïve forests can be expected to exert especially rapid and strong selection for host resistance because of high levels of susceptibility. Indeed, naïve lodgepole and jack pine forests exhibit lower defenses to MPB attack than those with a co-evolutionary history with the beetle (Clark et al., 2010; Cudmore et al., 2010; Raffa et al., 2013, 2017; Burke et al., 2017).

We focused on two tree species that have suffered high mortality by MPB in the recent outbreak. One is a relatively naïve host, whitebark pine (*Pinus albicaulis*), and the other is a highly co-evolved host, lodgepole pine (*P. contorta*). Whitebark pine is a high elevation tree that is considered a keystone in western subalpine ecosystems of the United States and Canada (Tomback et al., 2016). Historically, outbreaks in whitebark pine appear to have been rare and limited in size (Logan et al., 2010). During warm periods, beetles sometimes moved upslope from lower elevation outbreaks (Bartos and Gibson, 1990) where they killed some whitebark pine, but either did not reproduce successfully due to winter mortality, or completed only one or a few generations before the return of cold conditions once again limited them to lower elevations (Logan et al., 2010). The recent outbreak in whitebark pine has been extensive and has been driven by chronic warm temperatures that allowed the beetle to move into the subalpine and to persist there for an extended period (Buotte et al., 2016, 2017). With climate change, the presence of MPB in high elevation whitebark pine forests is expected to be persistent rather than occasional (Buotte et al., 2016, 2017). Whitebark pine exhibits many of the characteristics of a naïve host, including lower levels of defense chemicals and resin (Raffa et al., 2013, 2017). Reduced snow packs may also result in greater drought stress that may increase susceptibility (Larson and Kipfmueller, 2012). Outbreaks in this tree have been devastating in some areas, including the Greater Yellowstone Area, contributing to the recommendation that it be listed as an endangered species (United States Fish, and Wildlife Service [USFWS], 2011).

The second species studied was lodgepole pine, a co-evolved host that has experienced repeated extensive outbreaks in much of its range, likely over a long evolutionary period. Vigorous lodgepole pine typically exhibits strong constitutive and inducible defensive responses to beetle attack (Burke et al., 2017; Raffa et al., 2017). Outbreaks of MPB in lodgepole pine are considered natural disturbances that, much like fire, help maintain lodgepole pine forests by periodically regenerating new stands free of many diseases, initiating nutrient cycling, and stimulating regeneration, understory productivity, and supporting biodiversity (Dordel et al., 2008; Diskin et al., 2011; Pec et al., 2015).

Our objective in this study was to investigate whether whitebark and lodgepole pine growing in a mixed high elevation stand that survived the outbreak are genetically distinct. If so, this may indicate an increased potential for these pines to persist in the face of the more frequent and extensive outbreaks predicted due to a changing climate. We would expect genetic change at loci underlying beetle resistance but not at a genome-wide scale. Without knowing the basis for resistance in survivors, we chose to use inter-simple sequence repeats (ISSRs) to develop genetic profiles for whitebark and lodgepole pine. ISSRs target highly variable sequences within microsatellite regions (Parasharami and Thengane, 2012). Because ISSR markers can be used to detect high levels of polymorphism and are highly reproducible, they provide a powerful approach for comparing genetic diversity between individuals as well as within and among populations of plants including pines (Mehes et al., 2007; Parasharami and Thengane, 2012; Lucas-Borja et al., 2016). In many studies, ISSR profiles have been useful in marker assisted selection when particular markers were associated with particular traits (REFS). In our screens, we looked for patterns that indicted differences between survivors and susceptible trees.

MATERIALS AND METHODS

Site Description

This study was conducted at Vipond Park, a high-elevation plateau supporting a patchwork of grassland and open forest stands located on the Beaverhead National Forest, Montana, United States (2,501 m elevation, 45.6974°N, 112.9106°W). The site is relatively xeric with an understory of sagebrush and a diverse mixture of annual and perennial forbs. Vipond Park was chosen to take advantage of the high mortality to pines that occurred there during a recent high elevation outbreak of MPB (2009–2013) when approximately 93 and 75% of mature *P. albicaulis* and *P. contorta*, respectively, were killed. The relatively flat topography of the plateau combined with its location at the transition zone between lodgepole and whitebark pine-dominated forests allowed us to study the effects of MPB selection on more than one pine species growing under the same conditions and experiencing the same level of beetle pressure. Although *P. contorta* existed at lower numbers than *P. albicaulis* at the site, they were abundant enough to allow sufficient sampling to make comparisons with whitebark pine. Additionally, white pine blister rust infection incidence and severity were very low reducing the potential for the presence of the disease to influence the choice of individual host trees by the beetle (Six and Adams, 2007).

Transects

Transects were established in 2015 (*P. albicaulis*) and 2016 (*P. contorta*). These were variable length belt transects 2 m in width that started on the edge of a stand and then followed a randomly chosen bearing until another edge was reached at which point a new bearing was adopted to establish a new transect in the same or an adjacent stand. This process was continued until the desired number of trees per species per treatment were measured. When trees occurred in clumps (resulting from seed caching by Clark's Nutcrackers), we restricted measurements and samples to one tree per clump to avoiding sampling trees potentially originating from the same cone/parent.

Determination of the Diameter Distribution of Mountain Pine Beetle-Killed Pines

In initial transects, the diameter at breast height (DBH, 1.4 m above the soil line) of 100 *P. albicaulis* and 45 *P. contorta* killed by MPB were measured to estimate the diameter distribution of MPB-killed trees for each species. This distribution was used to inform our sampling of "survivors" (mature trees that survived the outbreak) so that a similar distribution was achieved, and to determine the diameter below which trees were not attacked.

Collection of Samples for Genetic Analysis

In 2015, transects were established as previously described. Thirty survivor *P. albicaulis* with diameters representative of the diameter distribution of MPB-killed *P. albicaulis* were located on the transects. For each tree, DBH was measured and each was rated for white pine blister rust infection severity using the method of Six and Newcomb (2005). Then, approximately 30 current-year needles were collected and placed in a small plastic bag that was sealed and placed on ice in a cooler. In the lab, needles were placed into silica gel for drying and preservation. In 2016, this procedure was repeated for *P. contorta* ($n = 20$) (except for rust rating) in the same stands sampled the previous year.

The smallest diameters of *P. albicaulis* and *P. contorta* killed by MPB were 12 and 18 cm, respectively. Because beetle-killed trees did not yield DNA, we used this information to choose a second set of living trees for sampling of each species we designated as the "general population." These trees were expected to approximate the genetic structure of the population of each tree species at the site without beetle selection and so should contain a mix of survivor and "susceptible" genotypes. If our hypothesis was correct that survivors were genetically distinct from beetle-susceptible trees, then we expected only a few general population trees would have genotypes matching those of survivors (roughly reflecting the proportion of mature survivors to mature MPB-killed trees at the site). To sample general population trees, we established similar transects as before, but collected needles from trees between 9–11 and 14–17 cm DBH for *P. albicaulis* ($n = 36$) and *P. contorta* ($n = 20$), respectively.

DNA Extraction and Amplification

Needles (3–5) from each sample were ground to a fine powder in liquid nitrogen using a mortar and pestle. DNA was then isolated from each sample using a Qiagen DNeasy Plant Kit (Qiagen, Valencia, CA, United States) following the protocol provided by the manufacturer.

Five ISSR primers were chosen for use (**Table 1**). Not all primers worked equally well for both species of trees. Therefore, we chose three primers for use with *P. albicaulis* and four for *P. contorta*. Two primers overlapped in use for both trees (**Table 1**).

For amplification we used a 25 μl reaction mixture consisting of 12.5 μl Promega Master Mix (Promega, Madison, WI, United States), 2.5 μl RNA-free water, 8 μl of 0.5 M primer and 2 μl of DNA template. Reactions were run individually with one of the five ISSR primers. PCR was conducted with one cycle denaturation at 95°C for 5 min, followed by 42 cycles of denaturation at 95°C for 1.3 min, annealing at 47°C for 2 min, and extension at 72°C for 1 min. A final cycle was conducted at 72°C for 1 min and final products were held at 6°C (Parasharami and Thengane, 2012).

PCR products were visualized in a 1% agarose gel prepared using 1× tris borate bu! er (TBE) to which 2 μl ethidium bromide per 100 ml gel was added. A 100 bp ladder (Promega, Valencia, CA, United States) was placed in the first lane of each gel to provide a reference for scoring bands. Amplified DNA was loaded into the remaining lanes with bromophenol blue as a running dye. Each gel was run with 1× TBE as a running bu! er at 70 mA until the dye moved ¾ of the length of the gel. Gel images were captured using a UV table. Any sample that gave ambiguous results (no, faint, or smeared bands) was repeated. Approximately 20% of samples were rerun and compared to check for consistency in results. Only samples exhibiting clear bands were included in the final analysis. Bands were scored manually.

Data Analysis

Diameter Distributions

A two-sample t-test was used to compare mean diameters among groups (survivor, general population, and beetle-killed) using Statistix 7 (Analytical Software, Tallahassee, FL, United States).

Genetic Analysis

Bands were scored as present (1) or absent (0) to develop a binary matrix combining data for all primers by tree species. The matrices were analyzed in Popgene v. 1.32 (Yeh et al., 1997) (assuming each group was in Hardy-Weinberg equilibrium) to calculate percent polymorphism, the Shannon information index (I), Nei's gene diversity index (h), total genetic diversity (H_T), genetic diversity within groups (survivor, general population) (H_S), and evidence for deviations from neutrality (selection) with an overall Ewens–Watterson test for neutrality. Population genetic structure was investigated using STRUCTURE v. 2.3 (Pritchard et al., 2000). The *admixture* model was used with a 10,000 burn-in period and 10,000 Markov Chain Monte Carlo replications. Twenty runs were performed with each value from 1 to 10 to estimate the optimal number of clusters (K) using the ΔK statistic (Evanno et al., 2005).

For each tree species, we examined genetic variation between groups using analysis of molecular variation (AMOVA) in GenAlEx 6.5 (Peakall and Smouse, 2006). We then conducted

TABLE 1 | Primers used for ISSR amplification.

Primer ID	Sequence	Tree species
HB12	CAC CAC CAC GC	*Pinus albicaulis*
17899A	GTG TGT GTG TGT CA	*P. albicaulis, P. contorta*
17901	CAC ACA CAC ACA AG	*P. contorta*
UBC 807	AGA GAG AGA GAG AGA GT	*P. albicaulis, P. contorta*
UBC 811	GAG AGA GAG AGA GAG AC	*P. contorta*

a principle coordinates analysis (PCoA) in GenAlEx based on genetic distances between individual trees in the two groups for each species of tree. Genetic distance matrices were developed for each tree species in the *Restml* program and then imported into *Neighbor* in PHYLIP 3.67 (Felsenstein, 2005) to produce an unweighted neighbor-joining tree. The tree was visualized using TreeView 1.6.6 (Page, 1996).

RESULTS

Diameter Distributions and Blister Rust Infection Severity

The mean, median, and range of diameters of beetle-killed and survivor *P. albicaulis* were similar (**Table 2**). The mean diameter was not significantly different between survivor and beetle-killed trees, while the diameter of general population trees, as expected, differed significantly from both groups (**Table 2**). The same was true for *P. contorta* (**Table 2**). Similarly, mean diameters of MPB-killed and survivor *P. albicaulis* and *P. contorta* did not differ from one another. However, the minimum size of tree attacked by the beetle differed by tree species resulting in the choice of different diameter distributions for sampling general population trees (**Table 2**). Blister rust infection severity was overall very low at the site, but significantly lower in survivors (mean = 1.3, *SD* = 1.8) than in general population trees (mean = 1.7, *SD* = 2.4; *F* = 1.63, *df* = 65, *P* = 0.013; potential range 0–18).

Genetic Analyses

Pinus albicaulis

Three primers (17899A, HB12, and UBC807) resolved well for *P. albicaulis* and were used for ISSR analysis. A total of 28 loci (bands) were resolved using the three primers (**Table 3**). Mean percent band polymorphism (BP) for all primers for all trees (general population and survivors) combined was 96.4% and this value was similar to the BP for each group individually. The Shannon information index and Nei's gene diversity was lower in general population trees compared with survivors (**Table 2**). Nei's unbiased measure of genetic identity between the survivor and general population trees was 95% while genetic distance was a corresponding 5%.

H_T, the total genetic diversity between the two study groups, was 0.26, and the diversity within groups, H_S, was 0.24. Seven of 28 loci (25%) exhibited significant differences between observed and expected frequencies of bands between the two groups (data not shown). However, no bands were unique to either group. The Ewens–Watterson test for neutrality detected only one marginally non-neutral locus. AMOVA indicated 87% of the variation exhibited existed within groups and 13% existed between groups.

TABLE 2 | Summary statistics for diameter breast height (cm) of *Pinus albicaulis* and *P. contorta* by group.

Tree	Group	N	Mean (*SD*)	Median	Minimum	Maximum
P. albicaulis	Beetle-killed	75	24.5 (5.3)^{a}	24.2	12.0	37.3
	Survivor	30	25.0 (5.2)^{a}	24.1	17.0	37.3
	General	36	10.0 (0.6)^{b}	10.0	9.0	11.0
P. contorta	Beetle-killed	45	26.7 (5.0)^{a}	26.4	17.5	36.8
	Survivor	20	27.5 (5.4)^{a}	29.9	18	37.2
	General	20	15.3 (0.9)^{c}	15.2	13.9	16.8

Different letters following means denote statistically significant differences, α = 0.05.

The neighbor-joining tree resolved most general population trees together in the basal clades while one major terminal clade contained all survivor trees as well as eleven general population trees that were distributed throughout the clade (**Figure 1**). The results of Bayesian clustering using STRUCTURE indicated that the optimal *K*-value was 3 with the general population dominated by one cluster (red, **Figure 2**) and survivors dominated by the other two (blue and green, **Figure 2**). The eleven general population trees that clustered with survivor trees in the neighbor-joining tree exhibited predominantly blue and green profiles in the STRUCTURE bar graph (shown with asterisks) indicating similarity to survivors (**Figure 2**). In the PCoA, the first two principle coordinates explained a total of 33% of the variation associated with the two groups. Adding the third, 43.55% was explained. In general, the eleven general population trees that clustered with survivors in the neighbor-joining tree resolved separate from other general population trees and with survivors in the PCoA (**Figure 3**).

Pinus contorta

Four primers resolved well for this species (17899A, UBC807, UBC901, and UBC811). Using these primers, we were able to resolve a total of 85 bands. The mean percent BP across all primers and groups was 98.82. This was considerably higher than BP for the general population (89.4%) and survivor (88.2%) trees (**Table 2**). The mean number of effective alleles was slightly lower than the mean number of observed alleles. Shannon's information index was similar within and across groups while Nei's gene diversity was lowest in survivors and highest for both groups combined (**Table 2**). Nei's unbiased genetic identity and diversity between the two groups was 93 and 7%, respectively.

H_T was 0.26 and H_S was 0.25, similar to values for whitebark pine. Allele frequencies were significantly different between survivors and general population trees at 12 of 85 loci (14%) (**Table 3**). No bands were unique to either group. The Ewan–Watterson test for neutrality indicated that six loci in the general population and nine loci in the survivors were outside the 95% CI indicating non-neutrality. All had positive *F*-values greater than the upper bound indicating a potential for directional selection. AMOVA indicated that 89% of variation occurred within groups while 11% occurred between groups.

The neighbor-joining tree partitioned general population and survivor trees into several clades (**Figure 4**). Most (55%) general population trees resolved in one clade. The remainder resolved into two clades interspersed with survivors (**Figure 4**). The general population trees that resolved with survivors in the neighbor-joining tree shared clusters with survivor trees in the STRUCTURE analysis (**Figure 2**) and also partitioned with survivor trees in the PCoA (**Figure 3**). The first two principle coordinates in the PCoA explained 21.5% of the

TABLE 3 | Percent band polymorphism (BP), number of observed (N_a) and effective (N_e) alleles, Shannon's Information Index (*I*), Nei's gene diversity (*h*), and diversity between (H_T) and within groups (H_S), presented by tree species and group.

Tree species	Group	N	%BP	N_a	N_e	*I*	*h*	H_T	H_S
P. albicaulis	Survivor	30	96.58	1.97 (0.19)	1.39 (0.25)	0.40 (0.19	0.22 (0.14)		
	General	36	96.55	1.97 (0.19)	1.32 (0.27)	0.36 (0.14)	0.25 (0.14)		
	Combined	66	96.43	1.96 (0.19)	1.41 (0.19)	0.42 (0.18)	0.26 (0.14)	0.26 (0.10)	0.24 (0.01)
P. contorta	Survivor	20	88.24	1.88 (0.32)	1.40 (0.33)	0.25 (0.17)	0.39 (0.23)		
	General	20	89.41	1.89 (0.31)	1.40 (0.31)	0.26 (0.16)	0.40 (0.22)		
	Combined	40	98.82	1.90 (0.11)	1.41 (0.29)	0.27 (0.14)	0.42 (0.18)	0.27 (0.02)	0.25 (0.02)

Means are accompanied by standard deviations in parentheses.

variation between the two groups. Adding the third component explained 31%.

DISCUSSION

Knowledge of the effects of bark beetle outbreaks on host tree population genetic structure and resistance to attack will be increasingly valuable as climate change drives more frequent outbreaks and facilitates the movement of beetle species into naïve forests. Outbreaks of MPB seldom kill all mature trees despite high beetle numbers during population peaks. Our results suggest that surviving trees possess a wealth of information that can be used to inform our understanding of the genetic and phenotypic bases for resistance and to develop management approaches that support forest adaptation.

We found that surviving mature trees in a high elevation forest of whitebark and lodgepole pine were genetically distinct from "general population" trees that were assumed to represent the genetic structure of the population pre-outbreak and without selection by the beetle. In line with our hypothesis, a low percentage (<10%) of "survivor" genotypes were identified within the general population. The proportion of these survivors roughly mirrored the proportion of mature trees that survived the outbreak at Vipond Park. The neighbor-joining tree, the PCoA and the STRUCTURE analyses each indicated strong differentiation between survivors and "susceptible" individuals and identified the same trees as survivors within the general population. In the STRUCTURE analysis for both whitebark and lodgepole pine, susceptible trees belonged to one cluster while survivor trees belonged to two other clusters. This separation can also be seen in the PCoA. Further research will be needed to

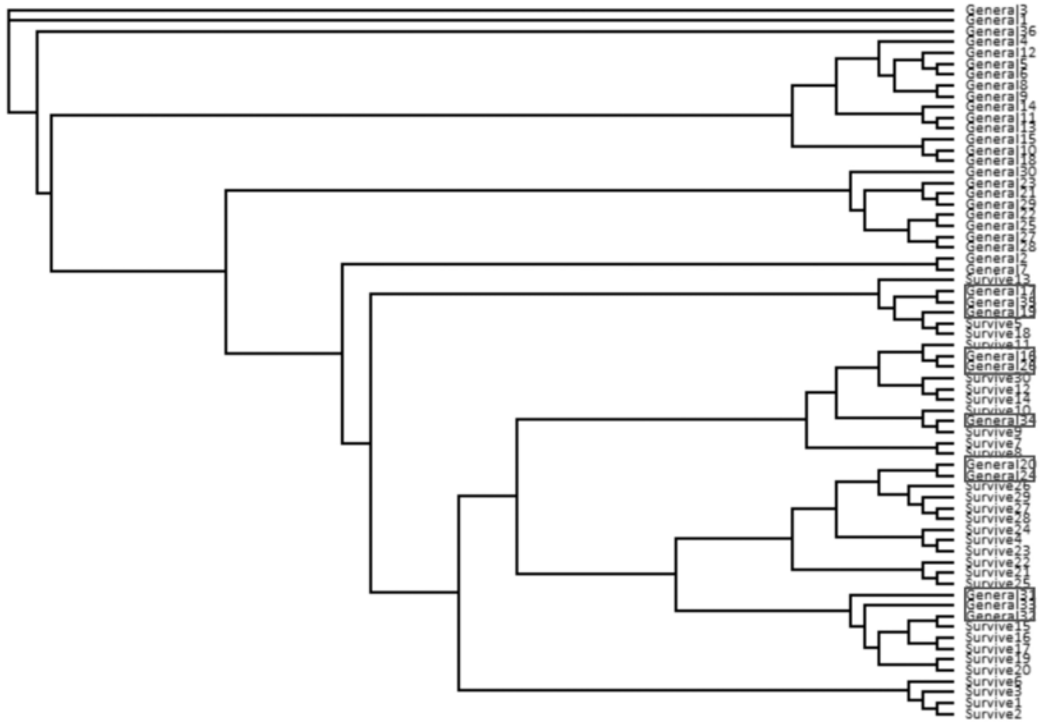

FIGURE 1 | Neighbor-joining tree from ISSR data for *Pinus albicaulis*. General = general population trees (with no *Dendroctonus ponderosae* selection). Survive = mature trees surviving *D. ponderosae* outbreak. Trees in boxes correspond to trees with arrows in **Figure 2** and in ellipses in **Figure 3**.

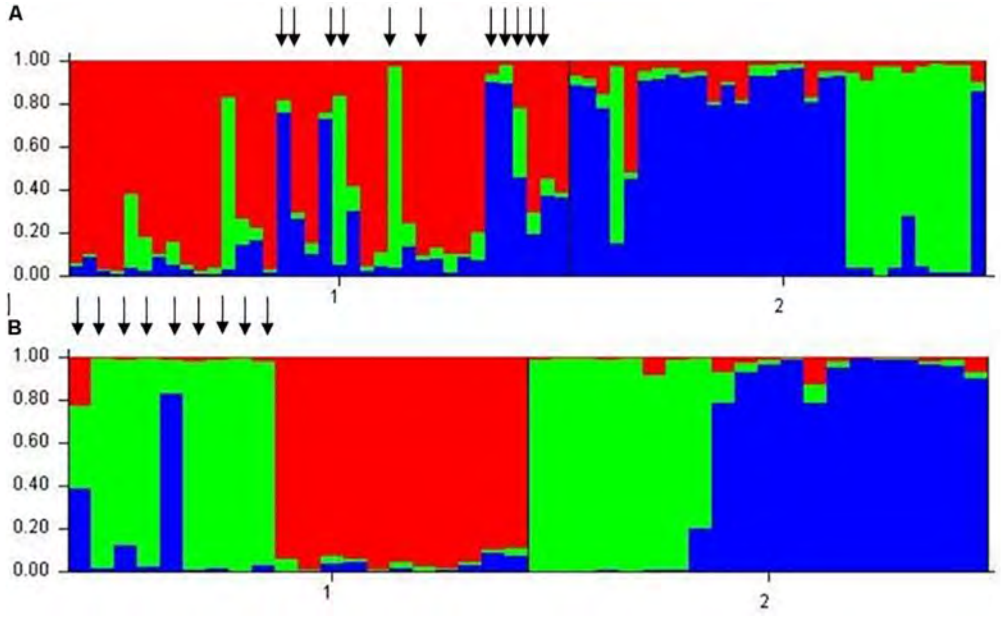

FIGURE 2 | Results of Bayesian clustering using STRUCTURE. Individual trees are represented by vertical bars. Colored segments represent the tree's estimated proportion similarity to each of the three clusters (red, blue, and green) optimally defined by STRUCTURE. **(A)** *Pinus albicaulis*. Arrows denote general population trees that resolved with survivors in neighbor-joining tree in **Figure 1**. **(B)**. *Pinus contorta*. 1 = general population trees. 2 = survivor trees.

determine whether the patterns we detected are indeed indicative of resistance, and if so, whether there are multiple or overlapping factors that account for survivorship.

