

Human-started wildfires expand the fire niche across the United States

Jennifer K. Balch^{a,b,1}, Bethany A. Bradley^{c,d,1}, John T. Abatzoglou^e, R. Chelsea Nagy^a, Emily J. Fusco^d, and Adam L. Mahood^{a,b}

^aEarth Lab, University of Colorado, Boulder, CO 80309; ^bDepartment of Geography, University of Colorado, Boulder, CO 80309; ^cDepartment of Environmental Conservation, University of Massachusetts, Amherst, MA 01003; ^dOrganismic and Evolutionary Biology Program, University of Massachusetts, Amherst, MA 01003; and ^eDepartment of Geography, University of Idaho, Moscow, ID 83844

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The economic and ecological costs of wildfire in the United States have risen substantially in recent decades. Although climate change has likely enabled a portion of the increase in wildfire activity, the direct role of people in increasing wildfire activity has been largely overlooked. We evaluate over 1.5 million government records of wildfires that had to be extinguished or managed by state or federal agencies from 1992 to 2012, and examined geographic and seasonal extents of human-ignited wildfires relative to lightning-ignited wildfires. Humans have vastly expanded the spatial and seasonal “fire niche” in the coterminous United States, accounting for 84% of all wildfires and 44% of total area burned. During the 21-y time period, the human-caused fire season was three times longer than the lightning-caused fire season and added an average of 40,000 wildfires per year across the United States. Human-started wildfires disproportionately occurred where fuel moisture was higher than lightning-started fires, thereby helping expand the geographic and seasonal niche of wildfire. Human-started wildfires were dominant (>80% of ignitions) in over 5.1 million km², the vast majority of the United States, whereas lightning-started fires were dominant in only 0.7 million km², primarily in sparsely populated areas of the mountainous western United States. Ignitions caused by human activities are a substantial driver of overall fire risk to ecosystems and economies. Actions to raise awareness and increase management in regions prone to human-started wildfires should be a focus of United States policy to reduce fire risk and associated hazards.

anthropogenic wildfires | fire starts | ignitions | modern fire regimes | wildfire causes

The United States has experienced some of the largest wildfire years this decade, with over 36,000 km² burned in 2006, 2007, 2012, and 2015 (1). There is national and global concern over how fire regimes have changed in the past few decades and how they will change in the future (2–4). In the western United States, there is strong evidence that regional warming and drying, including that directly attributed to anthropogenic climate change, are linked to increased fire frequency and size and longer fire seasons (5–9). However, the role that humans play in starting these fires and the direct role of human-ignitions on recent increases in wildfire activity have been overlooked in public and scientific discourse because of the difficulty in ascribing a cause, either human- or lightning-started (10). Humans primarily alter fire regimes in three ways: changing the distribution and density of ignitions, shifting the seasonality of burning, or altering available fuels (2, 3). Geographic variability in regional and continental-scale fire activity in the United States is strongly tied to proxies for these human-caused changes, including population and road density, and different land-use and development patterns (10–15). Although changing climate and fuels also influence fire regimes across the United States (10, 16, 17), there can be no fire without an ignition source. Here, we explore the role that human-started wildfires play in modern United States fire regimes.

Ignitions are often presumed to be saturated (18, 19), and therefore have limited ability to predict fire activity. However, several studies suggest that humans play an important role in

redistributing ignitions (20–22), particularly where lightning rarely occurs or where lightning is not concurrent with dry conditions (23). The human–fire connection in the modern era appears strongest at intermediate levels of development, as fires become less likely in the landscape beyond a certain population density, level of urbanization, or dependence on fossil fuels (11, 13, 24). Overall, humans expand the spatial and temporal “fire niche” by introducing ignitions into landscapes when fuels are sufficiently dry enough to ignite and carry fire, but when lightning is rare. Human ignitions are therefore a critical force acting to expand how the fire niche is realized across United States ecoregions.

National-scale analysis of human alteration of the fire niche is critical given that the annual expense of fighting wildfires has exceeded \$2 billion in recent years, and the accrued direct and indirect impacts of wildfire on infrastructure and communities could be 30 times that amount (25). Policies that govern wildfire management and response are also directed at the national level, demanding analysis at a national scale (10, 22, 26). Although recent human influence on fire regimes has been studied at local (13) to regional scales (14), human influence nationally remains poorly understood (10). National policies can strongly influence fire regimes (27) and, with sufficient information on human ignitions, policy directives could target human behavior in ways that remediate increasing trends in wildfire risk.

Here, we ask how human ignitions have altered the spatial extents, seasonality, and temporal trends in wildfire across the coterminous United States. We analyze over 1.5 million records of both human- and lightning-started fires in the United States from

Significance

Fighting wildfires in the United States costs billions of dollars annually. Public dialog and ongoing research have focused on increasing wildfire risk because of climate warming, overlooking the direct role that people play in igniting wildfires and increasing fire activity. Our analysis of two decades of government agency wildfire records highlights the fundamental role of human ignitions. Human-started wildfires accounted for 84% of all wildfires, tripled the length of the fire season, dominated an area seven times greater than that affected by lightning fires, and were responsible for nearly half of all area burned. National and regional policy efforts to mitigate wildfire-related hazards would benefit from focusing on reducing the human expansion of the fire niche.

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¹To whom correspondence may be addressed. Email: jennifer.balch@colorado.edu or bbradley@eco.umass.edu.

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1992 to 2012 (28). All of these wildfires necessitated an agency response to manage or suppress them, and therefore posed a threat to ecosystems or infrastructure; this record does not include intentionally set prescribed burns or managed agricultural fires. To our knowledge, this is the most comprehensive assessment of the role of human-started wildfires across the United States over the past two decades. We compare: (i) the spatial extents of human- vs. lightning-started wildfires, (ii) the seasonality of human vs. lightning wildfires, (iii) the climate niche for human- vs. lightning-started wildfires, and (iv) 21-y trends in large human vs. lightning wildfires. Our analysis documents the pronounced expansion of wildfire extent, seasonality of wildfires, and increasing numbers of large wildfires through time as a result of human-related ignitions across the United States.