We found surprisingly high levels of differentiation between survivor and general population trees in both species of pine. For whitebark pine, Nei's genetic distance between survivor and general population whitebark pines was 5%, a value that would indicate moderate differentiation if these comparisons had been made between tree populations. Likewise, AMOVA indicated 13% of the genetic variation present existed between groups. Considering that the trees in this analysis were not from different populations, but rather grew intermixed at the same site, these values seem strikingly high. Likewise, for lodgepole pine, Nei's genetic distance was 7%, and AMOVA indicated 11% of variation occurred between the groups.

These results indicate the presence of genetically based resistance in both pine species and that trees with resistant genotypes are not selected for attack. It has been thought that once MPB achieve high population levels during outbreaks, the selection of individual trees based on tree-produced compounds and condition becomes swamped by high levels of aggregation pheromone production and competition for increasingly rare hosts (Safranyik and Carroll, 2006). However, our results suggest that beetles remain selective even as outbreaks peak and collapse.

We chose ISSR profiling as a first step to determine whether survivors were different than trees chosen by MPB for colonization. This PCR-based method detects high levels of polymorphism, is highly reproducible, and allows the screening of a large number of trees relatively rapidly and economically. Unfortunately, this method cannot tell us why survivors are different, only that they are. Further study will be needed to further investigate whether survivors are indeed highly resistant and, if so, to determine the actual basis behind resistance. Ongoing studies are investigating correlations among genetic profiles of survivor and "susceptible" trees with phenotypic traits including defensive chemistry and growth rates in relation to climate. Genomic approaches will also be extremely useful to elucidate the basis of resistance.

This study corroborated the findings of other studies that found that MPB colonizes smaller diameter whitebark pine than lodgepole pine during outbreaks (Dooley et al., 2015). The mortality of younger whitebark pine trees indicates a more severe impact of MPB outbreaks on whitebark pine forests, at least in the short term, because advanced regeneration is killed along with large trees. However, the loss of large and mid-diameter trees may serve to open areas for nutcracker caching of seeds from the remaining resistant trees, potentially increasing the frequency of those genotypes and phenotypes at the site and within the larger population.

In a previous study, Six and Adams (2007) found that as infection severity increased so did the likelihood of attack by the beetle. However, while we found that white pine blister rust infection severity was significantly higher in general population trees than survivors, the mean level of infection severity at the site was very low and the size effect between means for survivors and general population trees was very small. Therefore, we feel it is unlikely blister rust played a significant role influencing beetle dynamics at the study site.

A caution is in order in interpreting our results. We were unable to amplify DNA from MPB-killed trees which forced us to use smaller diameter "general population" trees as a substitution

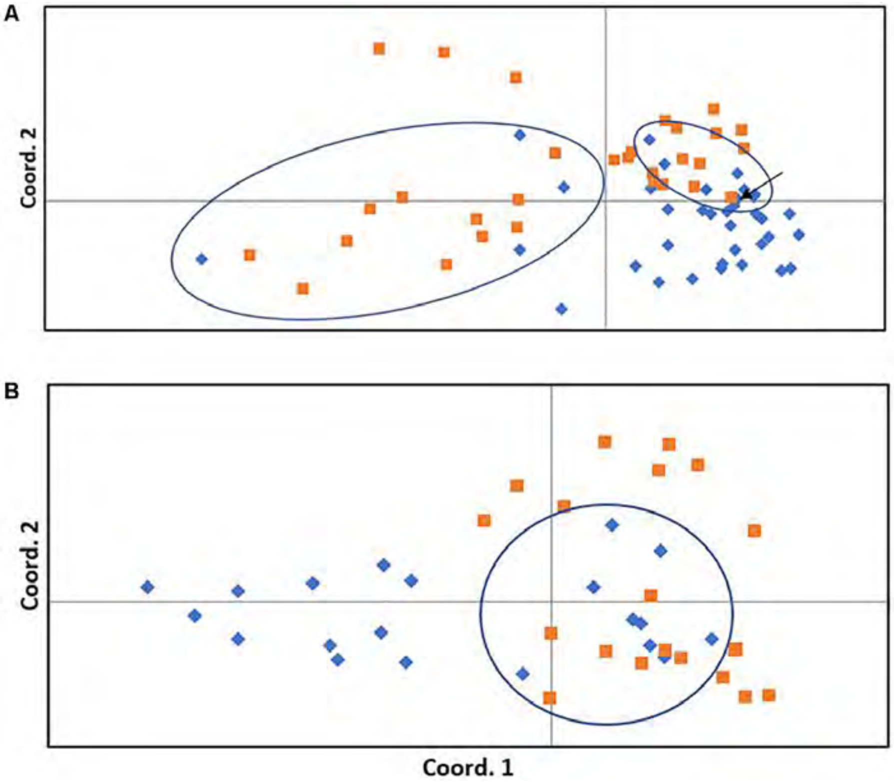

FIGURE 3 | Principle coordinates analysis of general (blue diamonds) and survivor (orange squares) trees. **(A)** *Pinus albicaulis.* The first and second coordinates explain 19.29 and 13.67% of the variation among trees, respectively (total 33%). **(B)** *Pinus contorta*. The first and second coordinates explain 10.98 and 10.55% of the variation among trees, respectively (total 21.5%). Ellipses surround general population trees that clustered with survivors in the neighbor-joining tree (**Figure 1** for *P. albicaulis*, **Figure 4** for *P. contorta*) and correspond to trees marked with an arrow in the STRUCTURE analysis (in this figure). Arrow indicates one general population tree within the ellipse that did not cluster with survivors in the neighbor-joining tree.

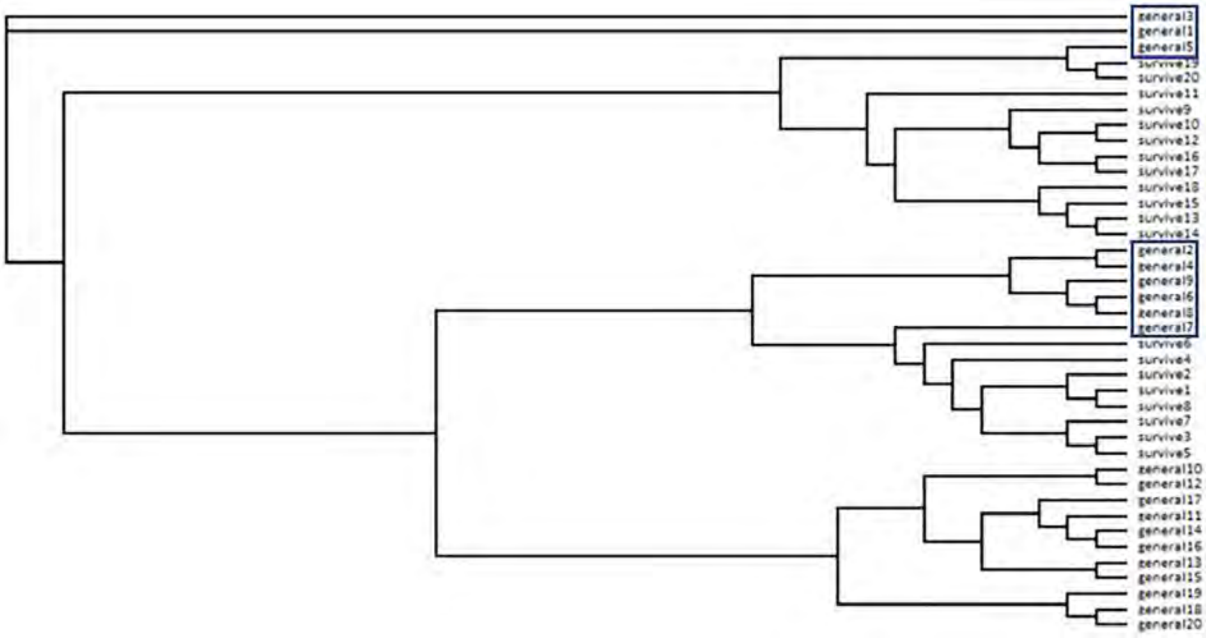

FIGURE 4 | Neighbor-joining tree from ISSR data for *Pinus contorta*. General = general population trees (with no *Dendroctonus ponderosae* selection). Survive = mature trees surviving *D. ponderosae* outbreak. Trees in boxes correspond to trees with arrows in **Figure 2** and in ellipses in **Figure 3**.

for "susceptible" trees. These trees were mature reproductive trees and only slightly smaller than trees selected by the beetle for colonization; however, some or all may constitute a cohort that regenerated under different environmental conditions resulting in a genetic structure unrepresentative of the larger trees that were available for selection by the beetle. However, the proportional distribution of survivor and "susceptible" trees in the neighbor-joining trees, PCoAs and STRUCTURE analyses indicate that the general population samples were likely appropriate proxies.

With climate change supporting the invasion of aggressive bark beetles into naïve forests, and predictions of more frequent and severe outbreaks, it is increasingly important to understand the capacity of trees to adapt and persist (Millar et al., 2007; Ramsfield et al., 2016). While the massive mortality of pines in western North America in recent years is cause for concern, we should also look at these hard-hit forests as opportunities to learn. In almost all cases, affected forests are not completely dead–they retain many living large diameter trees. If these trees are genetically different than those selected and killed by the beetles as our study suggests, these trees may aid in *in situ* adaptation and persistence. They may also be key to developing management and trajectories that allow for forest adaptation. For example, retaining surviving trees as a primary seed source, rather than removing them during salvage operations could support *in situ* adaptation. In contrast, the effects of natural selection in these stands could be instantly negated by clearcutting or replanting with general seed stock.

Supporting forest adaptation is critical in this time of rapid change (Millar et al., 2007). Given the great expanses of forest that are being affected by climate change and the fact that most will need to adapt *in situ*, it is imperative we begin to move past structural approaches to consider the genetic capacity of forest trees to adapt. The high degree of standing genetic variation found in most forest trees indicates many will have considerable ability to adapt. We need to be cognizant of adaptation that is occurring so that our management approaches act to support rather than hinder natural selection for traits needed under future conditions.

AUTHOR CONTRIBUTIONS

DS conceived of the project, participated in field work, conducted data analysis, and wrote the manuscript. CV conducted lab work on whitebark pine and participated in field work and data analysis. MC conducted field and lab work on lodgepole pine and contributed to data analysis.

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LETTER

Fire, water, and biodiversity in the Sierra Nevada: a possible triple win

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Keywords: wildfire, resilience, mixed conifer, climate change, adaption, hydrology

Abstract

Reducing the risk of large, severe wildfires while also increasing the security of mountain water supplies and enhancing biodiversity are urgent priorities in western US forests. After a century of fire suppression, Yosemite and Sequoia-Kings Canyon National Parks located in California's Sierra Nevada initiated programs to manage wildfires and these areas present a rare opportunity to study the effects of restored fire regimes. Forest cover decreased during the managed wildfire period and meadow and shrubland cover increased, especially in Yosemite's Illilouette Creek basin that experienced a 20% reduction in forest area. These areas now support greater pyrodiversity and consequently greater landscape and species diversity. Soil moisture increased and drought-induced tree mortality decreased, especially in Illilouette where wildfires have been allowed to burn more freely resulting in a 30% increase in summer soil moisture. Modeling suggests that the ecohydrological co-benefits of restoring fire regimes are robust to the projected climatic warming. Support will be needed from the highest levels of government and the public to maintain existing programs and expand them to other forested areas.

Introduction

Fire has been an integral ecosystem process in western U.S. forests for millennia. Lightning was the primary ignition source, and later, American Indians added ignitions by burning for cultural purposes. The invasion of Euro-Americans in the mid-1800s disrupted natural fire occurrence by both reducing the influence of Indigenous burning practices and introducing widespread livestock grazing, which limited fuel continuity and fire spread (Taylor *et al* 2016, Pyne 2019). Active fire suppression, which began in the early 20th century, further disrupted natural fire occurrence and ultimately led to a widely adopted policy of full fire suppression across all U.S. federally managed lands (Stephens *et al* 2016). This suppression policy was highly effective at eliminating fire for decades but recent wildfire activity has increased and this has been accompanied with severe land management problems (Calkin *et al* 2015).

In 1962, the Secretary of the Interior asked a committee to investigate wildlife management problems in the U.S. national parks. This committee, named after its chair, Dr Starker Leopold, took the broader ecological view

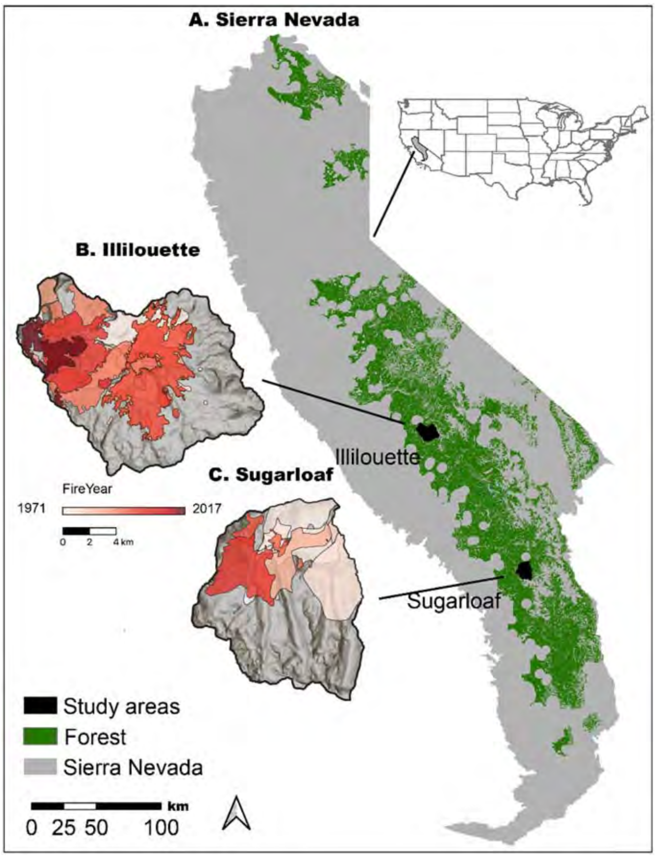

Figure 1. Sierra Nevada forests with managed wildfire potential, locations of study areas, and perimeters of wildfires that burned in Illilouette and Sugarloaf creek basins during the wildfire management program (~1972-present). Fire perimeters were obtained from a database generated by the state of California (FRAP 2020) and are shaded based on wildfire year (darker red = more recent). Forested areas with actual or potential managed wildfire use (green areas in A) are classified as those outside of the wildland urban intermix (WUI; Radeloff *et al* 2017) threat zone and where the contiguous land area is at least as large as our smaller study basin (Sugarloaf; ~13,000 ha). Forested areas are defined according to LANDFIRE biophysical settings data (Rollins 2009). WUI threat zone definition follows the strategic fire management zone alternative A of the Sierra National Forest land management plan (USDA 2019).

that parks should be managed as ecosystems (Leopold *et al* 1963). As a result, the U.S. National Park Service changed its policy in 1968 to recognize fire as an ecological process. Fires would be allowed to burn if they could be contained within fire management units and accomplished approved management objectives (figure 1).

Sequoia and Kings Canyon National Parks established a natural fire management zone in 1968 immediately after this policy change (Kilgore and Briggs 1972), and thus began the first tentative experiments with managing naturally ignited fires deep in park wilderness. This was followed in 1972 with a similar zone designation in Yosemite National Park (van Wagtendonk 1978). These three national parks have the longest periods of allowing lightning fires to burn in the USA. The objective of these programs was to restore the ecological role of fire under prescribed conditions (figure 2). Among land management agencies, these national parks have been world leaders in the increasingly difficult effort to allow lightning-ignited fires to burn. Concerns over smoke, at-risk species, the threat posed by fires to nonfederal lands, and the uncertainty of potential impacts should fires grow beyond expected boundaries have hindered full implementation of managed wildfire programs (Miller *et al* 2012). Even with these constraints, the parks and a few U.S. Forest Service wilderness areas remain committed to allowing wildland fires to play their ecological role. The U.S. Forest Service is currently moving ahead with plans to expand natural fire programs in California (Meyer 2015).

In this paper we summarize what has been learned from 50 years of managed fire programs in Sierra Nevada national parks. Very few areas with such a legacy of fire-use exist making these areas critical natural laboratories which have accordingly received increasing attention from scientists. As managers, policy makers, and the public work to create long-term solutions to conserve U.S. forests, these areas could prove invaluable in future program and policy design.

Figure 2. Repeat photographs taken from field plots in Illilouette Creek basin. The left two images (A), (B) were taken 1 and 9 years following low severity fire. The right two images (C), (D) were taken 1 and 9 years following moderate severity fire. Fire severity class for these plots was based on Landsat-derived Relative differenced Normalize Burn Ratio, using thresholds presented in Miller and Thode (2007). A small patch of fire-killed trees is also evident in Image D, just beyond the red oval, which contains numerous snags and saplings that regenerated following the 2001 Hoover Fire. Red ovals identify the same point in the photographs.

Fire severity and vegetation

Fire severity in the basins was assessed using the Relative differenced Normalized Difference Vegetation Index (RdNDVI) for fires prior to 1984 and Relative differenced Normalized Burn Ratio (RdNBR) for fires post 1984. RdNDVI and RdNBR were derived based on Parks *et al* (2018) Google Earth Engine algorithm. Both RdNDVI and RdNBR distributions for each fire was thresholded (Miller and Thode 2007), where values between 0 and 315 were classified as low severity, 316 and 640 as moderate severity, and values above 641 were classified as high severity. These thresholds were calibrated by Collins *et al* (2009), based on fires that occurred in Yosemite National Park. Despite 80–100 years of fire exclusion policies from ~1880 to 1970, the frequency of contemporary fire activity in both basins is similar to the pre fire exclusion period using dated fire scars (~1700–1880 C.E.; Collins and Stephens 2007). The long fire-free period (~1880–1970) coincided with substantial tree recruitment relative to the historical and contemporary natural fire periods (Collins and Stephens 2007) and allowed for considerable surface fuel accumulation (Parsons and Debenedetti 1979). Given these changes one might assume that fire severity, as measured using remotely sensed imagery (e.g., Miller and Thode 2007), would be elevated when fire was reintroduced. This was not the case in either basin. In Illilouette, the first widespread fire under the managed wildfire program, the 1974 Starr King Fire, burned nearly 1600 ha (van Wagtendonk 1978) and only 9% was at high severity (Collins *et al* 2009). Since then, only 14% of the total burned area in Illilouette was classified as high severity, and in Sugarloaf, high severity accounted for 16% of total burned area. For comparison, 27% of the area outside of the Illilouette and Sugarloaf basins in the Sierra Nevada burned at high severity from 1984 to 2018 (figure 3).

The return of fire to these basins has allowed investigation into the processes driving natural fire-vegetation dynamics. The fact that neither timber harvesting or road building occurred in either basin strengthens inferences from these investigations. Within individual fires, the dominant vegetation type (i.e., *Pinus*-dominated forest, *Abies*-dominated forest, montane chaparral) and weather were most strongly connected to fire severity (Collins *et al* 2007). At the landscape level, time-since-last-fire, previous fire severity (for reburns), and dominant vegetation type influenced fire severity (Collins and Stephens 2010, van Wagtendonk *et al* 2012).

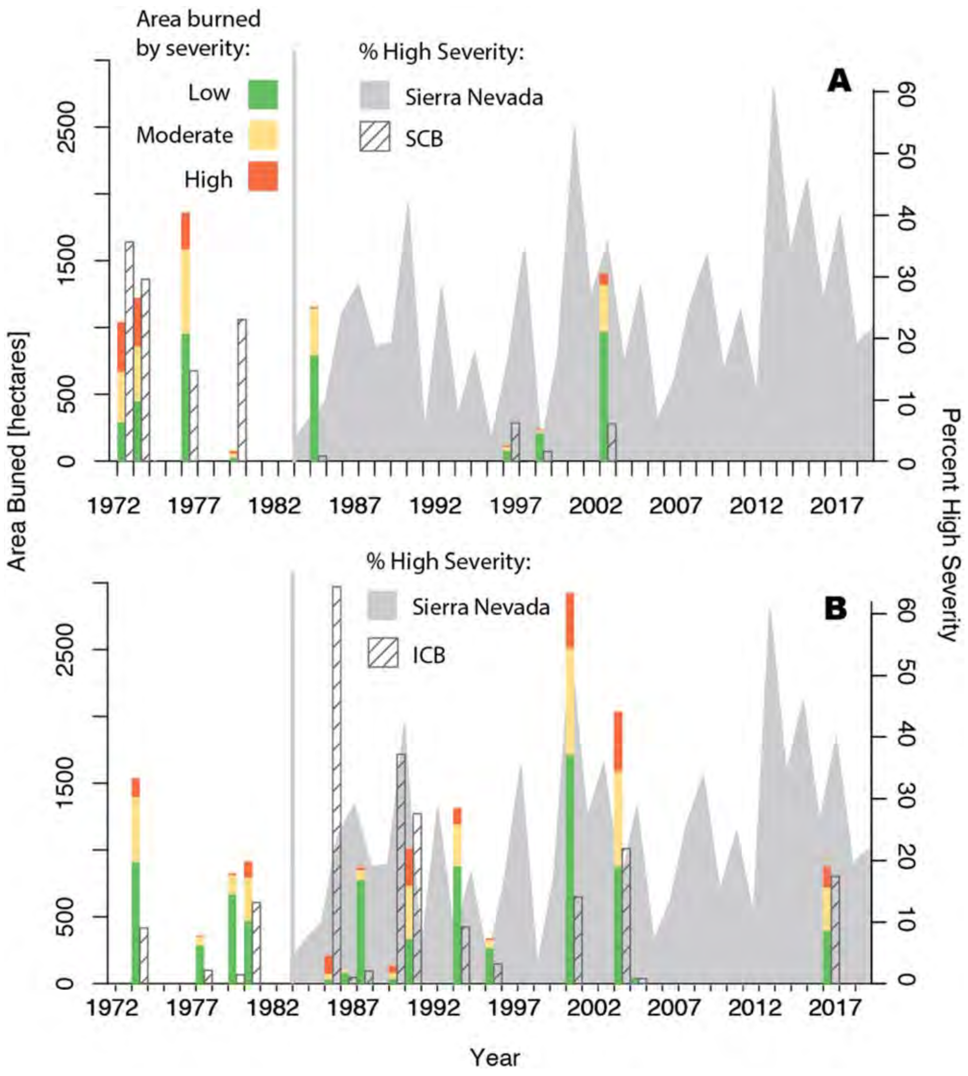

Figure 3. Proportion of fire area burned at low, moderate, and high severity as classified by LANDSAT-derived RdNDVI (prior to 1984) and RdNBR (post 1984) severity indices for fires burned in Sugarloaf Creek Basin-SCB (A) and Illilouette Creek Basin-ICB (B). Fire severity class thresholds were based on those in Collins *et al* (2009) and Miller and Thode (2007) for RdNDVI and RdNBR, respectively. Proportion of the yearly fire area burned at high severity is shown as vertical bars with diagonal line in both panels, which corresponds with the right vertical axis. For comparison, the proportion of yearly fire area burning at high severity in the entire Sierra Nevada bioregion (Rakhmatulina *et al* 2021a) is shown in light gray, also corresponding with the right vertical axis.

Time-since-last-fire also exerted a strong control on whether fires re-burned over previous fire areas (Collins *et al* 2009).

Assessments of landscape-scale vegetation change using aerial photography during the managed fire period revealed different outcomes for Illilouette (1970–2012; Boisramé *et al* 2017a) and Sugarloaf (1973–2014; Stevens *et al* 2020). In Illilouette, the proportion of the basin comprised of conifer forest decreased from 82% to 62%, being replaced by shrublands and meadows. In Sugarloaf, forest cover changed very little: from 83% to 82%. Accordingly, contemporary vegetation cover classes (forest, shrub, sparse and dense meadow) are more balanced, with greater landscape heterogeneity in Illilouette compared to Sugarloaf (Stevens *et al* 2020). Plot-level forest structure data collected in the early 1970s provided further evidence that forest stand structure in Sugarloaf did not change markedly as a result of the managed fire program (Stevens *et al* 2020). However, across both basins, conifer-dominated areas that burned in managed fires (including reburns) had highly variable structure and composition, ranging from open *Pinus jeffreyi* dominated forests, dominated by large trees (tree density: 104 ha^{-1}; basal area 19.5 m^{2}ha^{-1}) to dense, closed-canopy structures dominated by *Abies concolor and A. magnifica* (tree density: 446 ha^{-1}; basal area 53 m^{2}ha^{-1}) (Collins *et al* 2016). The two primary drivers of this variability were the local biophysical environment and recent fire severity. Despite this high variability, surface fuel loads and tree densities in both basins are markedly lower than in comparable portions of the Sierra Nevada where fire has been successfully excluded in the modern era (Collins *et al* 2016).

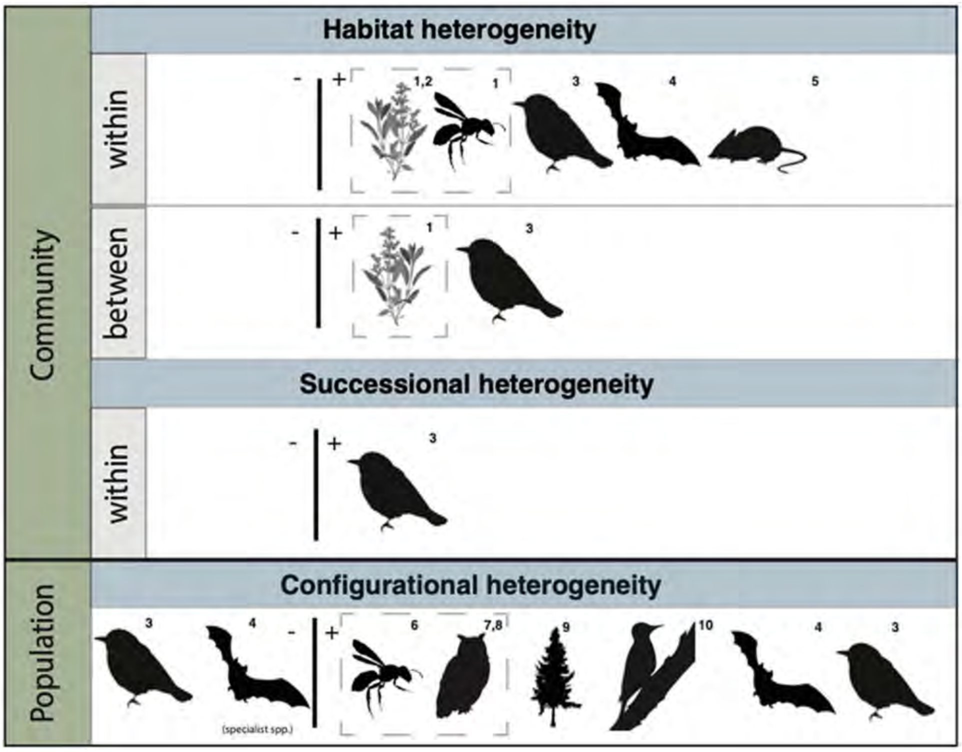

Figure 4. Studies finding evidence for (+) or against (−) the proposed mechanisms by which pyrodiversity begets biodiversity. Pyrodiversity may promote biodiversity by increasing variation in landscape composition (habitat and successional heterogeneity) and/or by increasing variation in the spatial arrangement of fire elements (configurational heterogeneity). The dashed grey boxes indicate studies were primarily conducted or at least partially in the Illilouette and Sugarloaf basins. Other studies examine the effect of mixed severity fires in the Sierra Nevada forests, the restoration of which is the intention of managed wildfire programs. 1 Flowering plants and bees- Ponisio *et al* 2016; 2 Understory plants - Wilkin *et al* 2021 (in press); 3 Birds - Tingley *et al* 2016; 4 Bats - Steel *et al* 2019; 5 Small mammals - Roberts *et al* 2015; 6 Bees- Ponisio 2020; 7,8 Birds (spotted owls) - Hobart *et al* 2021 and Kramer *et al* 2021; 9 Trees- Blomdahl *et al* 2019. 3,4 found evidence both for and against a specific mechanism depending on species.

The divergent effects of the managed fire program on vegetation in the two basins has several possible explanations. Illilouette has higher precipitation and vegetation productivity than Sugarloaf (Stevens *et al* 2020); therefore, it is possible that the increase in fuel during the fire exclusion period was greater in Illilouette, resulting in more frequent fires with larger high severity proportions that created larger patches of non-forest vegetation. Another possible reason for the difference is many fires have been suppressed in the last 15 years in Sugarloaf (Stevens *et al* 2020). The increase in vegetation heterogeneity in Illilouette is clearly related to the greater incidence of small high severity patches in this basin and the stability of fire severity classes over the decades (figure 3).

Biodiversity

Wilderness areas managed for wildfire in the Sierra Nevada support greater pyrodiversity (variability in fire severity, season, size, frequency) and consequently greater landscape heterogeneity (van Wagtendonk and Lutz 2007, Boisramé *et al* 2017a, Steel *et al* 2021) than comparable fire-suppressed areas. Ecological theory predicts that diversity, including pyrodiversity, begets biodiversity (Martin and Sapsis 1992). Multiple mechanisms by which pyrodiversity promotes biodiversity have been proposed at community and population scales (Kelly *et al* 2017, Jones and Tingley 2021, figure 4). Studies in Illilouette and Sugarloaf have shown that pyrodiversity created by managed wildfire is associated with higher biodiversity (bees and understory plants: Ponisio *et al* 2016, Ponisio 2020, Wilkin *et al* 2021 in press) and is compatible with at least some mature forest specialists (California spotted owl, *Strix occidentalis occidentalis*: Hobart *et al* 2021, Kramer *et al* 2021). Because few population- or community-level studies on the effect of fire management have been conducted primarily in Illilouette and Sugarloaf, we also considered studies conducted in similar Sierra Nevada landscapes. Corroborating Illilouette and Sugarloaf studies, pyrodiversity in other comparable regions is positively related to mammal, bird, bat, and tree biodiversity (Roberts *et al* 2015, Tingley *et al* 2016, Blomdahl *et al* 2019, Steel *et al* 2019) (figure 4). These lines of evidence suggest use of managed wildfire and restoration of pyrodiverse landscapes is broadly supportive of biodiversity in Sierra Nevada and similar ecosystems.

We also found support for a variety of mechanisms underlying the positive effect of pyrodiversity in and around the Illilouette and Sugarloaf basins. Within bird, bee, plant, and bat communities, habitat heterogeneity underlies enhanced biodiversity (figure 4). Specifically, pyrodiversity leads to local variation in fire history generating spatial niche diversity and allowing a greater number of species to coexist (Kelly *et al* 2017). Among communities, studies on flowering plants and birds found that the fire severity heterogeneity enhances beta-diversity (figure 4) because species are associated with different fire histories. These results highlight the potential for managed wildfire areas and their expansion to improve regional biodiversity, which is adversely affected by the homogenizing effects of both fire suppression and large high severity fires.

The successional heterogeneity mechanism has not been explicitly addressed for many taxa in the Sierra Nevada and is often conflated with habitat heterogeneity because different fire severities are often characterized as supporting species from different successional stages (e.g., higher severity fires support ‘early successional’ species) (Ponisio *et al* 2016). However, Tingley *et al* (2016) found that both habitat and successional heterogeneity enhanced bird coexistence in the Sierra Nevada. It is likely, therefore, that a combination of spatial and temporal heterogeneity of fire histories promotes biodiversity, as originally proposed by Martin and Sapsis (1992).

At the population scale, fire-generated heterogeneity promoted persistence in specific species of birds and bats that use areas with different fire histories for specific food resources/prey species, shelter, and/or avoid predation (Tingley *et al* 2016, Steel *et al* 2019, figure 4). For example, Black-backed woodpeckers (*Picoides arcticus*) benefited from configurational heterogeneity (number, size, and arrangement of habitat patches) along high severity patch edges perhaps reflecting the trade-offs of predation risk, nest site availability, and food resources within high severity patches (Stillman *et al* 2019, 2021). Similarly, fire refugia can support survival during and immediately following fire for California spotted owls (*Strix occidentalis occidentalis*) and some tree species (Blomdahl *et al* 2019, Hobart *et al* 2021, Kramer *et al* 2021). We would expect to find similar positive responses to configurational heterogeneity for other species that have resource/shelter needs associated with patches of different fire severities or unburned forest, but negative responses for some habitat specialists. In Illilouette, Ponisio (2020) found that the combination of local pyrodiversity enabled populations of species with the ability to switch floral interaction partners to persist through a severe drought. Fire-supported heterogeneity may therefore enhance community resistance to climate change in other species that, similar to bees, benefit from the different resources afforded by patches with disparate fire histories.

Together, the ample evidence across taxa (birds, mammals, insects and plants) and ecological scales (population, within and between communities) that pyrodiversity benefits biodiversity through a variety of mechanisms. This suggests that the expansion of the managed wildfire model to analogous areas in the Sierra Nevada mixed conifer forest would benefit biodiversity regionally and perhaps help ecological communities adapt to growing threats associated with global change.

Hydrology and climate change

The conversion of dense, fire-excluded forest to a mosaic of grasslands, wet meadows, shrublands, and forest stands of varying age and density changed the partitioning of the water balance in Illilouette (Boisramé, *et al* 2017b, figure 5). A statistical model trained on field moisture measurements suggested that the observed conversion of forest areas to meadows in the central area of the Illilouette basin between 1969 and 2012 led to increases in summer soil moisture by as much as 30 percentage points (Boisramé *et al* 2018). These estimates are supported by *in situ* soil moisture monitoring in Illilouette and Sugarloaf, which consistently shows soil water content under meadow and shrub canopies to be 10 to 30 percentage points greater than under neighboring forest canopies (Boisramé *et al* 2018, Stevens *et al* 2020).

Identifying the processes responsible for these relations between vegetation and water storage remains challenging. Simulation in Illilouette with ecohydrological models suggests that forest reduction was associated with reduced snowpack sublimation and summer transpiration so that 2012 vapor fluxes from the basin declined by approximately 40 mm year^{-1} relative to 1969, similar to the increase in streamflow (Boisramé *et al* 2019). Observations made with time-lapse cameras in Illilouette and Sugarloaf show that snowpack is thinnest and melts earliest beneath forest canopies compared to shrub and meadow areas (Boisramé *et al* 2019, Stevens *et al* 2020). Increased subsurface water storage and reduced transpiration demands probably contributed to very low tree mortality in Illilouette during the extreme drought years of 2014–2015 (Boisramé *et al* 2017b). Flow observations at the Happy Isles stream gauge on the Merced River and model predictions suggest that these water balance changes produced modest increases in annual streamflow, with approximately 50 mm year^{-1} additional flow from Illilouette after 40 years of managed wildfire (Boisramé *et al* 2019). Reassuringly, neither the modeling nor gauge observations show evidence of increased peak flows (floods), which are often identified as a potential hydrological risk of increasing fire frequency. In contrast to Illilouette, the less pronounced

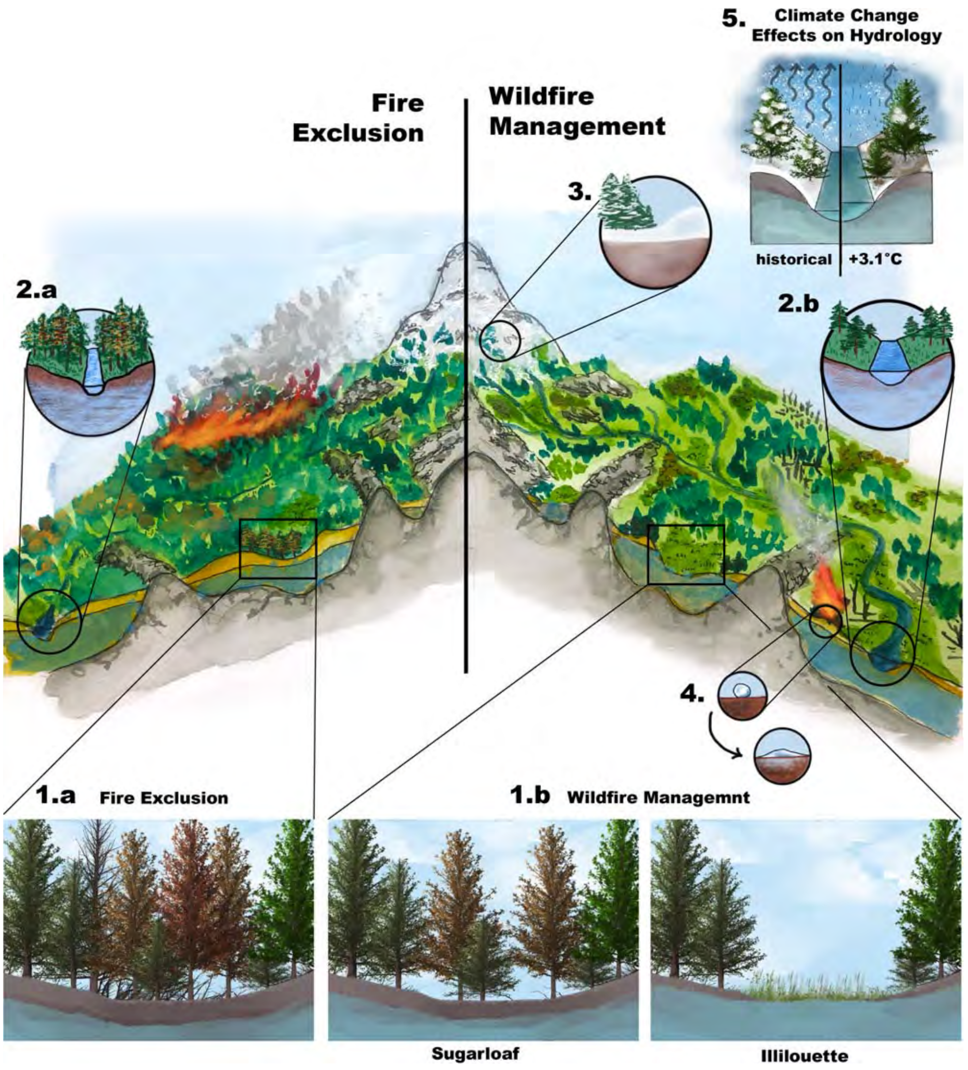

Figure 5. The left panel depicts a fire suppressed landscape, and the right panel shows a landscape experiencing frequent fires under a wildfire management strategy. The right panel is more representative of a landscape change that occurred in Illilouette basin, which experienced greater vegetation transitions from forest to shrublands and grasslands, resulting in an overall wetter landscape than Sugarloaf basin (1.b). As seen in Illilouette, wildfires increased basin streamflow (2), which is partially attributed to greater snow water equivalent in open areas compared to under canopies (3). No large-scale post-fire erosion is observed in Illilouette, likely due to frequent freeze-thaw cycles which reduce post-fire soil hydrophobicity (4). As climate is predicted to warm by 3.1 °C without significant change in precipitation totals, snowpack will be reduced, which is predicted to decrease basin evaporation through sublimation reduction, causing a marginal net increase in streamflow relative to historically observed conditions (5).

vegetation changes in Sugarloaf during the managed fire program do not appear to have resulted in noticeable hydrological changes (Stevens *et al* 2020).

Climatic warming is expected to impact the hydrology of the Sierra Nevada by increasing the fraction of precipitation falling as rain and moving peak streamflow earlier in the year (Rakhmatulina *et al* 2021a). Climate change is also likely to alter the characteristics of managed wildfires in Illilouette and Sugarloaf, although forecasting these changes is challenging (Gonzalez *et al* 2018). Observations over the past 50 years in Illilouette show no trends in fire severity or burned area in spite of climatic warming during that period (figure 3), presumably because both of these characteristics have been moderated by fuel consumption and associated disruptions in fuel continuity across the landscape (Collins *et al* 2009). Lightning ignitions, however, may become more frequent in Illilouette given warmer and drier weather. Increasing fire frequency from climate change accelerates the pace of hydrological changes without altering the long-term hydrological state (Rakhmatulina *et al* 2021a). These results suggest that the hydrological co-benefits of restoring fire regimes are robust to the projected climatic warming in the Sierra Nevada.

Considerable uncertainties remain, however, regarding the feedbacks between fire, vegetation, and the water cycle as climate changes. For instance, it is not clear how important the expansion of wet meadow areas might be in creating natural 'fire breaks' that constrain the extent of future fire. Even the modest increases in soil moisture that occurred in the basin to date could influence fires, with recent studies showing that fuel moisture can be significantly increased by wet soils, reducing ignition probabilities (Rakhmatulina *et al* 2021b). Similarly, several hydrological implications of the managed wildfire program, including the impacts on water quality, require more research. Examination of LIDAR imagery from before and after the 2017 Empire Fire in Illilouette, however, shows little evidence of large-scale erosion (Boisramé unpublished data 2020). The fact that freeze-thaw cycling in Sierra Nevada soils can rapidly erode post-fire hydrophobicity (Rakhmatulina and Thompson 2020) could contribute to rapid recovery of soil's ability to absorb and store water in these basins after fire.

Conclusion

Reducing the risk of large, severe wildfires while also increasing the security of mountain water supplies and enhancing biodiversity are urgent priorities. Here we found evidence for this synergism in Illilouette but not fully in Sugarloaf. While differences in the productivity of these forested areas could have contributed to this disparity, the shortage of managed wildfires in Sugarloaf is likely the biggest factor. The number of fires larger than 40 ha from 1973 to 2016 was much higher in Illilouette ($n = 21$) than Sugarloaf ($n = 10$). This disparity is particularly evident in recent decades, with Illilouette experiencing 12 fires larger than 40 ha since 1985 and Sugarloaf only experiencing 4 (Stevens *et al* 2020). The amount of recent fire activity in Sugarloaf may represent a deficit compared to the historical fire return interval (Collins and Stephens 2007). This recent fire deficit is illustrated by the fact that wildfires have burned only 1 ha in Sugarloaf between 2004 and 2017 with 59% of active ignitions suppressed, compared with 7,289 ha burned in Illilouette and only 23% of ignitions suppressed in the basin between 1969 and 2003 (Stevens *et al* 2020).

The challenges of maintaining a managed wildfire program are daunting, even in remote areas. Ignitions during droughts have been suppressed for fear of adverse fire effects or lack of public and political support in allowing fires to burn. Climate change is expected to create more alternating periods of drought and high precipitation (Abatzoglou and Williams 2016), which will probably be the environment that fire managers will have to adapt to. Political challenges were evident to Yosemite National Park managers when the 2017 Empire Fire was allowed to burn in Illilouette at the same time as the 2017 Wine Country fires were burning large areas of Napa, Sonoma, and Mendocino counties and destroying tens of thousands of structures. National park managers are to be commended for creating these managed wildfire programs and working to maintain them into the future.

Current revisions to the Land and Resource Management Plans for U.S. National Forests in the southern Sierra Nevada emphasize managed wildfire over 69% to 84% of National Forest land (Rakhmatulina *et al* 2021a). Areas that have similar characteristics to Illilouette and Sugarloaf in terms of forest type and remoteness are extensive in the Sierra Nevada (figure 1), demonstrating the potential to increase the area managed by wildfire. National Forest lands often have different land use histories than National Parks, including extensive historical logging which can change forest and fuel structures and create additional challenges to restoration by fire alone (Collins *et al* 2017, Jeronimo *et al* 2019), but the successes of the managed fire programs in the parks discussed here do provide a useful template for scaling up the landscape application of managed wildfire to other lands. If managers decide to implement managed fire programs they should be robust to climate change (fires continue to be self-limiting and fire severity classes remain stable) but may be more volatile as the time required to produce a fire mosaic is expected to be much shorter from the impacts of climate change (Rakhmatulina *et al* 2021a). Continued support at the highest levels of government, as well as from the public, would be needed to maintain existing managed wildfire programs and expand them to others forested areas. Were fire to be removed from managed fire areas, woody cover and water use would again increase, diminishing the positive impacts of these programs (continued fire use would produce relatively low levels of smoke for many months which could negatively impact some people). Perpetual support for these programs and for the scientific investigations that can interpret their effects is key if we want to avoid increasingly destructive high severity wildfires that damage ecosystems and human communities.

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Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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The forgotten stage of forest succession: early-successional ecosystems on forest sites

Mark E Swanson, Jerry F Franklin, Robert L Beschta, Charles M Crisafulli, Dominick A DellaSala, Richard L Hutto, David B Lindenmayer, and Frederick J Swanson

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The forgotten stage of forest succession: early-successional ecosystems on forest sites

Mark E Swanson[1*], Jerry F Franklin[2], Robert L Beschta[3], Charles M Crisafulli[4], Dominick A DellaSala[5], Richard L Hutto[6], David B Lindenmayer[7], and Frederick J Swanson[8]

Early-successional forest ecosystems that develop after stand-replacing or partial disturbances are diverse in species, processes, and structure. Post-disturbance ecosystems are also often rich in biological legacies, including surviving organisms and organically derived structures, such as woody debris. These legacies and post-disturbance plant communities provide resources that attract and sustain high species diversity, including numerous early-successional obligates, such as certain woodpeckers and arthropods. Early succession is the only period when tree canopies do not dominate the forest site, and so this stage can be characterized by high productivity of plant species (including herbs and shrubs), complex food webs, large nutrient fluxes, and high structural and spatial complexity. Different disturbances contrast markedly in terms of biological legacies, and this will influence the resultant physical and biological conditions, thus affecting successional pathways. Management activities, such as post-disturbance logging and dense tree planting, can reduce the richness within and the duration of early-successional ecosystems. Where maintenance of biodiversity is an objective, the importance and value of these natural early-successional ecosystems are underappreciated.

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Severe natural disturbances – such as wildfires, windstorms, and insect epidemics – are characteristic of many forest ecosystems and can produce a "stand-replacement" event, by killing all or most of the dominant trees therein (Figure 1). Typically, limited biomass is actually consumed or removed in such events, but many trees and other organisms experience mortality, leaving behind important biological legacies (structures inherited from the pre-disturbance ecosystem; Franklin *et al.* 2000), including standing dead trees and downed boles (tree trunks; Franklin *et al.* 2000). Such legacies provide diverse physical/biological properties and suitable microclimatic conditions for many species. Thereafter, species-diverse plant communities develop because substantial amounts of previously limited resources (light, moisture, and nutrients) become available. These emerging plant communities create additional habitat complexity and provide various energetic resources for terrestrial and aquatic organisms.