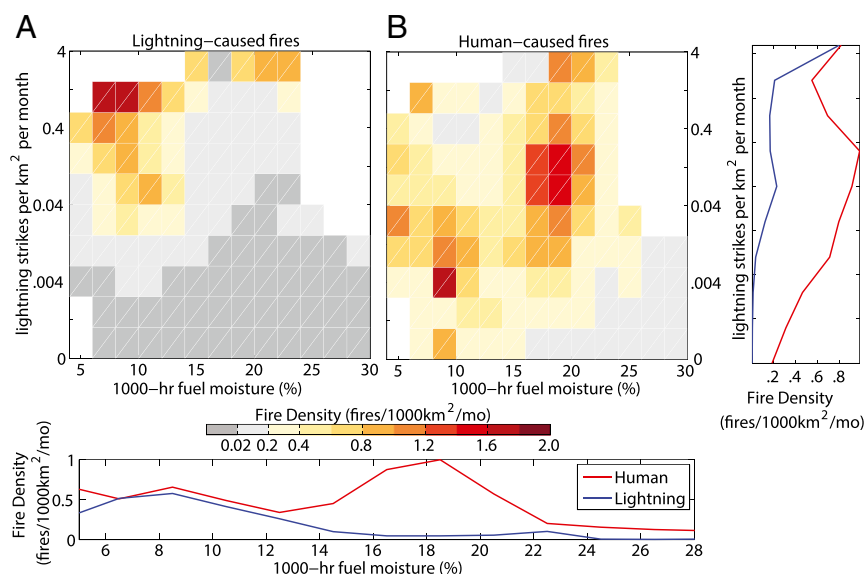
Human-started wildfires represented 84% of the 1.5 million wildfires included in this analysis ($n = 245,446$ lightning-started fires;

$n = 1,272,076$ human-started wildfires). The eastern United States and western coastal areas were dominated by human-started wildfires, whereas lightning-started fires dominated the mountainous regions of the western United States (Fig. 1, Table 1 and [Table S1](#)). Here we define a fire regime as dominated by either human or lightning ignitions when one cause accounts for more than 80% of the number of fires in a given 50×50 -km grid cell. Based on this definition, 5.1 million km^2 , or 60% of the total land area of the coterminous United States, was dominated by human-started wildfires, whereas only 0.7 million km^2 , or 8% of the area, was dominated by lightning-started fires. In addition to expanding the numbers of fires, humans also expanded the total area burned. Human-started wildfires burned a total of 160,274 km^2 , or $\sim 44\%$ of the total area burned from 1992 to 2012 (Table 1).

Human ignitions dramatically expanded the wildfire season in the United States, particularly during spring. The length of the human-started wildfire season [defined as the interquartile range (IQR) of human-ignited fires] was 154 d, more than triple that of the lightning wildfire season (IQR = 46 d) (Fig. 2 and Table 1). This national-scale expansion is driven by earlier (spring) human-started fires in eastern ecoregions coupled with later (late summer or fall) human-started fires in western ecoregions (Table S2). The median discovery date for human-started fires was over 2-mo (May 20th) earlier than lightning-started fires (July 25th). Summed across the 21-y record, the most common day for human-started fires by far was July 4th, US Independence Day, with 7,762 fires starting that day over the course of the record (Fig. 2), whereas, the most common day for lightning-started fires was July 22nd. Of all lightning-ignited fires, 78% occurred in the summer (June–August), 9% in the spring (March–May), and 12% in the fall (September–November). In contrast, human-ignited wildfires were more evenly distributed throughout the year, with 24% in summer, 38% in spring, 19% in fall, and 19% in winter. This pronounced expansion of the wildfire season was also evident spatially (Fig. 3), with human-ignited wildfires occurring predominantly in spring in the eastern United States and in the fall and winter in Texas and the Gulf states. See Table S1 for state-level analysis. When lightning-started fires were rare (<5% and >95% quantile; i.e., before May 13th or after September 16th), humans ignited 842,289 wildfires, effectively increasing the number of wildfires 35-fold compared with the 24,081 lightning-ignited wildfires during these spring, fall, and winter seasons.

Ecoregion	No. of fires		Human caused (%)	Area burned (ha)		Human caused (%)	Length (IQR, days)		Human expansion (%)
	Human	Light		Human	Light		Human	Light	
MC	87,274	2,855	97	2,143,282	253,210	89	85	45	189
NF	61,673	2,574	96	302,561	82,721	79	51	79	N/A
ETF	815,499	44,859	95	3,827,045	829,293	82	167	66	253
MWCF	14,586	925	94	19,251	27,291	41	67	52	129
GP	134,944	17,586	88	3,992,557	2,564,955	61	148	47	315
SSH	7,504	2,167	78	340,873	254,418	57	55	41	134
TWF	4,832	1,917	72	357,150	350,477	50	98	52	188
NAD	55,422	52,044	52	2,394,677	8,880,691	21	92	40	230
NFM	76,735	94,017	45	1,895,622	5,731,733	25	75	36	208
TS	13,607	26,502	34	754,393	1,152,064	40	85	39	218
CONUS	1,272,076	245,446	84	16,027,412	20,126,852	44	154	46	335

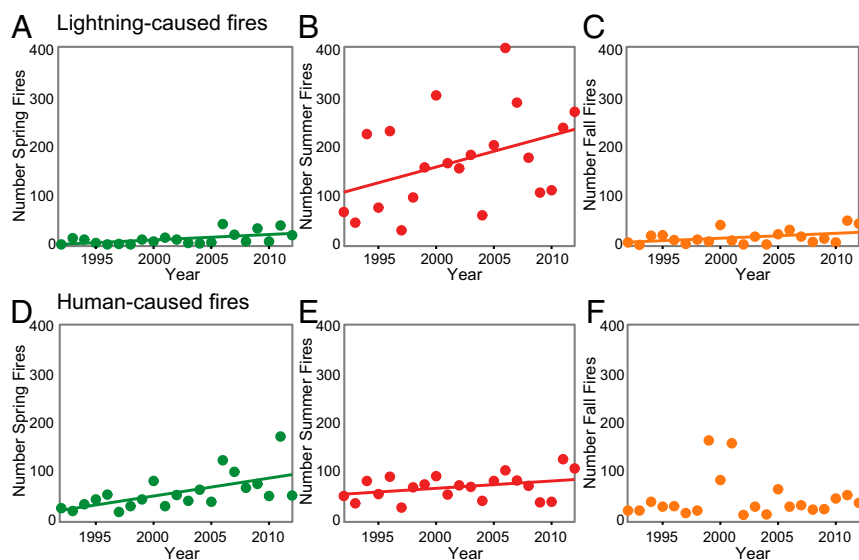
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wildfires were started by people from 1992 to 2012. Sixty percent of the total land area of the coterminous United States was dominated by human-started wildfires, whereas only 8% of the area was dominated by lightning fires. Humans tripled the length of the wildfire season, extending burning into the spring, fall, and winter months. During the spring, fall, and winter, people added more than 840,000 wildfires, a 35-fold increase over the number of lightning-started fires in those seasons. This expansion of the fire-niche was caused by human-related ignitions under higher fuel moisture conditions, compared with lightning-started fires. Moreover, during this 21-y record, large human-started wildfires increased significantly.

There was a strong national east-west dichotomy in the spatial distribution of human-started wildfires. Although human-started wildfires were pervasive across the United States (Fig. 1), the expansion of human-started wildfires relative to lightning-started fires was most dramatic in the eastern United States and central and southern California (Figs. 1 and 2C). Recent work for California confirms the important role of humans, with anthropogenic variables explaining half of the variability in fire probability over the past four decades (30). In contrast, lightning-started fires were

found primarily in the intermountain west and Florida and occurred predominantly in the summer, reflecting national lightning strike patterns (31) (Fig. 2C). This finding supports other studies of human vs. lightning ignition sources that have found an important distinction between eastern and western United States fire patterns (10, 21) and drivers (32). Some explanations for this distinction include higher population and housing densities, lower proportions of public land, and more extensive land use and development in the eastern United States (33, 34), all of which could lead to more sources of anthropogenic ignitions. Synchrony between lightning activity and the seasonal nadir of fuel moisture in the western United States also likely contributes to these geographic differences. However, even with a projected increase in the number of lightning strikes as a result of anthropogenic climate change (50% by 2100) (35), humans would still remain the dominant ignition source across the majority of the United States land area. The majority of the wildfires requiring agency suppression in the east can be attributed to escaped fires from debris burning occurring in the spring months (or winter in Texas and the Gulf Coast) (Fig. 3). Between 1992 and 2012, wildfires caused by debris burning tended to be small (median



fire size 0.4 ha, IQR: 0.14–1.62 ha), but still an important source of risk to surrounding ecosystems. At finer scales, there are also notable patterns in human- vs. lightning-started wildfires (Fig. S5). Increased wildfires can follow road networks (36), the wildland–urban interface (13), and boundaries between agricultural and forested areas (37), highlighting just a few examples of how human activities and cultural drivers provide ignitions that substantially change the distribution of fire across the United States (38).

Our findings reinforce the strong imprint of people on fire regimes through changes in wildfire seasonality, which has been documented globally (39). In the past few decades, early onset of warmer and drier conditions has promoted greater fire activity across the western United States (6, 7, 40). However, our study highlights the equally important role of human ignitions in changing modern fire regimes by increasing the fire season length to encompass the entire year. The vast majority (78%) of lightning-started fires occurred during the summer months, whereas 76% of human-started fires occurred during the spring, fall, and winter months. Moreover, this trend varies substantially by ecoregion, reflecting again the principle dichotomy between the eastern and western United States (Fig. 3). Human-started fires extend the fire season earlier in the east, and later in the west (Fig. 3 and Table S2). Observations suggest that climate change has extended the duration of the fire weather season across most of the globe, including parts of the United States by a couple of weeks over the past three decades (5, 9), whereas we show that human ignitions in the United States increased the length of the fire season by more than three mo. There was also a notable mark of American culture on the distribution of wildfires, with the peak day of wildfires occurring on July 4th, concurrent with Independence Day fireworks displays (Fig. 2). Indeed, Americans start over twice as many wildfires on July 4th as any other summer day. A similar cultural mark has also been demonstrated globally with a marked decline in wildfires on Sunday compared with other weekdays (41).

Thus, at the national scale, human ignitions dramatically expand the spatial and seasonal niche of fire. The key components that define the fire niche are ignition sources, fuel mass, and desiccation. By exploring the fire niche along these axes, our results show that lightning fires are primarily constrained to areas with a lightning-strike density of greater than 100 strikes per grid cell per month (0.04 strikes/km² per month) and are concurrent with drier fuels (< 15% fuel moisture) (Fig. 4). Human ignitions expand fires into regions with higher fuel moisture (Fig. 4) and higher NPP (Figs. S1 and S2), suggesting that humans create sufficient ignition pressure for wetter fuels to burn. As a consequence, human ignitions have expanded the fire niche into areas with historically low lightning-strike density, such as Mediterranean California, or low concurrence of lightning and dry conditions, such as Eastern Temperate Forests (Fig. 1).

Over the past two decades, there was a significant increase across the United States for both human- and lightning-caused large fires (Fig. S3). The significant increase in large lightning fires is driven primarily by fires in summer months (Fig. 5) in the Northwest Forested Mountains ecoregion of the western United States (Fig. S4). This finding is consistent with other studies that have demonstrated an increase in large fires across the western United States (6, 7, 40), likely as a consequence of changes in climate and fuels rather than ignitions. In contrast, the significant trend in human-caused fires is primarily driven by an increase in large fires during spring months (Fig. 5) in the Great Plains ecoregion of the United States (Fig. S4). This increasing trend suggests that earlier springs as a result of climate change (42, 43) may be interacting with human ignition sources to increase the risk of large fires in the central United States.

The strong year-to-year variability in human ignitions (Fig. S3 and S4) may reflect the degree to which human choices can affect fire regimes. However, interannual climate variability also influences fuel moisture, NPP, and short-term weather conditions that enable the spread of human-ignited wildfires (44). There was a significant temporal correlation between large human- and lightning-started

fires ($R = 0.75$). This pattern has been observed previously in the western United States (23) and suggests that large-scale climate drivers affect the frequency of both human- and lightning-caused fires. It is unknown how human actions will be affected by hotter and drier conditions, potentially increasing or decreasing ignitions from land use, recreation, and other sources. Increased public awareness and focused policy and management, particularly in years with elevated fire risk associated with climatic anomalies, are needed to reduce the number of human-caused ignitions.