In a nutshell:

- Naturally occurring, early-successional ecosystems on forest sites have distinctive characteristics, including high species diversity, as well as complex food webs and ecosystem processes
- This high species diversity is made up of survivors, opportunists, and habitat specialists that require the distinctive conditions present there
- Organic structures, such as live and dead trees, create habitat for surviving and colonizing organisms on many types of recently disturbed sites
- Traditional forestry activities (eg clearcutting or post-disturbance logging) reduce the species richness and key ecological processes associated with early-successional ecosystems; other activities, such as tree planting, can limit the duration (eg by plantation establishment) of this important successional stage

The ecological importance of early-successional forest ecosystems (ESFEs) has received little attention, except as a transitional phase, before resumption of tree dominance. In forestry, this period is often called the "cohort re-establishment" or "stand initiation" stage, with attention obviously focused on tree regeneration and the re-establishment of closed forest canopies (Franklin *et al.* 2002). Ecological studies have focused primarily on plant-community development and the needs of selected animal (mostly game) species, and not on the diverse ecological roles of ESFEs.

Here, we highlight important features of ESFEs, including their role in sustaining ecosystem processes and biodiversity, so that they may be appropriately considered by resource managers and scientists, and included within management/research programs dedicated to maintaining these functions, particularly at larger spatio-temporal scales. Most published examples focus on sites in western North America, but ESFEs are important elsewhere (Angelstam 1998; DeGraaf *et al.* 2003). We also discuss how traditional forestry practices, such as clearcutting, tree planting, and post-disturbance logging, can affect early-successional communities.

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Figure 1. *Stand-replacement disturbance events in forests create large areas free of tree dominance and rich in physical and biological resources, including legacies of the pre-disturbance ecosystem.*

(Franklin *et al.* 2002). Consequently, the duration of ESFEs varies inversely with rapidity of tree regeneration and growth, which, in turn, depend on such variables as tree propagule availability, conditions affecting seedling or sprout establishment, and site productivity. ESFE longevity after natural disturbances is therefore highly variable.

Development of a closed forest canopy may require a century or more in areas with limited seed sources, harsh environmental conditions, severe shrub competition (in some instances), or combinations thereof (Hemstrom and Franklin 1982). For example, tree canopy closure after wildfire in the Douglas fir region of western North America often requires several decades (Poage *et al.* 2009), but can occur much more rapidly when canopy seedbanks are abundant (eg Larson and Franklin 2005). Closed forest canopies may develop quickly in forests dominated by trees with strong sprouting ability (eg many angiosperms) or when windstorms "release" understories of shade-tolerant tree seedling banks by removing all or most of the overstory (Foster *et al.* 1997).

Early-successional ecosystems on forest sites

Initial conditions after stand-replacing forest disturbances vary generically, depending on the type of disturbance; this includes the types of physical and biological legacies available. For example, aboveground vegetation may be limited immediately after the disturbance, as in the case of severe wildfires or volcanic eruptions. Conversely, intact understory communities may persist where forests have been blown down by severe windstorms. Spatial heterogeneity in conditions is characteristic, given that disturbances vary greatly in the amount of damage they cause (Turner *et al.* 1998). For instance, severe wildfires frequently include substantial areas of unburned as well as low to medium levels of mortality, creating variability in shade, litterfall, soil moisture, seed distribution, and other factors.

We define ESFEs as those ecosystems that occupy potentially forested sites in time and space between a stand-replacement disturbance and re-establishment of a closed forest canopy. These ecosystems undergo compositional and structural changes (succession) during their occupancy of a site. Changes begin immediately post-disturbance, as a result of the activities of surviving organisms (eg plants, animals, and fungi), including plant growth and seed production. Developmental processes are enriched by colonization of flora and fauna from outside the disturbed area. Successional change is often characterized by progressive dominance of annual and perennial herbs, shrubs, and trees, although all of these species are typically represented throughout the entire sequence of forest stand development (or sere; Halpern 1988).

The ESFE developmental stage ends with re-establishment of tree cover that is sufficiently dense to suppress and often eliminate many smaller shade-intolerant plants

Attributes of early-successional ecosystems

After severe disturbances, forest sites are characterized by open, non-tree-dominated environments, but have high levels of structural complexity and spatial heterogeneity and retain legacy materials.

Environmental conditions

Removal of the overstory forest canopy during disturbances dramatically alters the site's microclimate, including light regimes. These changes lead to increased exposure to sunlight, more extreme temperatures (ground and air), higher wind velocities, and lower levels of relative humidity and moisture in litter and surface soil. Shifts in these environmental metrics favor some species, while creating suboptimal or intolerable conditions for others. For example, post-disturbance plant community composition, cover, and physiognomy are altered as shade-tolerant understory herbs are largely displaced by shade-intolerant and drought-tolerant species. New substrates deposited by floods or volcanic eruptions may lack nutrients, provide additional water-holding capacity, or have high albedo, all of which favor shifts in plant communities.

Survivors

Organisms (in a variety of forms) that survive severe disturbances are extremely important for repopulating and restoring ecosystem functions in the post-disturbance landscape. Even in severely disturbed areas, organisms may survive as individuals (mature or immature) or as reproductive structures (eg spores, seeds, rootstocks, and eggs), which become in situ propagule sources. For example, after the 1980 volcanic eruption of Mount St Helens (Washington State), most pre-eruption flora and many fauna (especially aquatic and burrowing terrestrial species) survived within the blast zone through several different mechanisms (Dale *et al*. 2005).

Surviving organisms are also often vital for the prompt re-establishment of important ecosystem functions, such as conservation of nutrients and stabilization of substrates. For instance, the important role of resprouting vegetation in curbing massive losses of nitrogen was demonstrated by experimentally clearcutting and applying herbicides in a watershed at Hubbard Brook Experimental Forest (Bormann and Likens 1979).

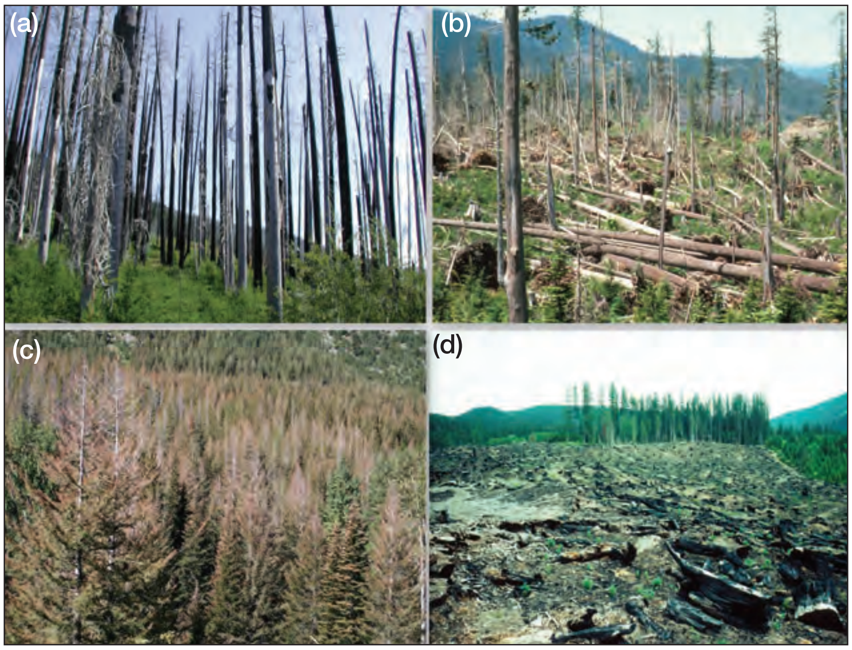

Figure 2. *Different types of disturbances produce different types of biological legacies, including living organisms and structures: (a) standing dead trees (snags) are dominant structural legacies after severe wildfires; (b) downed tree trunks and nearly intact understory communities are characteristic legacies after major windstorms; (c) standing dead trees are also dominant structural legacies after heavy insect infestations; and (d) clearcuts typically eliminate most aboveground structural legacies. Values for each metric are shown in Table 1 and are described in detail in the text.*

Structural complexity

The structural complexity of ESFEs depends initially on legacies, the general nature of which varies with the type of disturbance (Table 1; Figure 2); for example, snags and shrubs originating from belowground perennating (ie resprouting) parts or seeds are dominant legacies after wildfires, whereas downed boles and largely intact understories are typical post-disturbance characteristics of windstorms.

Woody legacies, such as snags and downed boles, play numerous roles in structuring and facilitating the development of the recovering ecosystem – providing habitat for survivors and colonists, moderating the physical environment, enriching aquatic systems in the disturbed area (Jones and Daniels 2008), and providing long-term sources of energy and nutrients (Harmon *et al*. 1986). Although subject to decomposition, these legacies can persist for many decades and sometimes even centuries.

Table 1. Different types of intense disturbances generate different types of biological legacies

	Disturbance				
Biological legacies	*Wildfire*	*Wind*	*Insect*	*Volcano*	*Clearcut*
Live trees	Infrequent	Variable	Variable (depends on stand composition)	Infrequent – confined to margins	Infrequent or absent
Snags	Abundant	Variable	Abundant	Abundant (spatially variable)	Infrequent or absent
Downed woody debris	Variable, but typically abundant	Abundant	Variable, but eventually abundant	Abundant (spatially variable)	Infrequent
Undisturbed understory	Infrequent	Abundant	Abundant	Infrequent – confined to disturbance margins	Infrequent
Spatial heterogeneity of recovery	High	Variable	High	High	Variable – usually low
Time in early-successional condition	Variable	Variable	Long	Variable – usually long	Variable – usually short

Figure 3. *Plant communities with well-developed shrub and perennial herb species are characteristic of early-successional communities on forest sites and provide diverse food resources. Twenty-five years after the Mount St Helens eruption in 1980, this community, which was within the blast zone, includes well-developed shrubs (eg* Sorbus *and* Vaccinium *spp), trees, and perennial herbs (eg* Epilobium angustifolium*).*

Structural complexity is further enhanced by the establishment and development of a variety of plant species, which often include perennial herbs and shrubs characteristic of open environments, as well as individual trees (Figure 3). The diversity of plant morphologies (maximum height, crown width, etc) increases structural richness, so that this associated flora contributes to both horizontal and vertical heterogeneity.

Spatial heterogeneity

Spatial heterogeneity is evident in early-successional ecosystems and has multiple causes: (1) natural variability in the geophysical template (topography and lithology) of the affected landscape; (2) variability in conditions in the pre-disturbance forest ecosystem; (3) variability in the intensity of the disturbance event; and (4) variability in rates and patterns of subsequent developmental processes in the ESFE. The first two sources relate to existing geophysical and biological patterns within the disturbed area. Land formations and patterns of geomorphic processes are certainly key geophysical elements (Swanson *et al.* 1988). The presence of surface water, such as streams and ponds, can be particularly influential in facilitating survival and re-establishment of biota.

Natural disturbances create heterogeneous environments at multiple spatial scales (Heinselmann 1973), because disturbances do not cause damage uniformly. Disturbances such as wildfires and windstorms are variable in intensity (eg "spotting", or initiation of new flame fronts by wind-thrown firebrands, during fire events). Alternatively, geographic variation in environmental conditions and topography (Swanson *et al.* 1988) influences the intensity of the disturbance and results in heterogeneity at multiple scales. Variability in the structure and composition of the pre-disturbance forest also creates spatial and temporal variability (Wardell-Johnson and Horowitz 1996). Some of these patterns may be transient, such as residual snowbanks protecting tree regeneration after the aforementioned Mount St Helens eruption (Dale *et al.* 2005).

Post-disturbance developmental processes also lead to spatial heterogeneity. For example, varying distances to sources of tree seed result in different rates and densities of tree re-establishment (Turner *et al.* 1998). Structural legacies can greatly influence the rates at which wind- or waterborne organic (including propagules) and inorganic materials are deposited. Finally, animal activity can strongly influence patterns of revegetation, as illustrated by the multiple effects that gophers (*Thomomys* spp) can have on post-disturbance landscapes (Crisafulli *et al.* 2005b) or the way ungulate browsing may impede tree regeneration (Hessl and Graumlich 2002).

■ Biological diversity

ESFEs in temperate forest seres show great diversity in the abundance of plant and animal species (Fontaine *et al.* 2009). Species composition may consist of a mix of forest survivors, opportunists, or ruderals (plants that grow on disturbed or poor-quality lands), and habitat specialists that co-exist in the resource-rich ESFE environment (Figure 3). Most forest understory flora can survive disturbances as established plants, perennating rootstocks, or seeds. In one study, in western North America, over 95% of understory species survived the combined disturbance of logging and burning of an old-growth Douglas-fir–western hemlock stand (Halpern 1988). Some important early-successional species (eg *Rubus* spp [blackberry; raspberry], *Ribes* spp [gooseberry], and *Ceanothus* spp [buckbrush]) may persist as long-lived seedbanks.

Opportunistic herbaceous species are often conspicuous dominants early in the development of ESFEs (Figure 4). Many of these weedy species (particularly annuals) decline quickly, although other opportunists will persist as part of the plant community until overtopped by slower growing shrubs or trees. Consequently, diverse plant communities of herbs, shrubs, and young trees emerge in ESFEs; this, combined with the structural legacies from the pre-disturbance ecosystem, often results in high levels of structural richness (Figure 3).

Many animals, including habitat specialists and species typically absent from the eventual tree-dominated communities, thrive under the conditions found in ESFEs. For some species, this is the only successional stage that can provide suitable foraging or nesting habitat. As an example, many butterflies and moths (Lepidoptera) found in forested regions depend on the high diversity and quality of plant forage in ESFEs (eg Miller and Hammond 2007), whereas jewel beetles (Coleoptera: Buprestideae) depend on abundant coarse woody debris. Also, a number of ground-dwelling beetle species occur as habitat specialists in early-successional communities (Heyborne *et al.* 2003).


Figure 4. *Early-successional communities are often dominated by annual herbaceous species for the first few years after disturbance; these are quickly displaced by perennial herbaceous species and shrubs.*

Many vertebrates also respond positively to ESFEs, which may provide the only suitable habitat at a regional scale for some species. Ectothermic animals, such as reptiles (eg Rittenhouse *et al.* 2007), generally respond favorably to sunnier and drier conditions, colonizing early-successional habitat or increasing in abundance if present as survivors. Many amphibians also thrive in ESFEs, provided resources such as water bodies and key structures (eg logs) are available. The diversity and abundance of amphibians in the area affected by the 1980 Mount St Helens eruption is illustrative (Crisafulli *et al.* 2005a); eleven of 15 amphibian species survived the event, and some (eg western toad, *Bufo boreas*) have since had exceptional breeding success.

The broad array of birds using the abundant and varied food sources (eg fruits, nectar, herbivorous insects) and nesting habitat in ESFEs includes many raptors and neotropical migrants, often making bird diversity highest during the ESFE stage of succession (Klaus *et al.* in press). Some species are habitat specialists that directly utilize the legacy of recently killed trees; for instance, black-backed woodpeckers (*Picoides arcticus*) are almost completely restricted to early post-fire conditions (Hutto 2008). Mountain bluebirds (*Sialia currucoides*) and several other woodpecker species also favor structurally rich, early-successional habitats (Figure 5). Observed population declines of many avian species in eastern North America – which, in some cases, have proceeded to a point of conservation concern – are linked to conversion of early-successional habitat to closed forest (Litvaitis 1993).

Small mammal communities in ESFEs typically show high levels of diversity as well, including some obvious habitat specialists. The eastern chestnut mouse (*Pseudomys gracilicaudatus*), for example, inhabits early-successional environments in coastal eastern Australia for 2–5 years after a wildfire, and then declines dramatically until these environments are burned again (Fox 1990). Populations of mesopredators (medium-sized predators, such as raccoons [*Procyon lotor*] and fox species) benefit from the abundance of small vertebrate prey items characteristic of ESFEs. Likewise, some species of large mammals are well known to favor ESFEs (Nyberg and Janz 1990). Utilizing the diverse and luxuriant forage characteristically present in these ecosystems, ungulates, such as members of the Cervidae, in turn serve to benefit large predators (eg wolves [*Canis lupus*]) as well as scavengers, making ESFEs important elements within those species' typically extensive home ranges. Omnivores, such as bears (*Ursus* spp), also rely on the diversity of food sources often present in ESFEs.

■ Food web diversity

ESFEs are exceptional in the diversity and complexity of food webs they support. Simply stated, a diverse plant community produces many food sources. Food resources for herbivores (grasses, shrubs, forbs) – as well as nectar, seeds, and shrub-borne fruit (eg produced by *Rubus* and *Vaccinium* spp [huckleberry]) – can reach high levels before site dominance by trees. In the temperate Northern Hemisphere, biologically important berry production is maximized in slowly reforesting ESFEs. Resource production in early-successional patches may even augment the richness of adjacent undisturbed forests, as in the case of fluxes of key prey species (Sakai and Noon 1997).

Aquatic biologists have, perhaps, best appreciated the greater complexity of food chains in early-successional versus closed forest environments (Bisson *et al.* 2003). In established forest stands, trees strongly dominate the physical and biological conditions in nearby small streams by controlling light and temperature, stabilizing channels, providing woody debris, and, importantly, offering allochthonous inputs (organic matter originating outside the aquatic ecosystem) – the primary energy and nutrient source for such ecosystems (Vannote *et al.* 1980).

Stand-replacement disturbances remove forest constraints on conditions and processes, and shift streams to an early-

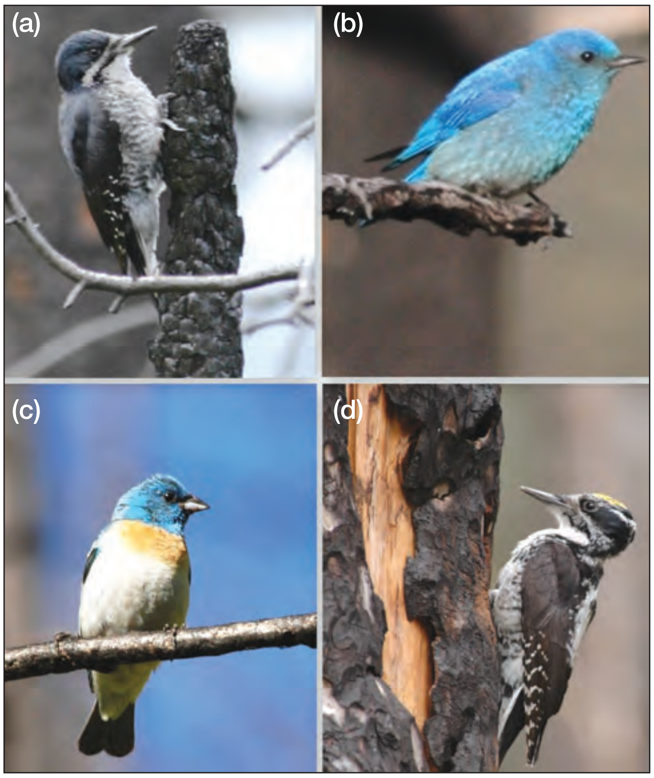

Figure 5. *Bird diversity is typically high in early-successional communities on forest sites and includes many habitat specialists: (a) black-backed woodpeckers (*Picoides arcticus*) are almost entirely restricted to early post-fire habitat; (b) mountain bluebirds (*Sialia currucoides*) favor early-successional ecosystems; (c) lazuli buntings (*Passerina amoena*) and (d) three-toed woodpeckers (*Picoides tridactylus*) have similar requirements.*

successional context (Minshall 2003; Figure 6). This greatly diversifies the types and timing of allochthonous inputs, as well as increases primary productivity. Allochthonous inputs are shifted from primarily tree-derived litter (coniferous-based in many systems) to material from a range of flowering herbs, shrubs, and trees, as well as from conifers. Consequently, litter inputs are highly variable in quality (eg decomposability) and delivery time, as compared with litterfall contributed primarily by evergreen conifer species. Also, inputs to post-disturbance streams often include material with a high nitrogen content, such as litter from the early-successional genera *Alnus* and *Ceanothus* (Hibbs *et al.* 1994).

Greater algal production may increase the diversity and abundance of aquatic invertebrate populations, which, in turn, become prey for fish and other organisms. However, increases in sediment production associated with disturbances can negate some benefits to aquatic processes and organisms (Gregory *et al.* 1987).

■ Processes in ESFEs

Ecosystem processes in ESFEs can be more diverse than those in closed forest systems, where the primary productivity of trees is dominant and organic matter is processed primarily through detrital food webs. Development of more diverse, and perhaps more "balanced", trophic pathways is possible when a disturbance opens a previously closed forest canopy. The contrast is probably greatest in forests dominated by a single tree type, such as evergreen conifers, as opposed to more diverse forests, such as mixed evergreen associations.

Recharging nutrient pools

ESFEs provide major opportunities for recharge of nutrient pools, such as additions to the nitrogen pool by leguminous (eg *Lupinus*) and some non-leguminous early-successional (eg *Alnus* and *Ceanothus*) plant species. These genera are commonly absent from late-successional forests, but are well represented in ESFEs. Nitrogenous additions from these sources are particularly important where the disturbance – eg a wildfire – has volatilized a substantial amount of the existing nitrogen pool.

Mineralization rates of organic material are typically accelerated (sometimes profoundly) after disturbances, as a result of warmer growing season temperatures. Diversified litter inputs in ESFEs, including a greater proportion of easily decomposed litter from herbs and deciduous shrubs, also result in more rapid mineralization. Finally, successional changes in the fungal and microbial communities can also hasten decomposition processes. As noted, these changes will be most profound in forest ecosystems dominated by a single species, including evergreen conifers or hard-leaved, evergreen hardwoods (such as the ash-type eucalypt forests of southeastern Australia).

In aquatic ecosystems that experience fire in adjacent forests, greater post-disturbance light and nutrient availability enhance primary productivity within the water body, causing shifts in food webs from the level of primary producers up through high-level consumers, such as fish (Spencer *et al.* 2003).

Modifying hydrologic and geomorphic regimes

Hydrologic regimes associated with ESFEs contrast greatly with those characterizing closed forest cover. For example, transpiration and interception are dramatically reduced and recover only gradually as forest canopies redevelop. Increases in normally low summer flows and annual water yields may occur immediately after a disturbance, as compared with levels in the dense young forests that may subsequently develop (Jones and Post 2004). The opposite may be true in systems where condensation of cloud or fog on tree crowns is an important component of the hydrologic cycle. ESFEs may also contribute to increased discharge peak runoff flows in hydrologic events of smaller magnitude (Harr 1986), but appear to have little effect on the magnitude of peak flows during large runoff events (Grant *et al.* 2008). From an ecological perspective, this may have a positive outcome, however, because floods restructure and rejuvenate many riparian communities (Gregory *et al.* 1991).

Rates and patterns of geomorphic processes, such as erosion and nutrient leaching losses, are also different between ESFEs and later successional stages. Tree death results in a loss of root strength that is critical for stabilizing soils and deeper rock layers on mountain slopes (Perry *et al.* 2008). Erosion and landslides may occur at higher rates in ESFEs, contributing to the variability of sediment budgets in watersheds (Reeves *et al.* 1995) and creating long-lasting substrates for ruderals. While enhancing erosion processes, ESFEs also provide materials and processes that counteract this effect, such as woody debris, which retain sediments and organic materials, and surviving vegetation, which stabilizes slopes and nutrient stores (eg Bormann and Likens 1979).