In conclusion, we demonstrate the remarkable influence that humans have on modern United States wildfire regimes through changes in the spatial and seasonal distribution of ignitions. Although considerable fire research in the United States has rightly focused on increased fire activity (e.g., larger fires and more area burned) because of climate change, we demonstrate that the expanded fire niche as a result of human-related ignitions is equally profound. Moreover, the convergence of warming trends and expanded ignition pressure from people is increasing the number of large human-caused wildfires (Fig. 5). Currently, humans are extending the fire niche into conditions that are less conducive to fire activity, including regions and seasons with wetter fuels and higher biomass (Figs. 3 and 4). Land-use practices, such as clearing and logging, may also be creating an abundance of drier fuels, potentially leading to larger fires even under historically wetter conditions. Additionally, projected climate warming is expected to lower fuel moisture and create more frequent weather conditions conducive to fire ignition and spread (45), and earlier springs attributed to climate change are leading to accelerated phenology (42). Although plant physiological responses to rising CO₂ may reduce some drought stress (46), climate change will likely lead to faster desiccation of fuels and increased risk in areas where human ignitions are prevalent.

Uncertainty remains regarding how anthropogenic climate change will alter wildfire activity geographically and seasonally (47, 48), particularly in areas where human-caused fires dominate. Moreover, the current wildland–urban interface, where houses intermingle with natural areas, constitutes 9% of the United States total land area (33) but is projected to double by 2030, predominantly in the intermountain West (49). This expected development expansion will increase not only ignition pressure, but also the vulnerability of new infrastructure. Human-driven expansion of the spatial and temporal distribution of ignitions makes national- and regional-scale policy interventions and increased public awareness critical for reducing national wildfire risk.

Materials and Methods

For this analysis, we used the publicly available US Forest Service Fire Program Analysis-Fire Occurrence Database (FPA-FOD) (28). This comprehensive dataset includes United States federal, state, and local records of wildfires (both on public and private lands) that were suppressed from 1992 to 2012, a total of ~1.6 million records. Previous studies have focused on the western United States (20), federal lands (22), or records from just one agency (21). Each entry includes at minimum the location, discovery date, and cause of the wildfire. We excluded 114,191 wildfires with an unknown cause and analyzed the spatial, seasonal, and temporal patterns of human- vs. lightning-started wildfires. In total, 1,517,522 wildfires were included in the analysis. Human-started wildfires were caused by a variety of sources, including the US Forest Service-designated categories of equipment use, smoking, campfire, railroad, arson, debris burning, children, fireworks, power line, structure, and miscellaneous fires (28). Spatially, we calculated the proportion of human- vs. lightning-caused wildfires within equal-area 50 × 50-km grid cells across the coterminous United States. This grid size corresponds roughly to the size of an average United States county. For each grid cell, we calculated the season (winter, spring, summer, or fall) when the majority of human-caused and lightning-caused wildfires were started. All spatial analyses were conducted in the Albers-Conical equal-area projection. To determine the seasonal distribution of wildfires, we plotted the distribution of human- and lightning-started fires by the day of year for the coterminous United States and for individual ecoregions. We used the level 1 ecological regions of North America, developed by the Commission for Environmental Cooperation (50). We calculated the length of the human- and lightning-caused fire seasons as the IQR of the Julian day of recorded fire ignition: that is, the difference between the first and third quartiles.

We determined how humans expanded the fire niche by comparing the lightning-strike density (i.e., natural ignition pressure) and fuel-moisture conditions under which actual human- and lightning-started fire events occurred. We obtained daily 1,000-h dead fuel moisture data from the surface meteorological data (51) on a 4-km grid from 1992 to 2012, and computed monthly averages across the 21-y study period. We obtained 4-km gridded monthly lightning-strike data from the Vaisala National Lightning Detection Network (<https://www.ncdc.noaa.gov/data-access/severe-weather/lightning-products-and-services>) and averaged the data over the 21-y study period. To account for fuel limitations, we also explored the fire niche as a function of fuel amount (approximated by NPP). We used MODIS mean annual NPP data (1-km resolution, from 2002 to 2015) (52) for this purpose. These three datasets were aggregated to the common 50 × 50-km grid cell. We calculated the number of human- and lightning-started fires by grid cell using the FPA-FOD dataset (28). We excluded any grid cells from subsequent analyses that did not report at least one lightning-caused or human-caused wildfire over the period of record. We tested whether fire niche expansion (as determined by fuel moisture and lightning-strike density) caused by human ignitions was significant based on Mann-Whitney tests between human- vs. lightning-started fires.

To assess trends in human- vs. lightning-caused wildfires through time, we used only large fires that were independently verified by the

Monitoring Trends in Burn Severity (MTBS) project (53). We specifically focused on these large fires (>400 ha in the west, >200 ha in the east; $n = 8,455$) for comparability with previous research, which has examined temporal trends in the western United States and the link to climate warming (6, 7, 40), but has not investigated the relative contribution of human-started fires at a national scale. In addition to overall temporal trends, we tested for significant trends by ignition source versus season (spring, summer, fall) and versus ecoregion based on the level I ecological regions of North America (50). We explored a similar analysis using all available FPA-FOD data, but changes in reporting frequency through time for some states precluded a robust temporal analysis. We tested for trends in wildfire numbers through time using the nonparametric Theil-Sen estimator (54) and tested for trend significance using nonparametric Mann-Kendall tests (55).

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Postfire Management on Forested Public Lands of the Western United States

ROBERT L. BESCHTA,*††† JONATHAN J. RHODES,† J. BOONE KAUFFMAN,‡
ROBERT E. GRESSWELL,§ G. WAYNE MINSHALL,** JAMES R. KARR,†† DAVID A. PERRY,‡‡ ‡‡‡
F. RICHARD HAUSER,§§ AND CHRISTOPHER A. FRISSELL***

*Department of Forest Engineering, Oregon State University, Corvallis, OR 97331, U.S.A.

†Senior Fishery Scientist-Hydrologist, Columbia River Inter-Tribal Fish Commission, 729 NE Oregon Street, Portland, OR 97232, U.S.A.