J Halofsky

Figure 6. *Streams within early-successional forest ecosystems contrast with forest-dominated reaches in many ecosystem attributes, including physical parameters (temperature and insolation), structure, plant and animal composition, and ecosystem processes, such as primary productivity.*

■ Land management implications

Incorporating ESFE attributes into forest policy and management is highly desirable, given the numerous advantages provided by these ecosystems. Many species and ecological processes are strongly favored by conditions that develop after stand-replacement disturbances. Rapid, artificially accelerated "recovery" of disturbed forest areas (eg via dense planting) to closed forest conditions has serious implications for many species. Clearly the term "recovery" has a different meaning for such early-successional specialists or obligates.

To fulfill their full ecological potential, ESFEs require their full complement of biological legacies (eg dead trees and logs) and sufficient time for early-successional vegetation to mature. Where land managers are interested in conservation of the biota and maintenance of ecological processes associated with such communities, forest policy and practices need to support the maintenance of structurally rich ESFEs in managed landscapes. Natural disturbance events will provide major opportunities for these ecosystems, and managers can build on those opportunities by avoiding actions that (1) eliminate biological legacies, (2) shorten the duration of the ESFEs, and (3) interfere with stand-development processes. Such activities include intensive post-disturbance logging, aggressive reforestation, and elimination of native plants with herbicides.

In particular, post-disturbance logging removes key structural legacies, and damages recolonizing vegetation, soils, and aquatic elements of disturbed areas (Foster and Orwig 2006; Lindenmayer *et al.* 2008). Where socioeconomic considerations necessitate post-disturbance logging, variable retention harvesting (retention of snags, logs, live trees, and other structures through harvest) can maintain structural complexity in logged areas (Eklund *et al.* 2009).

Prompt, dense reforestation can have negative consequences for biodiversity and processes associated with ESFEs, by dramatically shortening their duration. Such efforts reduce spatial and compositional variability characteristic of natural tree-regeneration processes, promote structural uniformity, and initiate intense competitive processes that eliminate elements of biodiversity that might otherwise persist. Artificial reforestation can also reduce genetic diversity by favoring dominance by fewer tree species/genotypes, and may make the system more prone to subsequent, high-severity disturbances (Thompson *et al.* 2007). The elimination of shrubs and broad-leaved trees through herbicide application can alter synergistic relationships, such as the belowground mycorrhizal processes provided by certain shrub species (eg *Arctostaphylos* spp).

Naturally regenerated ESFEs are likely to be better adapted to the present-day climate and may be more adaptable to future climate change. The diverse genotypes in naturally regenerated ESFEs are likely to provide greater resilience to environmental stresses than nursery-grown, planted trees of the same species. Given that climate change is also resulting in altered behavior of pests and pathogens (Dale *et al.* 2001), encouraging greater tree species diversity may also increase ecosystem resilience.

Clearcutting has been proposed as a technique to create ESFEs, but this can provide only highly abridged and simplified ESFE conditions. First, traditional clearcuts leave few biological legacies (eg Lindenmayer and McCarthy 2002), limiting habitat and biodiversity potential. Second, clearcuts are often quickly and densely reforested, and often involve the use of herbicides to limit competition with desired tree species. Clearcuts can provide some early-successional functionality (eg serving as nurseries or post-breeding habitat for many bird species in the southern US; Faaborg 2002), but this service is often truncated by prompt reforestation.

Management plans should provide for the maintenance of areas of naturally developing ESFEs as part of a diverse landscape. This should be in reasonable proportion to *historical* occurrences of different successional stages, as based on region-specific historical ecology. Major disturbance events provide managers with opportunities to incorporate a greater diversity of species and processes in forest landscapes and to enhance landscape heterogeneity. Some aspects of ESFEs can be incorporated into areas managed for production forestry as well, such as through variable retention harvest methods, the incorporation of natural tree regeneration, and extending the duration of herb/shrub communities in some portions of a stand by deliberately maintaining low tree stocking levels.

Finally, we suggest that adjustments in language are needed. Ecologists and managers often refer to "recovery" when discussing post-disturbance ecosystems, inferring that early seral conditions are undesirable and need to be restored to closed canopy conditions as quickly as possible. Emphasizing recovery as the management goal fails to acknowledge the essential ecological roles played by early-successional ecosystems on forest sites. It should also be considered that climate change and other factors may not permit "recovery" to pre-disturbance conditions.

■ Conclusions

Twentieth-century forest management objectives were centered on wood production and, later, on conservation and development of late-successional forests. Rapid regeneration of dense timber stands was frequently seen as a way to address both of these divergent objectives. Recognizing the ecological value of early-successional ecosystems on forest sites extends the ecological concerns associated with old growth to another "rich" period in a forest sere. This represents an important development in the evolution of holistic management of forest ecosystems, whereby large landscapes are managed for diverse seral stages.

ESFEs provide a distinctive mix of physical, chemical, and biological conditions, are diverse in species and processes, and are poorly represented and undervalued in traditional forest management. Forest policy and practice must give serious attention to sustaining substantial areas of ESFEs and their biological legacies. Similarly, scientists need to initiate research on the structure, composition, and function of ESFEs in different regions and under different disturbance regimes, as well as on the historical extent of these systems, to serve as a reference for conservation planning.

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REVIEW

Impacts of salvage logging on biodiversity: A meta-analysis

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Abstract

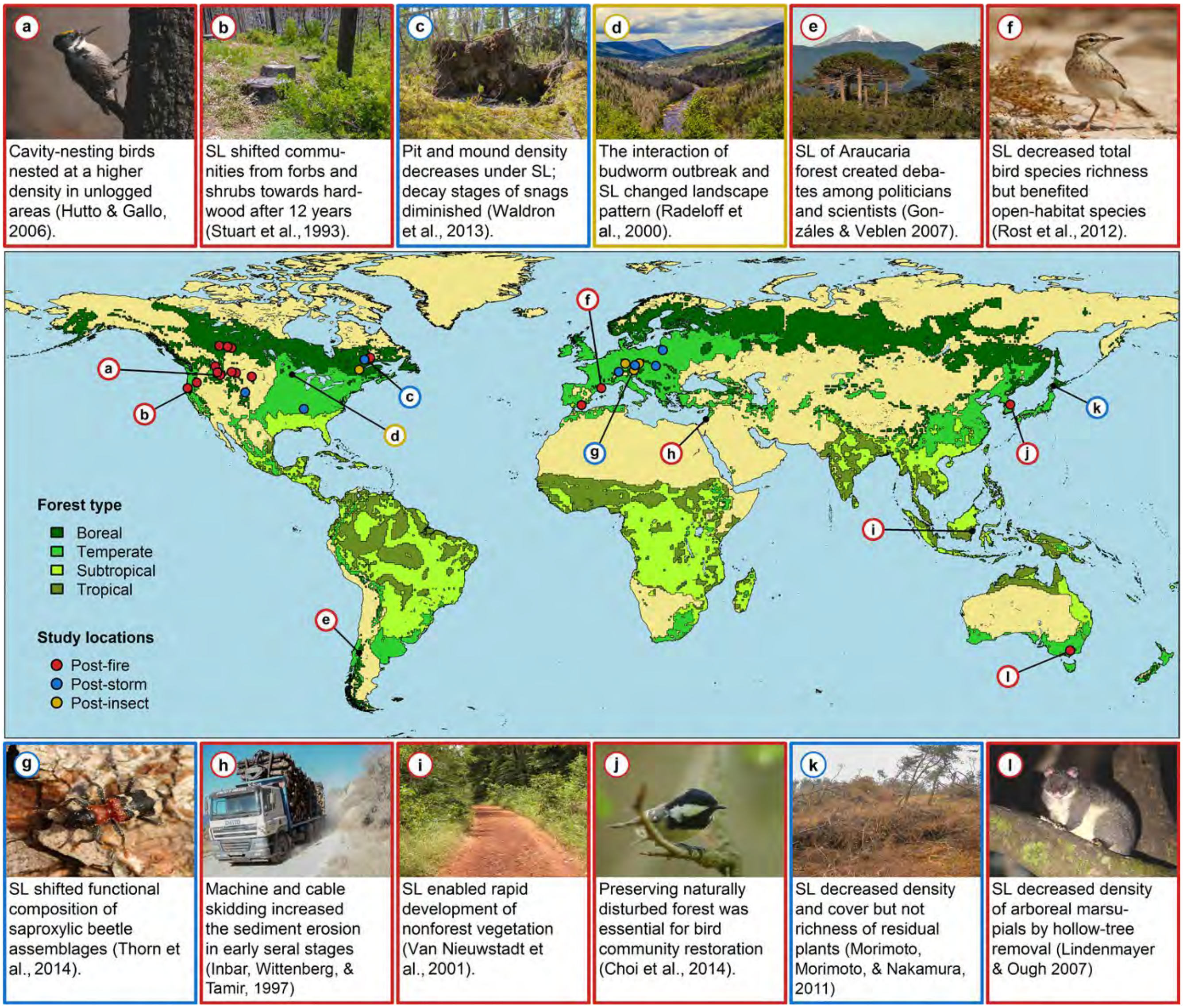
1. Logging to “salvage” economic returns from forests affected by natural disturbances has become increasingly prevalent globally. Despite potential negative effects on biodiversity, salvage logging is often conducted, even in areas otherwise excluded from logging and reserved for nature conservation, inter alia because strategic priorities for post-disturbance management are widely lacking.
2. A review of the existing literature revealed that most studies investigating the effects of salvage logging on biodiversity have been conducted less than 5 years following natural disturbances, and focused on non-saproxylic organisms.
3. A meta-analysis across 24 species groups revealed that salvage logging significantly decreases numbers of species of eight taxonomic groups. Richness of dead wood dependent taxa (i.e. saproxylic organisms) decreased more strongly than richness of non-saproxylic taxa. In contrast, taxonomic groups typically associated with open habitats increased in the number of species after salvage logging.
4. By analysing 134 original species abundance matrices, we demonstrate that salvage logging significantly alters community composition in 7 of 17 species groups, particularly affecting saproxylic assemblages.
5. *Synthesis and applications*. Our results suggest that salvage logging is not consistent with the management objectives of protected areas. Substantial changes, such as the retention of dead wood in naturally disturbed forests, are needed to support biodiversity. Future research should investigate the amount and spatio-temporal distribution of retained dead wood needed to maintain all components of biodiversity.

KEYWORDS
bark beetle, climate change, dead wood, disturbed forest, fire, natural disturbance, post-disturbance logging, salvage logging, saproxylic taxa, windstorm

1 | INTRODUCTION

The frequency and extent of stand-replacing natural disturbances, such as wildfires, windstorms and insect outbreaks, has increased considerably during recent decades, particularly in the Northern Hemisphere (Kurz et al., 2008; Seidl, Schelhaas, Rammer, & Verkerk, 2014). Natural disturbances can enhance the structural heterogeneity of forests, create habitats for species-rich assemblages of high conservation value and increase the long-term resilience of forests to future stressors (Swanson et al., 2011). However, societal demand for timber and/or pest reduction compels forest managers to “salvage” timber by logging before it deteriorates, a common practice even in locations otherwise exempt from conventional green-tree harvesting, such as national parks or wilderness areas (Figure 1) (Chylarecki & Selva, 2016; Thorn et al., 2014). Such salvage logging reduces the amount of dead wood, alters successional trajectories, affects biodiversity, and can influence restoration costs and subsequent fire hazards (Lindenmayer, Burton, & Franklin, 2008; Waldron, Ruel, & Gauthier, 2013). Consequently, conflicts often emerge between natural resource managers, policy-makers and conservationists on how to handle naturally disturbed forests (González & Veblen, 2007; Lindenmayer, Thorn, & Banks, 2017; Lindenmayer et al., 2004; Schmiegelow, Stepnisky, Stambaugh, & Koivula, 2006). This has resulted in intense public debates (Lindenmayer et al., 2017; Nikiforuk, 2011; Stokstad, 2006).

Different natural disturbance regimes leave distinct types of biological and/or structural legacies (Franklin et al., 2000). For instance, forests killed by wildfire or insect outbreaks are characterized by large numbers of snags, while windstorms create uprooted trees (Swanson et al., 2011). Salvage logging typically removes or alters these legacies. The responses of saproxylic and non-saproxylic species groups to salvage logging thus depend on their relation to (dead wood) legacies affected by salvage logging (Lindenmayer et al., 2008). Consequently, different taxonomic groups in different types of natural disturbances may respond differently to salvage logging (Zmihorski & Durska, 2011). Numerous studies have focused on the effects of salvage logging after natural disturbances on species richness and the community composition of various taxa such as vascular plants (Blair, McBurney, Blanchard, Banks, & Lindenmayer, 2016; Macdonald, 2007; Stuart,



a Cavity-nesting birds nested at a higher density in unlogged areas (Hutto & Gallo, 2006).

b SL shifted communities from forbs and shrubs towards hardwood after 12 years (Stuart et al., 1993).

c Pit and mound density decreases under SL; decay stages of snags diminished (Waldron et al., 2013).

d The interaction of budworm outbreak and SL changed landscape pattern (Radeloff et al., 2000).

e SL of Araucaria forest created debates among politicians and scientists (González & Veblen 2007).

f SL decreased total bird species richness but benefited open-habitat species (Rost et al., 2012).

g SL shifted functional composition of saproxylic beetle assemblages (Thorn et al., 2014).

h Machine and cable skidding increased the sediment erosion in early seral stages (Inbar, Wittenberg, & Tamir, 1997)

i SL enabled rapid development of nonforest vegetation (Van Nieuwstadt et al., 2001).

j Preserving naturally disturbed forest was essential for bird community restoration (Choi et al., 2014).

k SL decreased density and cover but not richness of residual plants (Morimoto, Morimoto, & Nakamura, 2011)

l SL decreased density of arboreal marsupials by hollow-tree removal (Lindenmayer & Ough 2007)

FIGURE 1 Salvage logging (SL) is commonly applied after wildfires, windstorms or insect outbreaks, and leads to changes in habitats and community compositions in various forest ecosystems around the world (as highlighted by the studies illustrated in panels (a–l). Study locations (coloured circles) represent study sites that contributed data to our meta-analysis. Photographs by authors. [Colour figure can be viewed at wileyonlinelibrary.com]

Grifantini, Fox, & Fox, 1993), carabids (Cobb, Langor, & Spence, 2007; Koivula & Spence, 2006; Phillips, Cobb, Spence, & Brigham, 2006), birds (Castro, Moreno-Rueda, & Hódar, 2010; Choi, Lee, Nam, Lee, & Lim, 2014; Nappi & Drapeau, 2009; Saab, Russell, & Dudley, 2009; Thorn, Werner, et al., 2016; Zmihorski, 2010), and saproxylic organisms (i.e. those depending on dead wood during some part of their life cycles; Cobb et al., 2011; Norvez, Hébert, Bélanger, Hebert, & Belanger, 2013).

Two main effects of salvage logging on biodiversity arise recurrently from the existing body of literature. First, salvage logging reduces the richness of taxonomic groups or abundance of particular species that depend on dead wood. For instance, salvage logging decreased nesting density of cavity-nesting-birds that usually breed in fire-killed trees (Hutto & Gallo, 2006). Similarly, post-storm logging decreased the total number of saproxylic beetle species and the number of threatened species (Thorn et al., 2014). Second, studies that investigate a set of different taxonomic groups have demonstrated that salvage logging can alter the community composition of both saproxylic and non-saproxylic organisms, while the effects on the overall number of species can be small (Thorn, Bässler, Bernhardt-Römermann, et al., 2016). For instance, post-storm salvage logging in Minnesota greatly diminished bird communities, while fewer differences in the tree cover were detected (Lain, Haney, Burris, & Burton, 2008). However, previous attempts to summarize knowledge on the effects of salvage logging on biodiversity have focused mainly on salvage logging of burned forests (Lindenmayer & Noss, 2006; Lindenmayer et al., 2008; McIver & Starr, 2000; Thorn, Bässler, Svoboda, & Müller, 2016), and a quantitative assessment of salvage logging impacts on biodiversity is still lacking, particularly across different taxonomic groups and in response to different types of disturbances (Figure 1).

Here, we reviewed the scientific literature and compiled existing data to quantify the effects of salvage logging after wildfire, windstorms and insect outbreaks on (1) species numbers via a meta-analysis of 238 individual comparisons of salvaged/unsalvaged areas; and (2) community composition, based on a subset of 134 original species abundance matrices. We also tested the hypothesis that the impacts of salvage logging are more pronounced for saproxylic species groups than for non-saproxylic groups regarding the number of species and community composition within different types of natural disturbances.

2 | MATERIALS AND METHODS

2.1 | Literature search

We followed guidelines for systematic literature reviews (Pullin & Stewart, 2006) to compile comparisons of species richness between salvaged and unsalvaged fire-, wind- or insect-affected forests. We screened the electronic databases Web of Science, Scopus and Google Scholar on 15 February 2016 by using the simplified search strings [salvage logging OR post$disturbance* OR salvaging] and [forest$ OR vegetation OR disturbance OR ecosystem]. From this body of literature (>2,000 articles), we retained only field-based studies after having screened the title and abstract. Modelling studies were excluded. We also added relevant papers from reference lists in published studies. We restricted studies to those providing comparisons between completely salvage logged plots and completely unsalvaged control plots according to the information given in the respective studies. This means that on salvage logged plots, more than 75% of the trees were affected by natural disturbance and then completely salvage logged without further treatment such as tree planting or legacy retention. Lower intensities of natural disturbances have been rarely targeted by scientific studies. Salvage logging operations thus resembled conventional clear-cutting. Unsalvaged control plots had to be affected by the same natural disturbance event but without any human intervention. Salvage logged plots had to be of similar size, surveyed with the same field methods during the same study period and with the same sampling effort as unsalvaged control plots.

To examine whether pseudo-replication (i.e. all plots nested within one area) might bias the results of our meta-analysis (Ramage et al., 2013), we carefully selected the studies according to their designs, and we used statistics that account for pseudo-replication (see below). The spatial arrangement of plots in all studies was checked based on method descriptions and/or original geographic coordinates. We contacted authors to provide data or to clarify their study designs where necessary (see Data sources section). Studies without true replicates (e.g. all salvaged plots nested and separated from unsalvaged control plots) were excluded from the analysis to ensure valid effect sizes (Halme et al., 2010). Studies using the same set of field plots and/or the same study area (e.g. Samcheok Forest, Korea) were identified and nested in all subsequent statistical analyses to control for pseudo-replication within study areas. We also excluded studies that sampled forests undergoing multiple types of disturbances. Salvage logging had to be conducted immediately (<12 months) after natural disturbance took place. Mean number of species and standard deviation values per sampling unit were extracted from published text and tables, or from figures using PLOT DIGITIZER 2.6.2. (www.plotdigitizer.sourceforge.net). Last, we compiled data on covariates by extracting information on the disturbance type and the time since disturbance, and the time since subsequent salvage logging. In addition, we compiled original species abundance matrices that underpinned the published papers, which allowed us to explore the effects of salvage logging on community composition.

2.2 | Meta-analysis

All analyses were conducted in R 3.3.1 (www.r-project.org). Prior to statistical analysis, species were assigned to one of the following taxonomic groups and to association with dead wood (i.e. saproxylic/non-saproxylic) based on the description in the articles. These where: amphibians, ants, bats, bees and wasps, birds, carabids, epigeal lichens, epigeal mosses, epigeal spiders, epixylic lichens, epixylic mosses, harvestmen, hover flies, land snails, nocturnal moths, non-saproxylic beetles (excluding carabids), reptiles, rodents, saproxylic beetles, scuttle flies, springtails, true bugs, vascular plants and wood-inhabiting fungi. For the analysis comparing responses of saproxylic and non-saproxylic species groups, we defined saproxylic beetles, wood-inhabiting fungi, and epixylic lichens and mosses as saproxylic and all other species groups as non-saproxylic.

For comparing numbers of species between salvaged and unsalvaged naturally disturbed plots described in the published literature, we used Hedges'*d*, which accounts for differences in sampling effort across studies and for small sample sizes (Hedges & Olkin, 1985). Positive values of Hedges'*d* indicate higher numbers of species in salvage logged plots, whereas negative values indicate a loss in numbers of species attributed to salvage logging (i.e. higher numbers of species in unsalvaged naturally disturbed plots). Mean absolute effect sizes of $d = 0.2$ indicate a small effect, $d = 0.5$ a moderate effect, and $d = 0.8$ a large effect (Koricheva, Gurevitch, & Mengersen, 2013).

We used multi-level linear mixed-effects models, provided by the R function "rma.mv" in the "metafor" package (Viechtbauer, 2010), to test the effect of taxonomic group as a categorical predictor and year since disturbance as a numerical covariate on Hedges'*d* as the response variable. Hedges'*d* values were weighted by the corresponding sampling variance within the statistical model. Furthermore, the study site was included as a random effect in the model (i.e. moderator term) to control for unmeasured site specificities and repeated measurements (pseudo-replication) within one study site. This means that multiple data points per study were possible if studies examined multiple taxonomic groups or if studies lasted for more than 1 year. We subtracted the intercept from the effect sizes (by including "−1" in the model formula) to evaluate if observed Hedges'*d* differed significantly from zero (for details and model formula see Table S1).

To evaluate the effects of salvage logging on saproxylic vs. non-saproxylic groups, we fitted a second model with Hedges'*d* as response variable. We again included the year after natural disturbance and subsequent logging as a numerical predictor variable and study site as well as taxonomic group as random factors. Furthermore, we added the interaction of dead wood dependence (i.e. saproxylic/non-saproxylic) with natural disturbance type as predictors to test whether the effect of salvage logging on the number of species in saproxylic and non-saproxylic groups differed within different types of natural disturbances. We implemented a simultaneous inference procedure to compare saproxylic and non-saproxylic species groups within each disturbance type (Hothorn, Bretz, & Westfall, 2008). This procedure allowed us to test if responses of saproxylic and non-saproxylic taxa vary among fire-, wind- and insect-disturbed forests (for details and model formula see Table S2). Last, we conducted funnel plots by means of the function “funnel” from the “metafor” package to assess publication bias (Koricheva et al., 2013; Figure S1).

2.3 | Analysis of community composition

Based on the reviewed literature, we compiled original species abundance matrices to quantify changes in community composition induced by salvage logging. Quantifying changes in community composition among large heterogeneous datasets is challenging and requires statistical methods able to deal with issues such as unbalanced sampling effort and which generate a standardized effect size that is comparable among different species groups and survey techniques. Thus, we used permutational multivariate analysis of variance using distance matrices (Legendre & Anderson, 1999), performed by means of the function “adonis” in the package “vegan” (Oksanen et al., 2016). This analysis provides a pseudo *F*-value, based on 999 permutations, that quantifies the deviance from the null-hypothesis, while simultaneously accounting for imbalanced study designs (McArdle & Anderson, 2001). Consequently, large values of *F* correspond to large changes in community composition induced by salvage logging. This *F*-value represents the standardized difference between communities in salvage logged and unsalvaged naturally disturbed plots within one species abundance matrix (e.g. differences in bird communities 6 years after wildfire and salvage logging in Oregon). We rigorously restricted this analysis to those abundance matrices that yielded valid pseudo *F*-values over the course of permutations; that is, those matrices which generated less than 99 real permutations were excluded. These restrictions resulted in a total number of 134 matrices, which supplied *F*-values for the analysis outlined below.