‡Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, U.S.A.

§U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, U.S.A.

**Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, U.S.A.

††Box 305020, University of Washington, Seattle, WA 98195-5020, U.S.A.

‡‡Department of Forest Science, Oregon State University (Emeritus), Corvallis, OR 97331, U.S.A.

§§Flathead Lake Biological Station, University of Montana, Polson, MT 59860, U.S.A.

***The Pacific Rivers Council, Polson, MT 59860, U.S.A.

Abstract: *Forest ecosystems in the western United States evolved over many millennia in response to disturbances such as wildfires. Land use and management practices have altered these ecosystems, however, including fire regimes in some areas. Forest ecosystems are especially vulnerable to postfire management practices because such practices may influence forest dynamics and aquatic systems for decades to centuries. Thus, there is an increasing need to evaluate the effect of postfire treatments from the perspective of ecosystem recovery. We examined, via the published literature and our collective experience, the ecological effects of some common postfire treatments. Based on this examination, promising postfire restoration measures include retention of large trees, rehabilitation of firelines and roads, and, in some cases, planting of native species. The following practices are generally inconsistent with efforts to restore ecosystem functions after fire: seeding exotic species, livestock grazing, placement of physical structures in and near stream channels, ground-based postfire logging, removal of large trees, and road construction. Practices that adversely affect soil integrity, persistence or recovery of native species, riparian functions, or water quality generally impede ecological recovery after fire. Although research provides a basis for evaluating the efficacy of postfire treatments, there is a continuing need to increase our understanding of the effects of such treatments within the context of societal and ecological goals for forested public lands of the western United States.*

Key Words: ecological principles, postfire treatments, restoration, salvage logging, wildland fire

Gestión Post-Incendio en Terrenos Boscosos Públicos en el Oeste de E. U. A.

Resumen: *Los ecosistemas boscosos en el oeste de Estados Unidos evolucionaron a lo largo de muchos milenios en respuesta a perturbaciones tales como incendios naturales. Sin embargo, las prácticas de uso y gestión del suelo han alterado estos ecosistemas, incluyendo los regímenes de fuego en algunas áreas. Los ecosistemas boscosos son especialmente vulnerables a las prácticas de gestión post-incendio porque tales prácticas pueden influir en la dinámica del bosque y en los sistemas acuáticos de décadas hasta siglos. Por tanto, hay una mayor necesidad de evaluar el efecto de tratamientos post-incendio desde la perspectiva de la recuperación*

†††email robert.beschta@oregonstate.edu

‡‡‡Current address: P.O. Box 8, Kapua'u, HI 96755, U.S.A.

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del ecosistema. Examinamos, vía la literatura publicada y nuestra experiencia colectiva, los efectos ecológicos de algunos tratamientos post-incendio comunes. Con base en esa examinación, las medidas de restauración post-incendio prometedoras incluyen la retención de árboles grandes, la rehabilitación de guardarrayas y caminos y, en algunos casos, la siembra de especies nativas. Las siguientes generalmente son inconsistentes con los esfuerzos para restaurar funciones del ecosistema después del incendio: siembra de especies exóticas, pastoreo, colocación de estructuras físicas en y cerca del canal de arroyos, tala post-incendio, remoción de árboles grandes y construcción de caminos. Las prácticas que adversamente afectan la integridad del suelo, la persistencia o recuperación de especies nativas, las funciones riparias o la calidad del agua generalmente impiden la recuperación ecológica después del incendio. Aunque la investigación proporciona una base para evaluar la eficacia de los tratamientos post-incendio, existe la necesidad de incrementar nuestro entendimiento de los efectos de dichos tratamientos en el contexto de metas sociales y ecológicas para los terrenos boscosos públicos del oeste de Estados Unidos.

Palabras Clave: incendio en terreno silvestre, principios ecológicos, restauración, tala de salvamento, tratamientos post-incendio

Introduction

Wildland fires are disturbances that occur with long recurrence intervals and generally high severity in some forest types and with shorter intervals and lower severity in others (Pyne 1984; Walstad et al. 1990; Agee 1993). For millennia, wildland fires have arguably been the most important disturbance process throughout many western forests (Hessburg & Agee 2003). Seedling germination and establishment, growth patterns, plant community composition and structure, rates of mortality, soil productivity, and other properties and processes of western forest ecosystems are often strongly influenced and shaped by fire disturbance regimes. Even so, perhaps the most controversial aspect of western land management at present is the ecology of fire and fire management.

Land and fire management practices across the western United States have profoundly affected forest, grassland, and aquatic ecosystems by fragmenting ecosystems, simplifying or destroying habitats, and modifying disturbance regimes (McIntosh et al. 1994; Keane et al. 2002; Hessburg & Agee 2003). Cumulatively, these practices have altered ecosystems to the point where local and regional extirpation of sensitive species is increasingly common (Rieman et al. 1997; Thurow et al. 1997). Consequently, the integrity of many terrestrial and aquatic systems has been severely degraded at every level of biological organization, among populations, communities, assemblages, and species (Nehlsen et al. 1991; Frissell 1993; Rieman et al. 2003).

For more than a century, wildland fires have been perceived as the major "threat" to the health of forest ecosystems, and management programs have too often ignored the interaction of human activities and altered fire regimes as a force for change in regional landscapes. For example, human perturbations often produce conditions outside the evolutionary and ecological tolerance limits of native species. In our quest as a society to control some types of forest disturbances, such as wildland fire, insects, and

diseases, we have often failed to recognize the vital role these forces play in sustaining ecosystem integrity and biodiversity. In other instances, we have created additional anthropogenic disturbances (e.g., increased sediment production and altered water quality) without adequately recognizing the significance of those activities to landscapes and aquatic systems. Thus, a continuing emphasis on fire suppression and postfire salvage logging on public lands addresses symptoms rather than causes and does not acknowledge the natural dynamics and restoration needs of forest ecosystems.

We reviewed postfire management practices within the context of ecological restoration. Based on this review, we propose guidelines for postfire management aimed at maintaining or restoring the integrity of forested landscapes and their dependent freshwater systems. Only by maintaining crucial ecological processes can we expect to sustain renewable resource systems. Two general themes emerge throughout this paper: (1) native species are adapted to natural patterns and processes of disturbance that produce and maintain diverse ecosystems, and (2) reducing the negative effects of past management practices and avoiding additional impacts of future practices will promote regional recovery of biodiversity. We suggest that understanding these themes is necessary for maintaining viable populations of native species, protecting critical ecosystem functions and services, and meeting stated objectives in laws governing federal land management in the United States (e.g., the Wilderness Act, the Clean Water Act, the Threatened and Endangered Species Act, the National Forest Management Act).

Wildland Fire and Postfire Management in a Landscape Context

Scientific assessments of the current condition of forested systems in the western United States consistently yield the

same broad conclusions: a century or more of road building, logging, grazing, mining, fire suppression, and water withdrawals, in conjunction with the loss of key species and the introduction of exotic species, have degraded watersheds, modified streamflows and water quality, altered ecosystem processes, and decreased biological diversity (e.g., Chamberlin et al. 1991; Furniss et al. 1991; Fleischner 1994; Terborgh et al. 1999; U.S. Department of Agriculture Forest Service 2000). Such conclusions have been documented for a variety of areas and over a wide range of scales (Leopold 1937; Henjum et al. 1994; McIntosh et al. 1994; CWW 1996; Espinosa et al. 1997; Kessler et al. 2001). Past and present actions limit the capacity for ecosystem recovery and reduce the range and abundance of many native species (Williams & Miller 1990; Nehlsen et al. 1991; Quigley & Arbelbide 1997). Thus, forests of the western United States can be viewed as a sea of compromised or degraded ecosystems surrounding a few relatively intact "islands" (Frissell 1993). These intact areas typically retain the full complement of regionally appropriate species and the processes that sustain those species (all the "parts and processes" of healthy regional landscapes; Karr 2000).

Although postfire landscapes are often portrayed as "disasters" in human terms, from an ecological perspective they are the result of vital disturbance processes in forests. The biota of these landscapes is adapted to, and often dependent upon, the occurrence of fires having highly variable frequency (return interval), season of occurrence, size, severity, and ecological effect. Evidence of early fire is present in fossil charcoal deposits of 350–300 million years ago (Komarek 1973); some 100–165 million years later, wildfires were common (Cope & Chaloner 1985). Over time, plants (and other biota) evolved morphological, physiological, and/or reproductive characteristics—long-lived seeds stored in soil, serotinous cones, thick bark—that facilitate and may even be required for species persistence. Furthermore, species that become established early in the postfire environment influence forest dynamics for decades to centuries, through, for example, symbiotic nitrogen fixation, mycorrhizal hosts, pollination and seed dispersal, wildlife habitat, and soil protection (Kauffman 1990; Gresswell 1999).

Restoration Considerations in a Postfire Landscape

Following a wildland fire, a common assumption is that immediate actions are needed to rehabilitate or restore the "fire-damaged" landscape. Yet abundant scientific evidence suggests that commonly applied postfire treatments may compound ecological stresses. For example, soil exposure and the compaction effects of ground-based yarding equipment may substantially increase erosion following postfire salvage logging. Additionally, the removal

of standing and downed large wood may eliminate important structural components for the recovery of terrestrial and aquatic systems (Swanson 1981; Trotter 1990; May & Gresswell 2003).

Perhaps the most critical step in undertaking ecological restoration in the postfire environment is to forgo those activities and land uses that either cause additional damage or prevent reestablishment of native species, ecosystem processes, or plant succession (Ebersole et al. 1996; Kauffman et al. 1997). The avoidance of degradation is far easier and more effective than trying to rehabilitate degraded lands (Hicks et al. 1991; Frissell 1993; Rhodes et al. 1994). Reducing significant human impacts to forest ecosystems often enhances system recovery and taps the natural capacities of species to reproduce and survive within the context of natural disturbance regimes, including wildland fires (Frissell et al. 1997). Thus, a crucial priority of postfire management is enhancing the capacity of burned areas to recover naturally.

While "active restoration" may be required in some postfire situations (Kauffman et al. 1997), such activities should be carefully considered and aimed at complementing natural recovery processes. Beneficial active restoration activities might include reducing sediment production from firelines and roads, replacing faulty drainage structures, and planting native species depleted by fire or previous management activities. A logical, and necessary, first step in assessing postfire management needs includes reducing or eliminating factors that degrade forest ecosystems and prevent recovery. This strategy can sometimes be difficult to implement because it often requires changing land uses in a watershed.

Another flaw in management approaches today is the tendency to use the current, altered status of many watersheds in the western United States as a baseline for assessing restoration strategies in landscapes following wildfire. This ignores the chronic or continuing effects of past management activities and may relegate aquatic systems to a permanently degraded condition.

Promoting Natural Recovery Processes

Fire and other natural disturbances in landscapes where natural biological integrity is relatively intact are not detrimental to the maintenance of diverse and productive aquatic ecosystems (Minshall et al. 1997; Gresswell 1999; Minshall et al. 2001). For example, riparian vegetation is typically quite resilient to fire and rapidly recovers following fire. In landscapes altered by decades of resource extraction or fire suppression, however, the consequences of fire for forest ecosystems may be severe. Furthermore, recovery of stream ecosystems from the effects of fire may be slower, more sporadic, and potentially incomplete in landscapes where natural processes and ecosystem structures have been degraded or impaired. Under these conditions, prefire restoration of ecosystem integrity (i.e., at

the watershed scale and larger) is likely to be more effective than fire prevention or postfire attempts at protection and rehabilitation of the stream channel (Gresswell 1999).

Postfire treatments such as seeding of exotic species, livestock grazing, or salvage logging can alter succession and delay restoration by removing elements of recovery or by accentuating damage to soil and water resources. Instead, management priorities should aim at the prevention or minimization of activities that increase stress upon surviving native biota, disrupt the establishment of early seral native species, or alter microclimates. Postfire treatments should be implemented only when they are needed to facilitate ecosystem recovery and do not interfere with natural succession or to reduce human disruptions of natural ecosystem processes. For example, natural recovery could be augmented by rehabilitation of areas disturbed by fire-suppression activities or other management practices (e.g., dozed firelines, roads). In other instances, planting of conifers may be needed where seed sources of native species have been lost by fire.