To test if salvage logging changed community composition in different taxonomic groups, we modelled pseudo *F*-values in linear mixed models provided by the function “lmer” in the “lme4” package assuming a Gaussian error distribution (Bolker et al., 2009). We included the taxonomic group as a categorical predictor and the year since disturbance as a numerical covariate. Furthermore, we included the study site as a random effect to control for possible differences among study sites and repeated measurements within one study site. We omitted the intercept from the model formula to determine if *F*-values differed significantly from zero. Thus, significant changes in community composition of a taxonomic group due to salvage logging were indicated by *F*-values significantly larger than zero (for details and model formula see Table S3).

As for the analysis of Hedges’*d*, a second model was fitted to test whether the effects of salvage logging on community composition differed between saproxylic and non-saproxylic species groups in different types of disturbances. Therefore, we included the year after disturbance and the interaction of saproxylic/non-saproxylic with disturbance type as predictors. Taxonomic group and study site were included as random factors in this model. We implemented a simultaneous inference procedure to compare saproxylic and non-saproxylic species groups within each disturbance type (for details and model formula see Table S4).

3 | RESULTS

Our meta-analysis showed that the effects of salvage logging have been studied primarily for birds, vascular plants and carabids, particularly in burned forests. Studies were conducted primarily in North America and Europe, but lacking in tropical regions (Figure 1). Furthermore, there was a clear lack of studies investigating saproxylic taxa. Of the 238 compiled data points, 170 covered a period of 5 years or less after disturbance, with studies addressing the long-term effects of salvage logging being rare (Figure 2). Only one study (Hutto & Gallo, 2006) was available that provided data on the effects of salvage logging for more than 20 years after disturbances (Figure 2).

Half of the individual comparisons produced values of Hedges’*d* lower than zero, indicating higher numbers of species in non-salvage logged areas than salvage logged areas (Figure 3). We found significantly lower species numbers of epigeal and epixylic mosses, birds, wood-inhabiting fungi, saproxylic beetles, springtails and epixylic as well as epigeal lichens in salvage logged areas compared to non-salvage logged areas (Figure 3a). In contrast, the numbers of species of land snails, epigeal spiders and carabids were higher in salvage logged areas than in unsalvaged areas (Figure 3a). Thirteen of the 24 taxonomic groups, including vascular plants, exhibited no significant response in numbers of species to salvage logging (Figure 3a). The numbers of species of saproxylic taxa significantly decreased compared to non-saproxylic taxa in storm-affected and burned forests (Figure 4a). The negative effect of salvage logging on number of species increased with time elapsed since disturbance and subsequent salvage logging, although long-term data on salvage logging are scarce.

Salvage logging was associated with significant changes in community composition in 7 of 17 taxonomic groups (Figure 3b). These seven groups were epigeal spiders, carabids, vascular plants, birds, wood-inhabiting fungi, saproxylic beetles and epixylic lichens (Figure 3b). Time elapsed since disturbance had no effect on the strength of logging-induced changes to community composition (Table S3). Furthermore, logging-induced changes in community composition were stronger for saproxylic taxa than for non-saproxylic taxa in storm-disturbed forests. However, data availability was scarce in insect-affected forest and lacking in burned forests (Figure 4b).

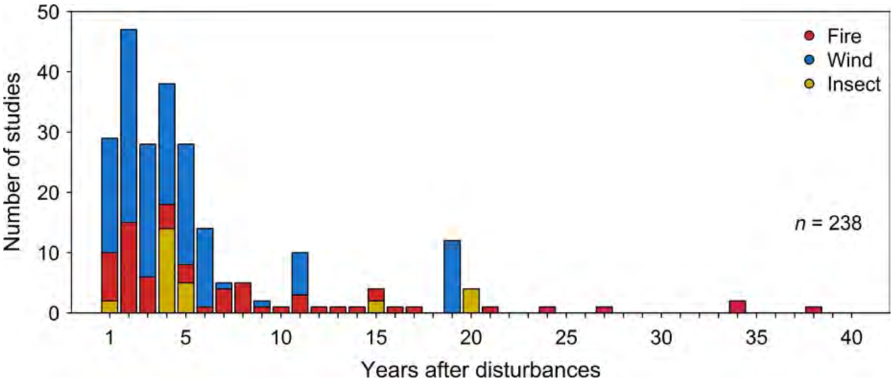


FIGURE 2 Distribution of studies investigating the effects of salvage logging on biodiversity after wildfire, windstorms and insect outbreaks according to the years after disturbance. [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Our study revealed that salvage logging can result in significant changes in species numbers and/or in altered community composition. Negative effects were particularly strong for taxa that depend on dead wood. In contrast, the numbers of species of taxa that are commonly characterized by species-rich communities in open habitats, such as carabids and epigeal spiders, responded positively to salvage logging. Despite positive effects of salvage logging on taxa associated with open habitats, strong negative effects on saproxylic groups call for substantial changes in how disturbed forests are routinely managed.

Naturally disturbed forests are characterized by large volumes of dead wood with high structural diversity (Swanson et al., 2011). In contrast, salvage logging typically reduces the amount and heterogeneity of dead wood by removing tree trunks (Keyser, Smith, & Shepperd, 2009; Priewasser, Brang, Bachofen, Bugmann, & Wohlgemuth, 2013). Not surprisingly, salvage logging reduced the numbers of species of saproxylic groups (Figures 3 and 4). However, not only a decreasing dead wood amount but likewise a logging-induced shift in dead wood quality may have additional impacts on saproxylic taxa. Salvage logging not only reduces the amount of large tree trunks but also alters characteristic conditions, such as decay stages or diameter distributions, of the remaining dead wood (Waldron et al., 2013). For instance, branches cut during post-storm logging remain on the ground but are overgrown by ground vegetation. The resulting shift in microclimatic conditions then modifies resource quality, leading to a loss of saproxylic beetles that depend on sun-exposed, dry branches (Thorn et al., 2014).

It is important to note that losses of saproxylic species can be present also within taxonomic groups that displayed no response in their overall species numbers (Figure 3a). For instance, birds (the most studied vertebrate group) were slightly negatively affected by salvage logging (Figure 3a), despite few species being directly dependent on dead wood. Nevertheless, several forest-dwelling bird species depend on snags, cavities or natural regeneration in post-disturbance forest stands. The removal of such legacies by salvage logging can cause a loss of associated bird species and consequently an overall lower number of bird species in logged areas (Hutto & Gallo, 2006; Werner, Müller, Heurich, & Thorn, 2015). Although the overall number of bird species decreased less strongly than, for instance, the number of saproxylic beetle species (Figure 3a), bird species that depend on post-disturbance habitat characteristics are often of high conservation interest. For instance, salvage logging after high severity wildfires can lead to lower site occupancies of Northern Spotted Owls (*Strix occidentalis caurina*) on logged than on unlogged sites in Oregon (Clark, Anthony, & Andrews, 2013).

Our study revealed that salvage logging caused significant changes in community composition for seven species groups (Figure 3b), with saproxylic species groups being affected most strongly (Figure 4b). Such alterations in community composition might reflect the establishment of open-habitat species and/or a simultaneous loss of forest specialists. For instance, salvage logging can increase the abundance of open-habitat carabid beetles (Koivula & Spence, 2006) or promote the establishment of non-forest vegetation (Stuart et al., 1993; Van Nieuwstadt, Sheil, & Kartawinata, 2001). Hence, species groups that are commonly characterized by species-rich communities in open habitats, such as carabids or epigeal spiders, can display an overall increase in numbers of species in response to salvage logging (Figure 3a). Likewise, salvage logging can cause an increase in herb- and grass-feeding moth species but a decrease in saproxylic and detritus-feeding moth species (Thorn et al., 2015). Such contrasting responses within and between species groups can mask the overall impact of salvage logging on biodiversity in coarse-scale analyses (i.e. Thom & Seidl, 2016). Numerous species of high conservation interest, such as the Red-cockaded Woodpecker (*Leuconotopicus borealis*), depend on dead wood in burned forests (Conner, Rudolph, & Walters, 2001). The results of our study therefore indicate that the biodiversity of saproxylic taxa could be enhanced by a modified management of naturally disturbed forests. In contrast, populations of species associated with open habitats, such as the Sharp-tailed Grouse (*Tympanuchus phasianellus*) in North America, may persist or even increase in the larger remaining area subject to unmodified management, that is, salvage logging (Radeloff, Mladenoff, & Boyce, 2000).

The two major incentives for salvage logging are to reduce economic losses caused by a natural disturbance and to omit mass reproduction and spread of insect pests that develop in trees killed or weakened by a preceding natural disturbance. For instance, salvage logging of storm-felled Norway spruce (*Picea abies*) decreased new infestations of nearby trees by the European spruce bark beetle (*Ips*

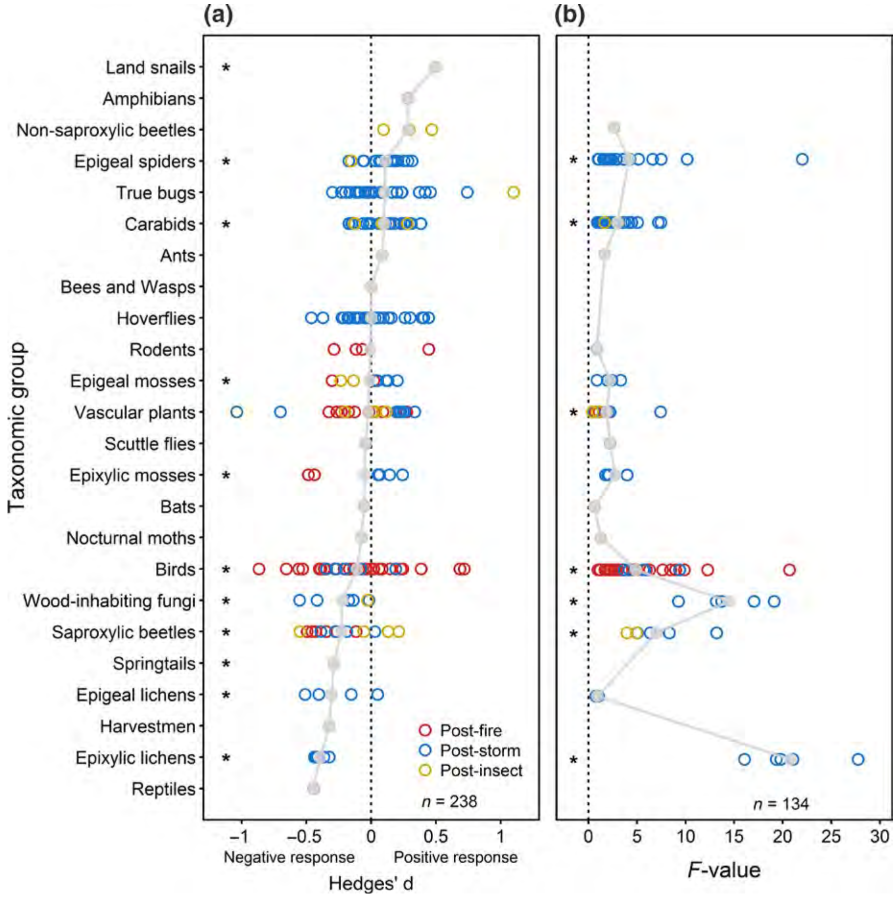


FIGURE 3 (a) Estimated response of Hedges' *d* based on 238 individual comparisons of species numbers in salvage logged and unsalvaged forests affected by natural disturbances. Higher species numbers in salvage logged areas correspond to positive Hedges' *d*, whereas negative values indicate lower species numbers in salvage logged areas. (b) Pseudo *F*-values of permutational multivariate analysis of variance based on 134 individual species abundance matrices. Larger pseudo *F*-values correspond to larger changes in community composition induced by salvage logging. Asterisks indicate significant responses (see Tables S1 and S2 for statistical details). For illustrative purposes, grey dots (and the grey line joining them for emphasis) represent the mean effect size in each taxonomic group. [Colour figure can be viewed at wileyonlinelibrary.com]

typographus) at a landscape scale (Stadelmann, Bugmann, Meier, Wermelinger, & Bigler, 2013). Salvage logging is therefore the predominant response to natural disturbances in wood production forests, but pest control is regularly used to justify salvage logging in protected areas. For instance, the Białowieża Forest National Park on the border between Poland and Belarus, which is the last primeval lowland forest in Europe, is currently obliged to salvage logging of areas affected by *I. typographus* on attempt to avoid further infestations (Chylarecki & Selva, 2016). Such an approach to disturbed forests neglects that regional factors, such as summer drought, can promote outbreaks of *I. typographus* more strongly than local stand variables (Seidl et al., 2015). Furthermore, salvage logged timber is usually of substantially lower economic value than normally harvested timber due to a rapid colonization by wood-inhabiting fungi and to the fact that disturbances affect forests of any age, so that generalized salvage logging operations necessarily include younger stands that otherwise would not be harvested (Leverkus, Puerta-Pinero, Guzmán-Álvarez, Navarro, & Castro, 2012). Our results demonstrate that salvage logging has strong and negative effects on many taxonomic groups, particularly those associated with dead wood, and that it is thus not consistent with biodiversity conservation goals. Along with questionable economic outputs and pest reducing effects, we argue that salvage logging should be excluded from protected areas such as national parks.

The incidence of stand-replacing natural disturbances remains spatially and temporally unpredictable (Berry et al., 2015), creating inherent uncertainty about appropriate management of naturally disturbed forests. Hence, management plans need to be jointly developed with (and confirmed by) stakeholders, scientists and natural resource managers before the next disturbance occurs (Lindenmayer, Likens, & Franklin, 2010). Such management plans could, for instance, encompass an a priori identification of salvage logging exclusion zones based on ecological data (e.g. Nappi et al., 2011). Forest managers also may target the preservation of structural key attributes in naturally disturbed forests, including snags or tipped uproot plates of windthrown trees (Hutto, 2006). Retention of trees during green-tree harvests has become an increasingly common tool around the globe to help conserve forest biodiversity (Fedrowitz et al., 2014; Gustafsson et al., 2012; Mori & Kitagawa, 2014). To obtain some economic return while retaining dead wood-dependent taxa, we recommend a simple expansion of the green-tree retention approach to include naturally disturbed forests. Retention approaches in naturally disturbed forests could be expected to be less costly than in green-tree harvest due to the lower opportunity cost of not harvesting disturbance-killed trees.

Approximately 70% of the studies we compiled spanned less than 5 years; studies addressing the long-term effects of salvage logging are rare (Figure 2). However, dead wood, and particularly snags, are long-lasting key biological legacies, and their loss can have long-lasting effects on biodiversity (Hutto, 2006). Hence, future research should target the long-term effects of salvage logging after natural disturbances. There are also taxonomic biases in existing studies investigating

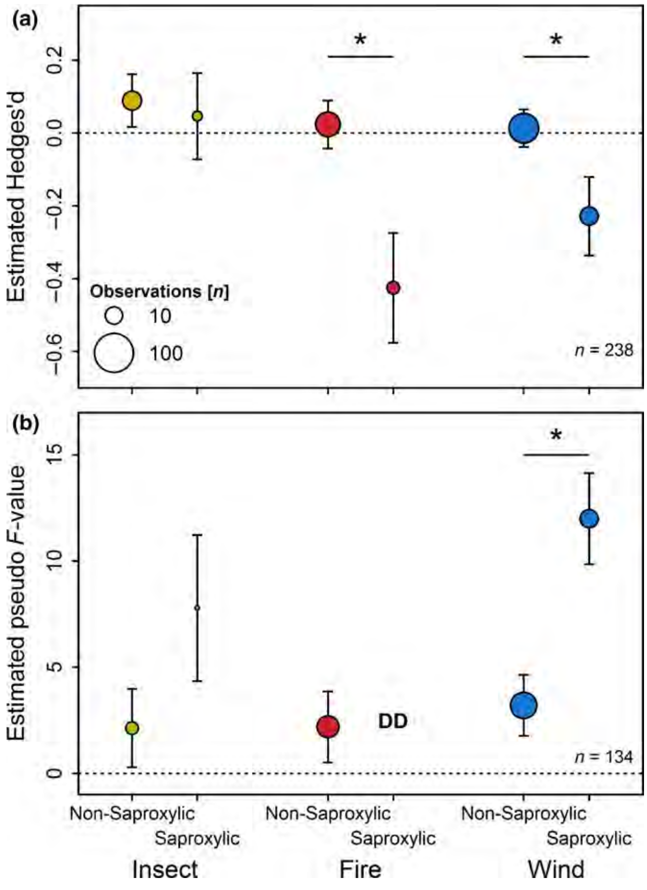


FIGURE 4 (a) Estimated response and corresponding standard error of saproxylic and non-saproxylic taxa to salvage logging based on 238 individual comparisons (based on Hedges' *d*) of numbers of species in burned, storm- and insect-affected forests. Negative estimates correspond to a decrease in numbers of species by salvage logging (Table S3). (b) Estimated response and corresponding standard error of community composition of saproxylic and non-saproxylic taxa based on pseudo *F*-values of permutational multivariate analysis of variance obtained from 134 individual species abundance matrices. Increasing *F*-values correspond to larger changes in community composition induced by salvage logging (Table S4). Note, insufficient data (DD) were available for saproxylic taxa in burned forests. Asterisks above dots indicate significant differences in the responses between saproxylic and non-saproxylic taxa within each disturbance type. Number of underlying data points is indicated by the size of the circles, with 10 and 100 size shown for reference. [Colour figure can be viewed at wileyonlinelibrary.com]

the effects of salvage logging after natural disturbances. In particular, saproxylic groups such as wood-inhabiting fungi have been underrepresented in empirical studies despite their high diversity and importance for ecosystem functioning. Future research should therefore target particularly saproxylic species groups. In contrast, other groups have been relatively well studied in one disturbance type (e.g. birds in burned forests), but less in others, and studies were conducted primarily in North America, Europe and Asia, but lacking in tropical regions (Figure 1). However, different types of natural disturbances in different parts of the world can act at very different spatial scales and may require different retention approaches (Kulakowski et al., 2016). Furthermore, coniferous forests of the Northern Hemisphere—in contrast to tropical forests—are naturally prone to large-scale natural disturbances (Lindenmayer et al., 2008), whereas disturbances in tropical forests mostly have anthropogenic causes associated with long-term land-use change (e.g. fire to open space for livestock grazing and agriculture; Peres, Barlow, & Laurance, 2006). Nevertheless, natural disturbances such as windstorms affect tropical forests as well as temperate forests, and salvage logging effects on tropical forests should be targeted in future research (e.g. Lawton & Putz, 1988).

In conclusion, these data from a wide range of studies demonstrate that salvage logging has a range of effects on species numbers and community composition of various taxonomic groups, with important negative consequences for several groups, especially saproxylic ones. While current policies for enhancing biodiversity and ecosystem services, such as green-tree retention (e.g., Gustafsson et al., 2012), focus mainly on forests subjected to traditional logging operations, such policies are largely absent from naturally disturbed forests. We therefore call for an expansion of the green-tree retention approach to include naturally disturbed forests by leaving substantial amounts of dead wood on site to reduce the impact of salvage logging on biodiversity.

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AUTHORS' CONTRIBUTIONS

S.T. and J.M. initiated the study. S.T. analysed and interpreted the data and wrote the first draft of the paper. The authors named from S.T. to J.M. are listed alphabetically, as they contributed equally in gathering field data, providing corrections to subsequent manuscript drafts and discussing ideas.

DATA ACCESSIBILITY

All data are from previously published articles, see "Data sources". Data from these articles can be made available upon reasonable request to original data owners. A list of data sources used in the study is provided in the Data Sources section.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Severe fire weather and intensive forest management increase fire severity in a multi-ownership landscape

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Abstract. Many studies have examined how fuels, topography, climate, and fire weather influence fire severity. Less is known about how different forest management practices influence fire severity in multi-owner landscapes, despite costly and controversial suppression of wildfires that do not acknowledge ownership boundaries. In 2013, the Douglas Complex burned over 19,000 ha of Oregon & California Railroad (O&C) lands in Southwestern Oregon, USA. O&C lands are composed of a checkerboard of private industrial and federal forestland (Bureau of Land Management, BLM) with contrasting management objectives, providing a unique experimental landscape to understand how different management practices influence wildfire severity. Leveraging Landsat based estimates of fire severity (Relative differenced Normalized Burn Ratio, RdNBR) and geospatial data on fire progression, weather, topography, pre-fire forest conditions, and land ownership, we asked (1) what is the relative importance of different variables driving fire severity, and (2) is intensive plantation forestry associated with higher fire severity? Using Random Forest ensemble machine learning, we found daily fire weather was the most important predictor of fire severity, followed by stand age and ownership, followed by topographic features. Estimates of pre-fire forest biomass were not an important predictor of fire severity. Adjusting for all other predictor variables in a general least squares model incorporating spatial autocorrelation, mean predicted RdNBR was higher on private industrial forests (RdNBR 521.85 ± 18.67 [mean ± SE]) vs. BLM forests (398.87 ± 18.23) with a much greater proportion of older forests. Our findings suggest intensive plantation forestry characterized by young forests and spatially homogenized fuels, rather than pre-fire biomass, were significant drivers of wildfire severity. This has implications for perceptions of wildfire risk, shared fire management responsibilities, and developing fire resilience for multiple objectives in multi-owner landscapes.

Key words: fire severity; forest management; Landsat; multi-owner landscape; Oregon; plantation forestry; RdNBR.

Introduction

The wildfire environment has become increasingly complicated, due to the unanticipated consequences of historical forest management and fire exclusion (Weaver 1943, Hessburg et al. 2005, Fulé et al. 2009, Naficy et al. 2010, Merschel et al. 2014), an increasingly populated wildland urban interface (Haas et al. 2013), and a rapidly changing climate (Westerling and Bryant 2008, Littell et al. 2009, Jolly et al. 2015). These factors are resulting in more intense fire behavior and increasingly negative ecological and social consequences (Williams 2013, Stephens et al. 2014). Fuels reduction via mechanical thinning and prescribed burning have been the dominant land management response for mitigating these conditions (Agee and Skinner 2005, Stephens et al. 2012), although there is an increasing recognition of the need to manage wildfires more holistically to meet social and ecological objectives. (North et al. 2015a, b). However, overcoming these challenges is inhibited by numerous disagreements in the scientific literature regarding historical fire regimes and appropriate policies and management of contemporary fire-prone forests (Hurteau et al. 2008, Hanson et al. 2009, Spies et al. 2010, Campbell et al. 2012, Odion et al. 2014, Collins et al. 2015, Stevens et al. 2016). These factors and others have resulted in a nearly intractable socioecological problem (Fischer et al. 2016); one that is compounded by the fact that many fire-prone landscapes consist of multiple owners and administrative jurisdictions with varying and often conflicting land management objectives.

Developing and prioritizing landscape fire management activities (i.e., thinning, prescribed fire, wildland fire use, and fire suppression) across jurisdictional and ownership boundaries requires landscape-scale assessments of the factors driving fire severity (i.e., the fire behavior triangle of fuels, topography, and weather). Researchers have focused on the influence of bottom-up drivers such as topography (Dillon et al. 2011, Prichard and Kennedy 2014, Birch et al. 2015), and fuels via fuel reduction effects (Agee and Skinner 2005, Raymond and Peterson 2005, Safford et al. 2009, Prichard and Kennedy 2014, Ziegler et al. 2017), as well as the top-down influence of weather on fire severity (Birch et al. 2015, Estes et al. 2017). They have also focused more broadly on how fire severity varies with vegetation and forest type (Birch et al. 2015, Steel et al. 2015, Reilly et al. 2017) and climate (Miller et al. 2012, Abatzoglou et al. 2017). While there is substantial value in further describing how components of the fire behavior triangle influence fire severity, we believe there is a need to account for these known influences on fire behavior and effects to understand

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how different management regimes interact with these controlling factors, so appropriate landscape management strategies can be developed to support social-ecological resilience in fire-prone landscapes (Spies et al. 2014, Schoennagel et al. 2017).