Protecting Soils

Fire intensities and patterns of fuel consumption vary across landscapes with weather, topography, and differences in fuel loads and condition; all these factors also influence the effect of fire on soils. With a moderate- to high-severity fire, litter and duff are consumed, and the soil surface experiences high temperatures. Over a 25-year period (1973–1998), burned-area reports for western forests indicate that moderate- and high-severity categories account for about one-half of the total burned area (Robichaud et al. 2000). Burned area varies substantially from decade to decade (Fig. 1).

To protect aquatic ecosystems in areas with moderate- to high-severity burns, postfire management should not increase soil erosion or reduce soil productivity. For example, use of ground-based logging equipment will cause additional site disturbance and soil compaction. Decreased

infiltration, increased overland flow, and accelerated sedimentation following ground-based logging not only degrade forest soils (Kattleman 1996; McIver & Starr 2000, 2001) but can also affect aquatic systems, including reduced survival of salmonids and other aquatic species (Young et al. 1991; Rhodes et al. 1994; Quigley & Arbelbide 1997). Furthermore, onsite impacts to early successional native plant species during postfire logging, where such species are nitrogen fixers, can significantly affect a major pathway of nutrient replenishment in the postfire environment.

After fire, some soils may exhibit a water-repellant (hydrophobic) condition that reduces the infiltration of water (DeBano et al. 1998). Although these changes can significantly alter the hydrologic properties of forest soils, the magnitude of change varies with soil texture and organic-matter content, vegetation, and fire behavior. Water-repellant soils mainly develop on sites that experience moderate- or high-severity burns with coarse-textured soils and certain vegetation, such as waxy-leaved shrublands and woodlands (Wells et al. 1979; DeBano et al. 1998).

Water-repellant soils occur naturally in the absence of fire (Kattleman 1996), and fire does not always cause hydrophobic conditions. Although comprehensive studies on water repellency following fire are uncommon, generally water-repellant conditions are spatially variable and diminish as vegetation and soils recover (Robichaud et al. 2000; Huffman et al. 2001; Letey 2001). If organic matter on the soil surface remains intact following a burn, the occurrence of hydrophobic soils and associated effects on erosion and runoff are greatly reduced.

Some researchers (McIver & Starr 2000) suggest that benefits can be derived from the mechanical disturbance of hydrophobic soils by postfire logging, whereby disruption of hydrophobic soil surfaces increases infiltration and reduces overland flow, peakflow, and sediment production to streams. For several reasons, such an approach would have far more persistent negative effects on soils, watersheds, and aquatic resources than would allowing soils to recover naturally. For example, soil disturbance during ground-based logging that is severe enough to “mix” or break through soil layers would also cause significant compaction, contributing to accelerated surface erosion and long-term reductions in soil productivity. Although cable-logging systems typically cause less compaction than ground-based systems, dragging logs across burned terrain without full suspension can still damage soils. Because salvage logging often occurs a year or more after a fire, and because water-repellant conditions usually last only a few years, at most, water-repellant soils may no longer exist by the time logging occurs, if they ever did. Finally, water-repellant soils can occur in the absence of fire, so the intensity and location of hydrophobic soils is generally not determined in postfire assessments (Robichaud et al. 2000).

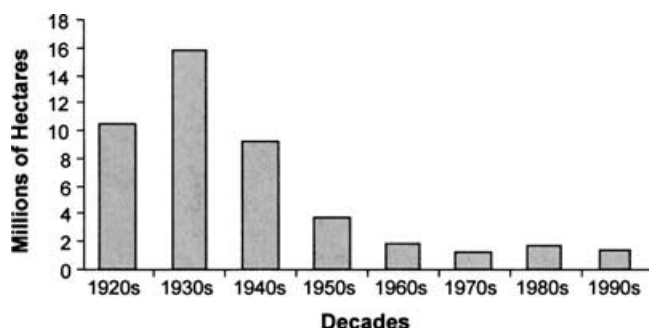


Figure 1. Area burned annually, by decade (1920–2000), for U.S. federal agencies (1994–2001) (U.S. Department of Agriculture Forest Service Annual Fire Statistics).

Evidence continues to mount of a direct relationship between mechanical disturbance to the postfire environment and accelerated erosion (Kattleman 1996; McIver & Starr 2000, 2001). Soil compaction can persist for 50–80 years in many forest soils (Quigley & Arbelbide 1997) and even longer in areas with high clay content, which is substantially longer than the negative influence on soils that may be associated with fire (U.S. Department of Agriculture Forest Service & BLM 1997).

Because soils and soil productivity are irreplaceable in human time scales, postfire management practices that compact soils, reduce soil productivity, or accelerate erosion should not be undertaken or allowed to continue. The recovery of organic matter in soils, which is essential to the recovery of soil productivity in areas with moderate- to high-severity burns, can be accomplished efficiently and inexpensively by leaving burned areas undisturbed (Kattleman 1996; Quigley & Arbelbide 1997). Although postfire treatments are often undertaken in an attempt to reduce soil erosion and impacts to water quality, prefire management practices—prescribed fire, obliteration of problem roads, removal of exotic species, reduced grazing pressure—may have an even larger payoff at both local and landscape scales.

Changing Postfire Practices

Dramatic changes are needed in forest management practices and policies that relate to land use and fire management in the western United States. Management with short- and long-term ecological goals should reduce human impacts to ecosystems and allow natural disturbance regimes to retain or reestablish some of their historical influence in maintaining the diversity and productivity of regional landscapes. Instead of focusing on the immediate effects of a given fire, land managers might more fruitfully direct their attention to historical and on-going land uses and policies, including the loss of natural disturbance regimes (i.e., fire exclusion).

Rehabilitating Sites Disturbed by Fire Suppression

The postfire environment is a reflection of not only the conditions that influence the spread and intensity of fire but also the magnitude of suppression efforts. For some fires, hundreds of kilometers of firelines may be constructed. Whether built by hand or machinery, these firelines involve soil disturbance and the removal of vegetation and litter. This can increase surface runoff, erosion, and sediment delivery to streams and facilitate the invasion of noxious weeds (Kattleman 1996). Firelines constructed by bulldozers are of greatest concern because of their width (up to 15 m) and the severity of soil disturbance and compaction. Firelines in riparian areas contribute to aquatic degradation by reducing recruitment of large wood, bank stability, and stream shading, and they increase sediment delivery to streams. Although hand-

lines are typically narrower and involve less severe impacts than bulldozer lines, negative effects can be substantial, especially in areas that are highly susceptible to erosion.