Understanding the relationships between forest management regimes and fire severity is especially important in multi-owner landscapes, where wildfire governance systems concerned about short-term property loss and public safety can reinforce perceptions of wildfire risk and hazard, resulting in individual property owners being less likely to make management decisions that reduce long-term risk exposure (McCaffrey 2004, Fischer et al. 2016). This is particularly important in landscapes that include intensive plantation forestry, a common and rapidly expanding component of forest landscapes at regional, national, and global scales (Cohen et al. 1995, Landram 1996, Del Lungo et al. 2001, Rudel 2009, FAO 2010, Nahuelhual et al. 2012). Researchers have hypothesized that intensive forest management reduces fire behavior and effects (Hirsch et al. 2001, Rodríguez y Silva et al. 2014). However empirical results have been mixed, with evidence that intensive forest management can either reduce (Lyons-Tinsley and Peterson 2012, Prichard and Kennedy 2014) or increase fire severity (Odion et al. 2004, Thompson et al. 2007), and that reduced levels of forest legal protection (a proxy for more active management) have been associated with increased fire severity in the western U.S. (Bradley et al. 2016). These conflicting results further complicate the development of fire governance and management strategies for increasing social-ecological resilience in a rapidly changing fire environment.

The quality, spatial scale, and spatial correlation of explanatory data (i.e., weather, topography, and fuels) are major limitations to empirically understanding how forest management activities influence fire severity across landscapes. Regional studies of fire severity often rely on spatially coarse climatic data (Dillon et al. 2011, Miller et al. 2012, Cansler and McKenzie 2014, Kane et al. 2015, Harvey et al. 2016, Meigs et al. 2016, Reilly et al. 2017), rather than local fire weather that can be a significant driver of fire area and severity (Flannigan et al. 1988, Bradstock et al. 2010, Estes et al. 2017). This is in part because finer-scale fire weather variables are often incomplete across the large spatial and temporal domains of interest. Additionally, regional studies often occur in areas with large elevation relief resulting in strong climatic gradients, while more local studies often have less elevation relief and potentially weaker climatic gradients. Perhaps more importantly, the geographic distribution of different ownership types and management regimes can confound quantification of the drivers of fire severity. For example, high elevation forests in the Pacific Northwest region of the United States are largely unmanaged as National Parks and congressionally designated wilderness areas, compared to intensively managed forests at lower elevations, resulting in differences in topography, weather, climate, forest composition, productivity, and historical fire regimes between ownerships and management regimes. While landscape studies of fire severity and management activities have used a variety of statistical techniques to account for spatial correlation of both response and predictor variables (Thompson et al. 2007, Prichard and Kennedy 2014, Meigs et al. 2016), these techniques may not overcome fundamental differences in response and predictor variables between management and/or ownership types.

In this study, we examined the drivers of fire severity within one large (~20,000 ha) wildfire complex that burned within the Klamath Mountains, an ecoregion with a mild Mediterranean climate of hot dry summers and wet winters in southwestern Oregon, USA. The fire burned within a checkerboard landscape of federal and private industrial forestry ownership. This spatial pattern of contrasting ownership and management regimes provided a unique landscape experiment where we quantified the effects of management regimes after accounting for variation in well-known drivers of fire behavior and effects. Leveraging geospatial data on fire severity, fire progression, fire weather, topography, prefire forest conditions, and past management activities, we asked two questions: (1) What is the relative importance of different variables driving fire severity? And (2) is intensive plantation forestry associated with higher fire severity?

METHODS

Study site

In the summer of 2013, the Douglas Complex burned 19,760 ha of forestland in southwestern Oregon, USA (Fig. 1). Starting from multiple lightning ignitions, individual small fires coalesced into two large fires (Dads Creek and Rabbit Mountain) managed as the Douglas Complex.

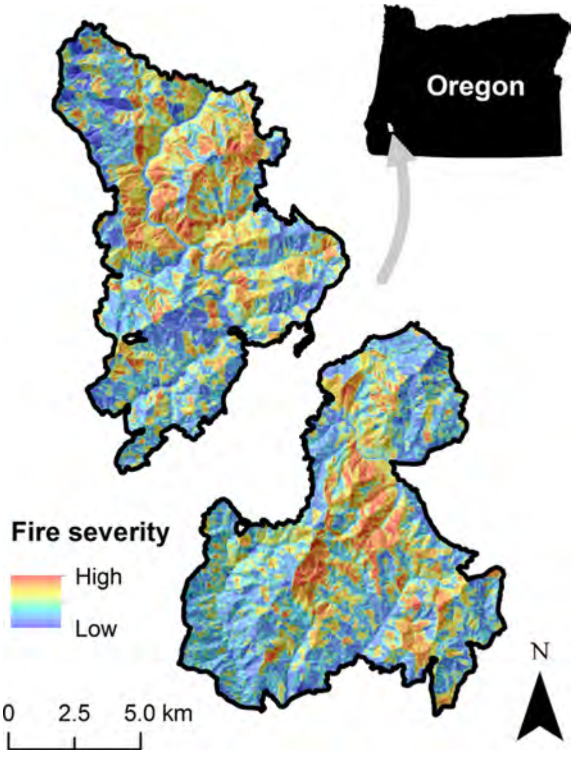

FIG. 1. Location of and fire severity within the Douglas Complex in Oregon, USA. Fire severity quantified using the Relative differenced Normalized Burn Ratio (RdNBR).

This fire burned within the Oregon and California Railroad Lands (hereafter O&C Lands). O&C Lands resulted from 19th century land grants that ceded every other square mile (259 ha) of federally held land to railroad companies along planned routes in Oregon and California to incentivize railroad development and homesteading settlement. The Oregon and California Railroad Company received a total of 1.5 million ha, but failing to meet contractual obligations, 1.1 million ha were transferred back to federal ownership under the Chamberlain-Ferris Revestment Act of 1916. The USDI Bureau of Land Management (BLM) is currently required to manage these lands for sustainable timber production, watershed protection, recreation, and wildlife habitat. Private industrial forestlands dominate the remaining O&C landscape, and are managed intensively as native tree plantations (primarily Douglas-fir, *Pseudotsuga menziesii* var. *menziesii*) for timber production typically on 30–50 yr harvest rotations. The Douglas Complex fires burned 10,201.64 ha of forests managed by the BLM, 9,429.66 ha of private industrial forests, and 129.33 ha managed by the Oregon Department of Forestry (ODF).

The Douglas Complex burned at elevations ranging from 213 to 1,188 m in mountainous terrain of the Klamath Mountains Ecoregion. Climate in the ecoregion is characterized by hot dry summers and wet winters, with greater winter precipitation at higher elevations and western portions of the ecoregion. Vegetation types within the region include oak woodlands and mixed hardwood/evergreen forests at low to mid elevations, transitioning into mixed-conifer forests at higher elevations (Franklin and Dyrness 1988). Forests within the Douglas Complex are dominated by Douglas-fir, ponderosa pine (*Pinus ponderosa*), and white fir (*Abies concolor*). Other conifer tree species present include incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), Jeffery pine (*Pinus jefferyi*), and knobcone pine (*Pinus attenuata*). Hardwood species include Oregon white oak (*Quercus garryana*), big-leaf maple (*Acer macrophyllum*), Pacific dogwood (*Cornus nuttallii*), Pacific madrone (*Arbutus menziesii*), canyon live oak (*Quercus chrysolepis*), California black oak (*Quercus kelloggii*), golden chinkapin (*Chrysolepis chrysophylla*), and tanoak (*Lithocarpus densiflourus*). Douglas-fir is the primary commercial timber species managed on private and public lands, while fire exclusion and historical management practices have expanded the density and dominance of Douglas-fir across much of the ecoregion (Franklin and Johnson 2012, Sensenig et al. 2013).

Data sources

We analyzed fire severity in relation to eight predictor variables representing topography, weather, forest ownership, forest age, and pre-fire forest biomass (Fig. 2). We quantified fire severity using the Relative differenced Normalized Burn Ratio (RdNBR), a satellite-imagery-based metric of pre- to post-fire change. Cloud-free pre-fire (3 July 2013) and post-fire (7 July 2014) images came from the Landsat 8 Operational Land Imager. Normalized Burn Ratio (NBR), which combines near-infrared and mid-infrared bands of Landsat imagery, was calculated for pre- and post-fire images. Differenced Normalized Burn Ratio (dNBR) was calculated by subtracting $\mathrm{NBR}_{\text{post-fire}}$ from $\mathrm{NBR}_{\text{pre-fire}}$ values, and RdNBR was then calculated following Miller et al. (2009), where:

$$\mathrm{RdNBR} = \frac{\mathrm{dNBR}}{\sqrt{\text{Absolute Value}\,(\mathrm{NBR}_{\text{pre-fire}}/1,000)}}. \quad (1)$$

We chose RdNBR over dNBR as our fire severity metric because RdNBR removes, at least in part, the biasing effect of pre-fire conditions, improving assessment of burn severity across heterogeneous vegetation and variable pre-fire disturbances (Miller and Thode 2007). We used the continuous RdNBR values as our response variable for fire severity at a 30-m resolution.

Elevation and other topographic variables were derived from the National Elevation Dataset 30 m digital elevation model (Gesch et al. 2002). We generated 30-m rasters of elevation (m), slope (%), topographic position index (TPI), and heat load ($\mathrm{MJ{\cdot}cm^{-2}{\cdot}yr^{-1}}$). TPI was calculated as the difference between elevation in a given cell and mean elevation of cells within an annulus around that cell, calculated at fine and coarse scales (TPI fine and TPI coarse) with 150–300 m and 1,850–2,000 m annuli, respectively. We also originally considered TPI at a moderate spatial scale (850–1,000 m annuli), but rejected it as an predictor variable due to its high correlation to TPI fine ($r = 0.64$) and TPI course ($r = 0.84$). TPI course had strong linear correlations with elevation ($r = 0.83$) and TPI fine ($r = 0.46$), so it was also removed to avoid multi-collinearity in statistical analyses. Heat load was calculated by least-squares multiple regression using trigonometric functions of slope, aspect, and latitude following McCune and Keon (2002).

Rasters of daily fire weather conditions were generated by extrapolating weather station data to a daily fire progression map. We obtained hourly weather data for the duration of active fire spread (7 July–20 August 2013) from the Calvert Peak Remote Automatic Weather Station (NWS ID 352919; 42°46′40″ N 123°43′46″ W, 1,165 m), approximately 30 km west-southwest of the Douglas Complex. We then subset each 24-h period of weather data to the daily burn period (10:00 to 18:00) when fire behavior is typically most active. We then calculated the daily burn period minimum wind speed (km/h), maximum temperature (°C), and minimum relative humidity (%). For each daily burn period we also calculated the mean energy release component (ERC), spread component (SC), and burning index (BI) using FireFamilyPlus Version 4.1 (Bradshaw and McCormick 2000). ERC is an index of fuel dryness related to the maximum energy release at the flaming front of a fire, as measured from temperature, relative humidity, and moisture of 1–1,000 h dead fuels. SC is a rating of the forward rate of spread of a head fire, and is calculated from wind speed, slope, and moisture of live fine and woody fuels (Bradshaw et al. 1983). BI is proportional to the flame length at the head of a fire (Bradshaw et al. 1983), calculated using ERC and SC, thus incorporating wind speed and providing more information than ERC and SC individually. ERC, SC, and BI vary by broadly categorized fuel types. We calculated ERC, SC, and BI using the National Fire Danger Rating System Fuel Model G, which represents short-needled

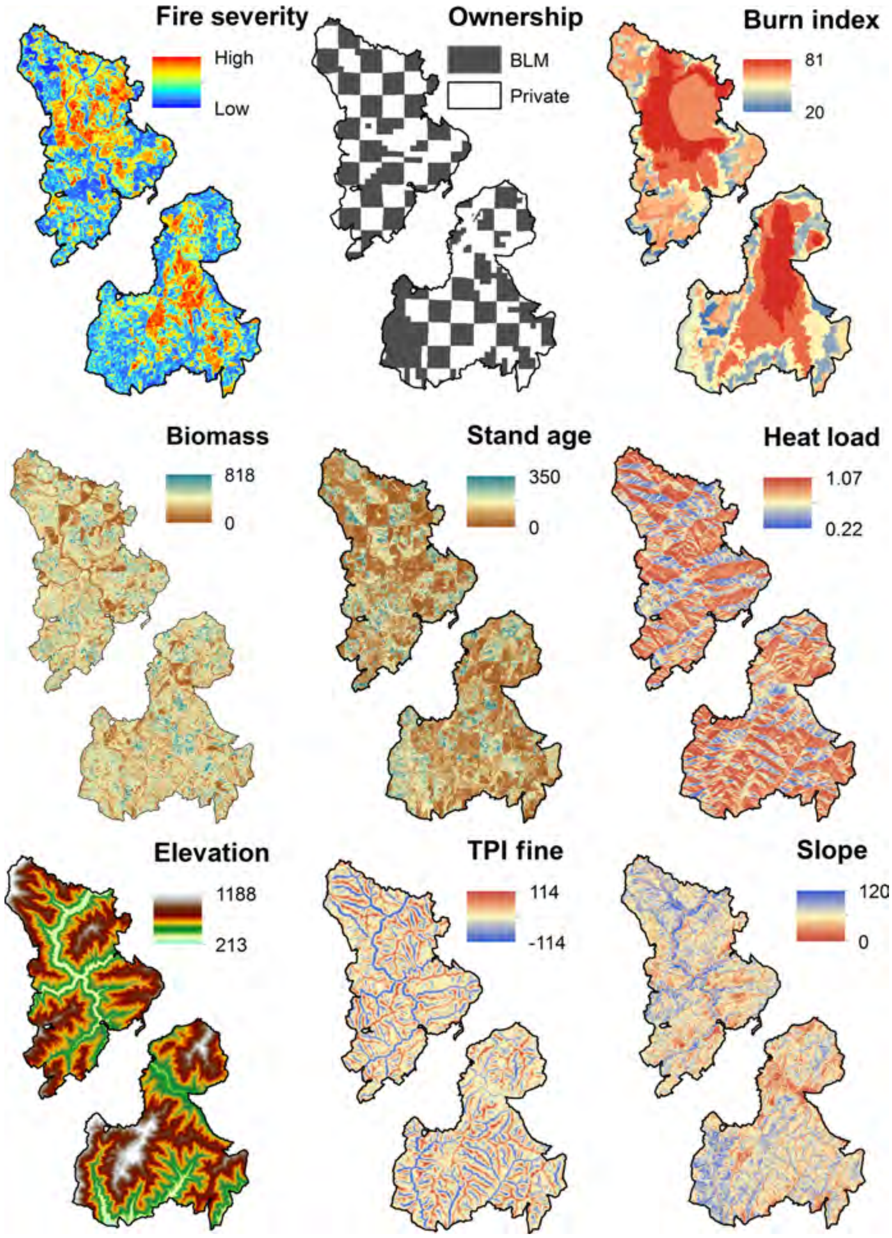

FIG. 2. Maps of response and predictor variables for Douglas Complex. TPI, topographic position index.

conifer stands with heavy dead fuel loads. Daily fire weather variables were then spatially extrapolated to the daily area burned based on daily fire progression geospatial data captured during the fire (GeoMAC 2013).

Forest ownership was derived from geospatial data representing fee land title and ownership in Oregon (Oregon Spatial Data Library 2015). We grouped ODF and BLM lands as a single ownership type, because ODF lands were a small component of the area burned and have management objectives closer to federal vs. private industrial forests (Spies et al. 2007). Pre-fire forest conditions were represented with 30-m rasters of live biomass (Mg/ha) and stand age, derived from a regional 2012 map of forest composition and structural attributes developed for the Northwest Forest Plan Monitoring Program (Ohmann et al. 2012, Davis et al. 2015). These maps were developed using the gradient nearest neighbor method (GNN), relating multivariate response variables of forest composition and structure attributes from approximately 17,000 federal forest inventory plots to gridded predictor variables (satellite imagery, topography, climate, etc.) using canonical correspondence analysis and nearest neighbor imputation (Ohmann and Gregory 2002). Biomass values are directly from the GNN maps, while we quantified forest age as a two-step process. First, we calculated pre-fire forest age in 2013 based on years since each pixel was disturbed in the Landsat time series (1985–2014) from a regional disturbance map generated for the Northwest Forest Plan Monitoring Program using the LandTrendr segmentation algorithm (Kennedy et al. 2010, Ohmann et al. 2012, Davis et al. 2015). Second, for pixels where no disturbance had occurred within the Landsat time series, we amended forest age derived from the Landsat time series using dominant and codominant tree age from the GNN maps.

Statistical analyses

All statistical analyses were conducted in the R statistical environment version 3.3.3 (R Development Core Team 2017). We sampled the burned landscape using a spatially constrained stratified random design, from which response and predictor variables were extracted for analysis. Sample points had to be at least 200 m apart to minimize short distance spatial autocorrelation of response and predictor variables. Our choice of minimum inter-plot distance to reduce spatial autocorrelation was confounded by the dominance of long distance spatial autocorrelation driven by large ownership patches, which would have greatly reduced sample size and potentially eliminated finer scale variability in the sample. For these reasons we based our 200 m minimum inter-plot distance in part on prior research (Kane et al. 2015), that found residual spatial autocorrelation in Random Forest models of fire severity in the Rim Fire of 2013 in the California Sierra Nevada was greatly diminished when inter-plot distances were at least 180 m apart. Additionally, point locations had to be at least 100 m away from ownership boundaries to minimize inter-ownership edge effects. Within these spatial constraints, sample points were located in a stratified random design, with the number of points proportional to area of ownership within the fire perimeter, resulting in 571 and 519 points located in BLM and private industrial forests, respectively. Mean response and predictor variables were extracted within a 90 × 90 m plot (e.g., 3 × 3 pixels) centered on each sample point location to minimize the effects of potential georeferencing errors across data layers and maintain a plot size comparable to the original inventory plots used as source data in GNN maps as recommended by Bell et al. (2015).

We observed high correlation between fire weather variables (mean absolute $r = 0.59$), likely due to their temporal autocorrelation during the fire event, which could result in multi-collinearity in statistical analyses. Therefore, we evaluated the relationships between each fire weather variable and daily mean fire severity, selecting a single fire weather variable as a predictor variable in subsequent analyses. We based our variable selection on visual relationships to daily RdNBR, variance explained in regressions of RdNBR and fire weather variables, and Akaike information criterion (AIC) scores of regressions of RdNBR and fire weather variables following Burnham and Anderson (2002).

The study's strength rests in part on the implicit assumption that the checkerboard spatial allocation of ownership types is a landscape scale experiment, where predictor variables directly modified by management activities (e.g., pre-fire biomass and forest age) are different between ownership types, but fire weather and topographic variables are not. We assessed this assumption by visualizing data distributions between ownerships using boxplots and violin plots, and testing if variables were different between ownership types using Mann–Whitney–Wilcoxon Tests.

To assess the relative importance and relationships between predictor variables and RdNBR, we used Random Forest (RF) supervised machine learning algorithm with the randomForest package (Liaw and Wiener 2002). As applied in this study, RF selected 1,500 bootstrap samples, each containing two-thirds of the sampled cells. For each sample, RF generated a regression tree, then randomly selected only one-third of the predictor variables and chose the best partition from among those variables. To assess the relative importance and relationships of predictor variables on RdNBR across the entire study area and within different ownerships, separate RF models were developed for all 1,090 sample plots across the entire burned area, as well as separately for plots on BLM and private industrial lands. For each of the three RF models, we calculated variable importance values for each predictor variable as the percent increase in the mean squared error (MSE) in the predicted data when values for that predictor were permuted and all other predictors were left unaltered. In addition to variable importance values, we determined which predictor variables should be retained in each RF model using multi-stage variable selection procedures (Genuer et al. 2010). We applied two-stage variable selection for interpretation to each RF model using the VSURF package (Genuer et al. 2016). Final RF models were then run including only the selected variables. Predictive power of the final RF models were assessed by calculating the variance explained, which is equivalent to the coefficient of determination (R^2) used with linear regressions to assess statistical model fit for a given dataset. Last, we visualized the relationships of individual predictor variables on RdNBR in the final RF models using partial dependency plots (Hastie et al. 2001).

Importance values in RF models are not the same as quantifying the fixed effects of predictor variables, nor is RF well suited to explicitly test hypotheses or quantify effects of predictor variables while accounting for other variables in a model. To test if ownership type increased RdNBR, we developed a generalized least squares (GLS) regression model with an exponential spherical spatial correlation structure using the nlme package (Pinheiro et al. 2017). The GLS regression used the distance between sample locations and the form of the correlation structure to derive a variance–covariance matrix, which was then used to solve a weighted OLS regression (Dormann et al. 2007). Using the same response and predictor data as in the RF model for the entire Douglas Complex, and a binary predictor variable for ownership type, we developed a GLS model from which we calculated the fixed effect of ownership on RdNBR. We then predicted the mean and standard error of RdNBR by ownership after accounting for the other predictor variables in the GLS model using the AICcmodavg package (Mazerolle 2017).

Results

Fire weather variables

Regression models of fire weather variables (except maximum temperature) described a significant proportion of the variance in daily mean RdNBR (Table 1; Appendix S1: Fig. S1). SC described the most variance in daily RdNBR, had the lowest AIC score, and was most likely to be the best model of those compared ($w_i = 0.8250$). However, BI described a comparable amount of the variance in daily RdNBR ($R^2 = 0.5815$), had a substantial level of empirical support (ΔAIC = 3.3816), was the second most likely model given the data ($w_i = 0.1521$), and contained additional metrics that influence fire behavior (influence of temperature, relative humidity, and drought on live and dead fuels) not incorporated in SC. For these reasons, we choose to use BI as the single fire weather variable in subsequent analyses, acknowledging that it may describe slightly less variation in RdNBR than SC.

Table 1. Regression models of daily mean Relative differenced Normalized Burn Ratio (RdNBR) in relation to daily burn period fire weather variables.

Models	R^2	AIC	ΔAIC	$L(g_i \mid x)$	w_i
RdNBR = SC^2	0.6532	210.0324	0.0000	1.0000	0.8250
RdNBR = BI^2	0.5815	213.4140	3.3816	0.1844	0.1521
RdNBR = min wind speed^2	0.4542	218.1948	8.1624	0.0169	0.0139
RdNBR = log (min relative RH)	0.3800	220.4903	10.4579	0.0054	0.0044
RdNBR = ERC^2	0.3675	220.8497	10.8173	0.0045	0.0037
RdNBR = max wind speed^2	0.2179	224.6700	14.6376	0.0007	0.0005
RdNBR = max temperature^2	0.1069	227.0592	17.0268	0.0002	0.0002
RdNBR = null model	0.0000	228.1855	18.1531	0.0001	0.0001

Notes: R^2, adjusted R squared; AIC$_c$, Akaike information criterion corrected for sample size; ΔAIC$_c$, AIC$_c$ differences; $L(g_i \mid x)$, likelihood of a model given the data; w_i, Akaike weights; SC, spread component; BI, burn index; RH, relative humidity; ERC, energy release component.

RdNBR and predictor variable differences by ownership

The majority of predictor variables were not statistically different by ownership, as expected given the spatial distribution of ownership. Based on Mann-Whitney-Wilcoxon tests, biomass and stand age were lower on private industrial vs. BLM managed lands (Table 2; Appendix S1: Fig. S2). TPI fine, heat load, slope, and BI were not different between ownership types. Elevation was different between ownership types, but only 44 m higher on BLM land across a range of 875 m for all sample plots. Mean RdNBR was higher (536.56 vs. 408.75) on private industrial vs. BLM lands.

Random forest variable importance values and partial dependency plots

Two-stage variable selection procedures retained seven, five, and six predictor variables in the final RF models for the entire Douglas Complex, BLM, and private forests, respectively (Fig. 3). Across the entire Douglas Complex, BI was the most important predictor variable of RdNBR (increasing MSE by 138.4%), while BI was also the most importance variable separately for BLM (105.4%) and private forests (83.2%). Age and ownership were the next most

Table 2. RdNBR (mean with SE in parentheses) and predictor variables on sampled plots for Bureau of Land Management (BLM) vs. private industrial (PI) ownership.

Variable	BLM	PI	w	P
RdNBR	408.75 (298.53)	536.56 (299.88)	111,124	<0.0001
Biomass (Mg/ha)	234.75 (87.24)	163.88 (74.47)	215,166	<0.0001
Age (yr)	108.81 (55.53)	52.18 (36.78)	236,021.5	<0.0001
BI (index)	62.99 (14.16)	63.64 (14.54)	142,575.5	0.2782
Elevation (m)	653.79 (153.48)	609.46 (161.62)	171,200	<0.0001
TPI fine	0.55 (32.51)	−1.08 (32.12)	152,275	0.4296
Heat load (MJ·cm^{-2}·yr^{-1})	0.77 (0.2)	0.77 (0.2)	150,363	0.6734
Slope (%)	48.4 (13.4)	47.05 (14.01)	156,435	0.1115

Notes: The w values and associated P values are from Mann–Whitney–Wilcoxon tests. TPI, topographic position index.

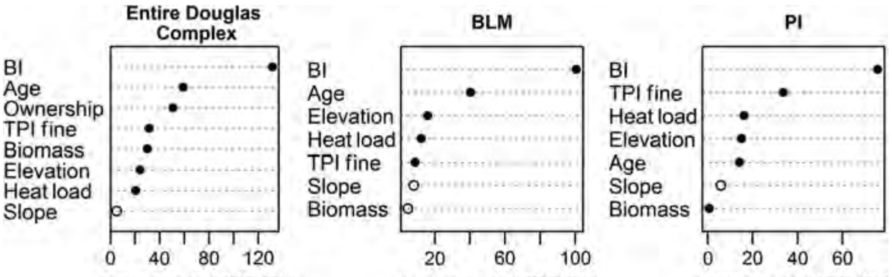

Fig. 3. Variable importance plots for predictor variables from Random Forest (RF) models of RdNBR for 1090 sample plots across the entire Douglas Complex (left panel), 571 plots on Bureau of Land Management (BLM) forests (middle), and 519 plots on private industrial (PI) forests (right). Solid circles denote variables retained in two-stage variable selection, open circles denote variables removed from the final RF models during variable selection. BI, burning index; MSE, Mean Squared Error.

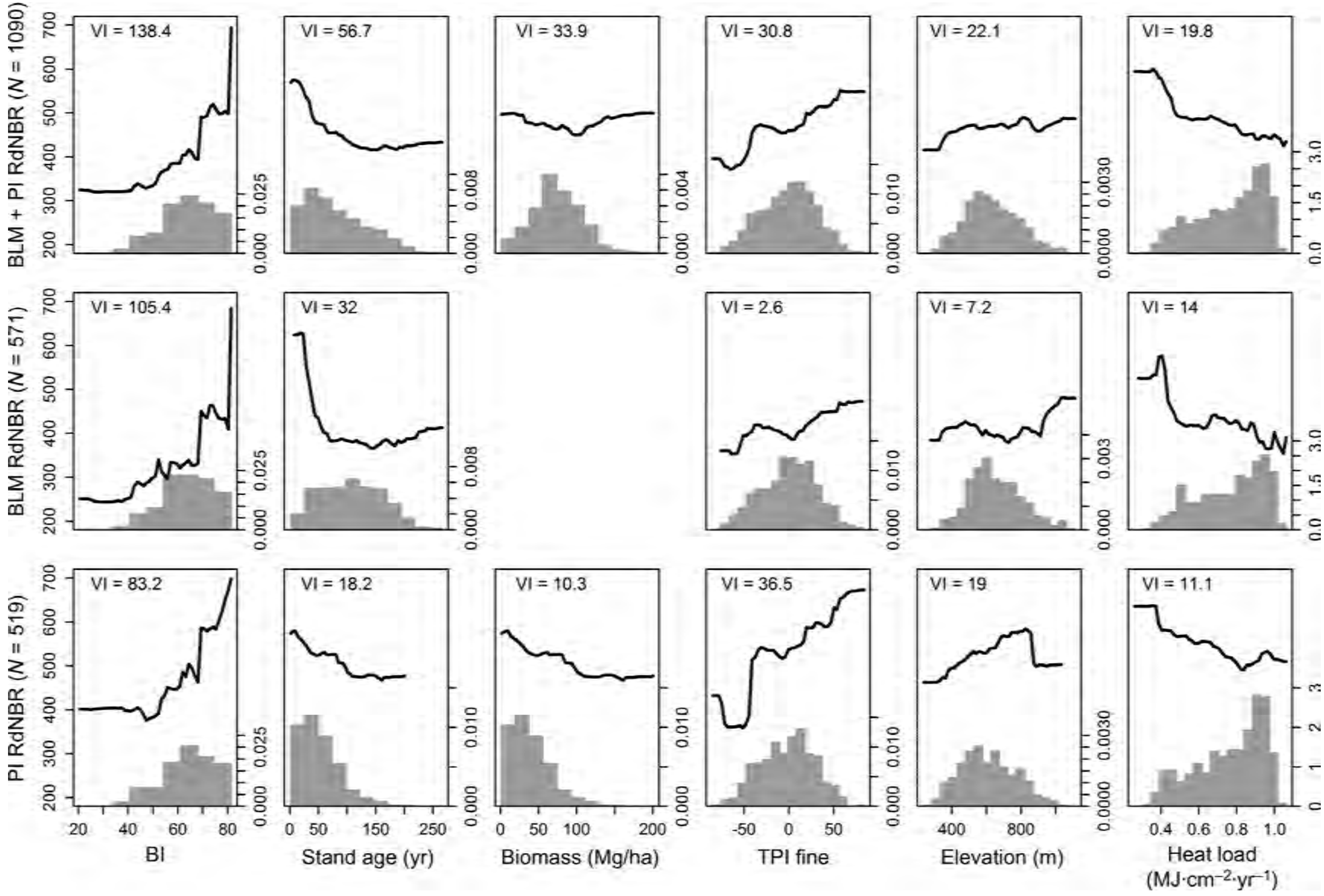

FIG. 4. Partial dependency plots showing relationships between each predictor variable and RdNBR in random forest models for all forests (BLM and PI, top panels), forests on Bureau of Land Management (BLM, middle panels), and private industrial land (PI, bottom panels). Number within each panel shows variable importance (VI; mean squared error increase [%]) of each predictor in the random forest model. Solid lines show trends in RdNBR in response to each predictor, histograms show the distributions of values for each predictor. Note there is no partial dependency plot for the relationship between RdNBR and biomass for BLM forests, as biomass was not a significant predictor variable for BLM forests based on two-stage variable selection procedures.

Table 3. Coefficients of predictor variables in generalized least squares model of RdNBR.

Variable	Parameter estimate	SE	*t*	*P*
Intercept	80.3321	90.4529	0.8881	0.3747
Age	−1.0544	0.2132	−4.9452	<0.0001
BI	6.1413	0.7618	8.0614	<0.0001
Ownership	76.3559	22.1111	3.4533	0.0006
Elevation	0.1179	0.0872	1.3512	0.1769
TPI fine	1.2839	0.2509	5.1169	<0.0001
Heat load	−150.0098	39.5750	−3.7905	0.0002
Slope	1.1321	0.5979	1.8933	0.0586
Biomass	0.1261	0.1194	1.0562	0.2911

important predictor variables, increasing MSE across the Douglas Complex by 56.7% and 53.2%, respectively. Age was the second most important variable in the final RF model for BLM forests (32%), but was the fourth most important variable for private forests (18.2%). Pre-fire biomass was the fourth most importance predictor variable in the RF model of the entire Douglas Complex (33.9%), but was not retained in the final RF model for BLM forests, and was the least important variable (10.3%) in the final RF model for private forests. Overall, topographic variables (TPI fine, heat load, and slope) were less important than BI, ownership, and age, increasing MSE across the Douglas Complex by 2.6–36.5%. RF models described 31%, 23%, and 25% of the variability in RdNBR across the entire burned area, BLM managed forests, and private forests, respectively.

Partial dependency plots displayed clear relationships between RdNBR and predictor variables (Fig. 4). RdNBR increased exponentially with BI across the entire Douglas Complex as well as for BLM and private forests separately, although RdNBR was shifted up by approximately 100 RdNBR on private forests vs. BLM forests for any given BI value. RdNBR was consistently higher in young forests on both ownerships. RdNBR declined rapidly on BLM forests between stand ages of 20 and 80 yr old, and remained roughly level in older forests. In contrast, RdNBR in private forests declined linearly with age across its range, although private lands had few forests greater than 100 yr old. RdNBR on both BLM and private forests increased with higher elevations, higher TPI fine, and steeper slope. Heat load was negatively correlated with RdNBR for all ownerships. Pre-fire biomass was not included in the final RF model for BLM lands, while, for the entire study and private lands, RdNBR appeared to decline slightly in forests with intermediate pre-fire biomass. However, the relationship between RdNBR and pre-fire biomass is more tenuous on private lands because they lacked forests with high pre-fire biomass.

Generalize least squares model

BI, age, ownership, TPI fine, and heat load were all significant predictors of RdNBR in the GLS model (Table 3). Slope had a suggestive relation with RdNBR ($P = 0.0586$), while elevation ($P = 0.1769$) and pre-fire biomass ($P = 0.2911$) were not a significant predictors. Relationships between predictors and RdNBR were consistent with partial dependency plots from RF models, with RdNBR increasing with BI and TPI fine and declining with age and heat load. Ownership had a fixed effect of increasing mean RdNBR by 76.36 ± 22.11 (mean ± SE) in private vs. BLM. Adjusting for all other predictor variables in the model, predicted mean RdNBR was higher on private (521.85 ± 18.67) vs. BLM forests (398.87 ± 18.23).

Discussion

Quantifying fire severity in the unique checkerboard landscape of the O&C Lands, this study disentangled the effects of forest management, weather, topography, and biomass on fire severity that are often spatially confounded. We found daily fire weather was the most important predictor of fire severity, but ownership, forest age, and topography were also important. After accounting for fire weather, topography, stand age, and pre-fire biomass, intensively managed private industrial forests burned at higher severity than older federal forests managed by the BLM. Below we discuss how the different variables in our analysis may influence fire severity, and argue that younger forests with spatially homogenized continuous fuel arrangements, rather than absolute biomass, was a significant driver of wildfire severity. The geospatial data available for our analyses was robust and comprehensive, covering two components of the fire behavior triangle (i.e., topography, weather), with pre-fire biomass and age serving as proxies for the third (fuel). However, we recognize there are limitations to our data and analyses and describe these below. We conclude by suggesting how our findings have important implications for forest and fire management in multi-owner landscapes, while posing important new questions that arise from our findings.

Fire weather was a strong top-down driver of fire severity, while bottom-up drivers such as topography and pre-fire biomass were less important. Across the western United States, evidence suggests bottom-up drivers such as topography and vegetation exert greater control on fire severity than weather, although the quality of weather representation confounds this conclusion (Dillon et al. 2011, Birch et al. 2015). At the same time, it is recognized that bottom-up drivers of fire severity can be overwhelmed by top-down climatic and weather conditions when fires burn during extreme weather conditions (Bradstock et al. 2010, Thompson and Spies 2010, Dillon et al. 2011). Daily burn period BI values were used in our analyses, but it is important to place fire weather conditions for any single fire within a larger historical context. We compared these daily BI values to the historical (1991–2017) summer (1 June–30 September) BI data we calculated from the Calvert RAWS data used in this study (3,296 total days). Within this historical record, mean burn period BI during the Douglas Complex for days with fire progression information was above average (79th percentile), but ranged considerably for any given day of the fire (15th–100th percentile). Fire severity was consistently higher on private lands across a range of fire weather conditions for the majority of days of active fire spread (Appendix S1: Fig. S3), leading us to conclude that while fire weather exerted top-down control on fire severity, local forest conditions that differed between ownerships remained important, even during extreme fire weather conditions.

Variation in pre-fire forest conditions across ownerships were clearly a significant driver of fire severity, and we believe they operated at multiple spatial scales. Private industrial forests were dominated by young trees, which have thinner bark and lower crown heights, both factors known to increase fire-induced tree mortality (Ryan and Reinhardt 1988, Dunn and Bailey 2016). At the stand scale, these plantations are high-density single cohorts often on harvest rotations between 30 and 50 yr, resulting in dense and relatively spatially homogenous fuel structure. In contrast, public forests were dominated by older forests that tend to have greater variability in both tree size and spatial pattern vs. plantations (Naficy et al. 2010), arising from variable natural regeneration (Donato et al. 2011), post-disturbance biological legacies (Seidl et al. 2014), and developmental processes in later stages of stand development (Franklin et al. 2002). Fine-scale spatial patterns of fuels can significantly alter fire behavior, and the effects of spatial patterns on fire behavior may increase with the spatial scale of heterogeneity (Parsons et al. 2017), which would likely be the case in O&C Lands due to the large scale checkerboard spatial pattern of ownership types.

Management-driven changes in fuel spatial patterns at tree and stand scales could also reconcile differences in prior studies that have found increases (Odion et al. 2004, Thompson et al. 2007) and decreases (Prichard and Kennedy 2014) in fire severity with intensive forest management. The two studies that observed an increase in fire severity with intensive forest management were conducted in the Klamath ecoregion of southwestern Oregon and northwestern California, the same ecoregion as this study. In contrast, Prichard and Kennedy (2014) examined the Tripod Complex in north-central Washington State, where harvests mostly occurred in low to mid elevation forests dominated by ponderosa pine, Douglas-fir, lodgepole pine (*Pinus contorta* var. *latifolia*), western larch (*Larix occidentalis*), and Engelmann spruce (*Picea engelmannii*). These forests have lower productivity compared to those studied in the Klamath ecoregion, with more open canopies and longer time periods to reach canopy closure after harvest, which likely results in more heterogeneous within stand fuel spatial patterns. Furthermore, forest clearcut units were relatively small in the Tripod Complex (mean 53 ha; Prichard and Kennedy 2014), and while these harvest units were spatially clustered, they were not large contiguous blocks as found in the O&C Lands. Last, it is unclear if the harvest units evaluated by Prichard and Kennedy (2014) experienced the full distribution of fire weather or topographic conditions compared to unharvested units, as our study does, which may confound their conclusions and our understanding of the relative importance of the factors driving fire behavior and effects.

Limitations

Our study examined a landscape uniquely suited to disentangling the drivers of wildfire severity and quantifying the effects of contrasting management activities. Additionally, we leveraged a robust collection of geospatial data to quantify the components of the fire behavior triangle. However, it is important to recognize the inherent limitations of our study. First, this study represents a single fire complex, instead of a regional collection of fires analyzed to elucidate broader system behaviors (sensu Dillon et al. 2011, Birch et al. 2015, Meigs et al. 2016). However, given the challenges of obtaining high quality fire weather information and accurate daily fire progression maps for fires that have occurred in landscapes with contrasting management regimes, we believe the landscape setting of our study provides key insights into the effects of management on fire severity that are not possible in large regional multi-fire studies. Second, while Landsat imagery is widely used to estimate forest conditions and fire severity, it has specific limitations. The GNN maps used in this study to derive pre-fire biomass and stand age are strongly driven by multi-spectral imagery from the Landsat family of sensors, whose imagery is known to saturate in forests with high leaf area indices and high biomass (Turner et al. 1999). Third, GNN maps of forest attributes used in this study were originally developed for large regional assessments, and as such have distinct limitations when used for analyses at spatial resolutions finer than the original source data (Bell et al. 2015), while application of GNN at fine spatial scales can underestimate GNN accuracy compared to larger areas commonly used by land managers (Ohmann et al. 2014). We addressed potential limitations of using GNN predictions at fine spatial scales in two ways. First, our sample plots are 90-m squares (3 × 3 30 m pixels) which more closely represents the area of the inventory plots used as GNN source data compared to pixel level analyses (Bell et al. 2015). Second, we visually assessed GNN predictions of live biomass and stand age within the Douglas Complex in relation to high resolution digital orthoimagery collected in 2011 by the USDA National Agriculture Imagery Program. From this qualitative assessment we concluded that GNN predictions characterize both between and within ownership variation in pre-fire biomass and age (Appendix S1: Fig. S4). Fourth and perhaps most fundamentally important, we relied on pre-fire biomass and stand age as proxies for fuel, in part because Landsat and other passive optical sensors have limited sensitivity to vertical and below-canopy vegetation structure (Lu 2006). Accurate and spatially complete quantitative information of forest surface and canopy fuels were not available for the Douglas Complex. More broadly, there are significant limitations to spatial predictions of forest structure and fuels using GNN and other methods that rely on passive optical imagery such as Landsat (Keane et al. 2001, Pierce et al. 2009, Zald et al. 2014), which is why we relied on the more accurately predicted age and pre-fire biomass variables as proxies. Surface and ladder fuels are the most important contributors to fire behavior in general (Agee and Skinner 2005), and surface fuels have been found to be positively correlated to fire severity in plantations within the geographic vicinity of the Douglas Complex (Weatherspoon and Skinner 1995). Yet correlations between biomass and fuel load can be highly variable due to site conditions and disturbance history (i.e., mature forests with frequent surface fires may have high live biomass but low surface fuel loads, while dense young forests that have regenerated after a stand replacing wildfire will have low live biomass but potentially high surface fuel loads as branches and snags fall). Therefore, GNN predicted pre-fire biomass may represent the total fuel load, but not the available surface and ladder fuels that have the potential to burn during a specific fire, and this is supported by the low importance of pre-fire biomass as a predictor of fire severity in our study. Furthermore, it is important to recognize that in addition to total surface and ladder fuels, the spatial continuity of these fuels strongly influences fire behavior (Rothermel 1972, Pimont et al. 2011). Fifth, while private industrial and BLM forests in our study area had very different forest conditions due to contrasting management regimes, ownership alone misses management activities (e.g., site preparation, stocking density, competing vegetation control, partial thinning, etc.) that can influence fuels and fire behavior. Sixth, while our spatial extrapolation of fire weather correlated well with daily fire severity and area burned, it did not account for topographic mediation of weather that can influence fine scale fire behavior, nor did it examine the underlying weather patterns such as temperature inversions that are common to the region and may play a key role in moderating burning index (Estes et al. 2017). Finally, we were unable to discern the effects of fire suppression activities and whether they varied by ownership, since incident documentation of suppression activities are generally not collected or maintained in a manner consistent with quantitative or geospatial statistical analyses (Dunn et al. 2017).

Management Implications

Although only one fire complex, the contrasting forest conditions resulting from different ownerships within the Douglas Complex are consistent with many mixed-ownership or mixed-use landscapes, such that we believe our results have implications across a much broader geographic area. First, it brings into question the conventional view that fire exclusion in older forests is the dominant driver of fire severity across landscapes. There is strong scientific agreement that fire suppression has increased the probability of high severity fire in many fire-prone landscapes (Miller et al. 2009, Calkin et al. 2015, Reilly et al. 2017), and thinning as well as the reintroduction of fire as an ecosystem process are critical to reducing fire severity and promoting ecosystem resilience and adaptive capacity (Agee and Skinner 2005, Raymond and Peterson 2005, Earles et al. 2014, Krofcheck et al. 2017). However, in the landscape we studied, intensive plantation forestry appears to have a greater impact on fire severity than decades of fire exclusion. Second, higher fire severity in plantations potentially flips the perceived risk and hazard in multi-owner landscapes, because higher severity fire on intensively managed private lands implies they are the greater source of risk than older forests on federal lands. These older forests likely now experience higher fire severity than historically due to decades of fire exclusion, yet in comparison to intensively managed plantations, the effects of decades of fire exclusion in older forests appear to be less important than increased severity in young intensively managed plantations on private industrial lands.

Furthermore, our findings suggest challenges and opportunities for managing intensive plantations in ways that reduce potential fire severity. Increasing the age (and therefore size) of trees and promoting spatial heterogeneity of stands and fuels is a likely means to reducing fire severity, as are fuel reduction treatments in plantations (Crecente-Campo et al. 2009, Kobziar et al. 2009, Reiner et al. 2009). The extent and spatial arrangement of fuel reduction treatments can be an important consideration in their efficacy at reducing fire severity at landscape scales (Finney et al. 2007, Krofcheck et al. 2017). However, optimal extent and landscape patterns of fuels reduction treatments can be hampered by a wide range of ecological, economic, and administrative constraints (Collins et al. 2010, North et al. 2015a, Barros et al. 2017). In the past, pre-commercial and commercial thinning of plantations (a potential fuel treatment) in the Pacific Northwest were common, economically beneficial management activities that improved tree growth rates and size, but these practices have become less common with improved reforestation success, alternative vegetation control techniques, and shorter harvest rotations (Talbert and Marshall 2005). This suggests there may be strong economic limitations to increased rotation ages and non-commercial thinning in young intensive plantation forests. More broadly, the development of large-scale forest management and conservation strategies can face legal and equitability challenges in multi-owner landscapes given existing laws constraining planning among private organizations (Thompson et al. 2004, 2006).

We believe two major questions arise from our findings that are important to fire management in multi-owner landscapes, especially those with contrasting management objectives. Plantations burned at higher severity, and this implies they are a higher source of risk to adjacent forest ownerships. However, a more explicit quantification of fire severity and susceptibility is needed to understand how risk is spatially transmitted across ownership types under a variety of environmental conditions. Second, we suggest the need for alternative management strategies in plantations to reduce fire severity at stand and landscape scales. However, the economic viability of such alternative management regimes remains poorly understood. Optimization models integrating spatial allocation of fuel treatments and fire behavior with economic models of forest harvest and operations could be used to determine if alternative management activities in plantations are economically viable. If alternative management activities are not economically viable, but wildfire risk reduction is an important objective on lands adjacent to industrial forestlands, strategic land purchases or transfers between ownership types may be required to achieve landscape level goals. This may be particularly important given the previously stated legal and equitability challenges in multi-owner landscapes. Regardless of the landscape-level objectives and constraints, it is clear that cooperation among stakeholders will be necessary in multi-ownership landscapes if wildfire risk reduction, timber harvesting, and conservation objectives remain dominant yet sometimes conflicting objectives for these landscapes.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1710/full

Data Availability

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.3gv5c78