Fireline locations cause additional ecological concerns. Although this issue has received increased attention in recent years, firelines continue to be constructed in riparian areas and down the fall line of steep slopes when deemed necessary by fire managers. Unfortunately, little can be done to remedy adverse effects if firelines are constructed in areas prone to erosion. Although less significant than firelines at the watershed scale, fire camps can sometimes result in local soil damage. Furthermore, water-drafting sites can damage soils near streams and disrupt channel banks.

As Kattleman (1996) has suggested, the principal objectives of postfire rehabilitation efforts should be to avoid additional damage, repair potential problems from fire-suppression activities (e.g., firelines and fire camps), and enhance the reestablishment of native vegetation to provide soil cover and organic matter. Consequently, highly disturbed sites should be rehabilitated (e.g., through water bars and seeding with native species) immediately following fires. It should be recognized, however, that such treatments may not eliminate persistent effects from areas that are prone to erosion or that have been severely affected.

Banning Introduction of Exotic Species

The rationale for seeding burned areas with non-native grasses includes reducing onsite erosion, decreasing sediment runoff into streams, reducing noxious weed invasions, and increasing the availability of forage for grazing animals (Barro & Conard 1987, Sexton 1998, Robichaud et al. 2000). Although the efficacy of seeding for accomplishing these objectives has not been well evaluated, results of studies show that seeding grasses in burned ecosystems can lead to long-term changes in ecosystem composition and structure (Nadkarni & Odion 1986; Barro & Conard 1987). Comparing seeded burned areas to those that were not burned or seeded, Sexton (1998) found no differences in total herbaceous cover but did quantify a significantly greater cover of exotic grasses and a lower cover of native flora in seeded areas. Furthermore, rates of growth and survival of shrubs and conifer seedlings were reduced in areas seeded following fire (Amaranthus et al. 1993; Sexton 1998). Establishing a dense cover of seeded grasses, which decreases survival of woody plant seedlings, may cause long-term diminution of many important functional roles of species that shape ecosystem structure and productivity, roles including nitrogen accumulation, alternative hosts to mycorrhizal fungi, wildlife habitat, and erosion control.

Established exotic grasses can increase the flammability of burned sites; thus, reburns through these sites can

have severe ecological consequences (Zedler et al. 1983). Furthermore, a dense stand of exotic grasses will increase the likelihood of a reburn because (1) there is a continuous fuel bed with a high surface-to-volume ratio that is conducive to rapid rates of fire spread, (2) annual foliage dies and moisture content is low by late summer, and (3) fine fuels such as dried grasses and grass litter are more susceptible to ignition (Barro & Conard 1987).

Grass seeding has a low probability of reducing postfire erosion in the first season of erosion because any benefits of grass cover occur after the initial damaging runoff events (Barro & Conard 1987; Amaranthus 1989). In reviews of grass seeding and postfire erosion, Barro and Conard (1987), Kattleman (1996), and Raubichaud et al. (2000) could not find a significant relationship between establishment of grass cover and reduction in erosion in the years following wildland fire. Furthermore, they note the potential for grass seeding to exacerbate long-term erosion rates. Even so, seeding remains a widely used postfire rehabilitation activity, considered a panacea by many.

From an ecological perspective, seeding or planting should be avoided unless the prefire landscape has been severely degraded or dominated by alien or nonindigenous species. When species introductions are initiated, only species and seed sources native to the site should be utilized.

Curtailling Livestock Grazing

Livestock grazing, as practiced throughout much of the western United States, significantly damages soils, elevates erosion, thwarts vegetative recovery, contributes to invasions of exotic species, and degrades stream and riparian conditions (Platts 1991; Fleischner 1994; Belsky et al. 1999). Consequently, this land use has been a major contributor to declines in native salmonids across western states (Rhodes et al. 1994; CWW 1996; NRC 1996, 2002). Furthermore, postfire livestock grazing is widely recognized as an inhibitor of soil recovery and plant succession following fire, delaying the recovery of burned areas. Thus, livestock grazing should not occur in burned areas, particularly riparian areas, until vegetation recovery has occurred.

Avoiding Use of Structures in and Near Stream Channels

The installation of structures such as sediment traps, wood additions, bank stabilizations, weirs, check dams, and gabions in and along streams often occurs in conjunction with postfire recovery activities. The cost of these structures, combined with their limited functional utility and short lifetimes, limits their value, especially in streams with elevated sediment and flow (Frissell & Nawa 1992). Instream structures often interfere with important interactions among sediment flux, channel form, and erosion

(Frissell & Nawa 1992; Thompson 2002), thus negatively affecting the maintenance and diversity of aquatic habitats (Schmetterling et al. 2001). Managers should not assume that these structures mitigate the negative effects of other postfire management practices (e.g., road construction, postfire logging) that might accelerate sediment delivery to streams.

Restricting Postfire Logging

In the past, logging of fire-affected forest stands often occurred with little consideration of potential ecological consequences. However, postfire salvage logging inherently involves the removal of large trees that play important roles in numerous biological and physical processes and provide habitat for a variety of species (Thomas 1970; Harmon et al. 1986; Perry et al. 1989; Rose et al. 2001). In Oregon and Washington, for example, at least 96 wildlife species are associated with snags in forests. Most use snags >36 cm diameter at breast height (dbh); about one-third use snags >74 cm dbh. Hollow trees >51 cm dbh are often the most valuable for animal shelter, roosting, and hunting (Rose et al. 2001). Salvage logging may be especially detrimental in those watersheds where only a few large trees or snags remain following fire.

Large wood has multiple roles in the ecological recovery of disturbed aquatic ecosystems. Salvage logging conducted in or near riparian zones or streams diminishes the source of large wood important for stream structure and function (Maser et al. 1988; McMahon & deCalesta 1990; Hauer et al. 1999). Postfire wood inputs are important in creating physical habitat, recycling nutrients, and providing structural components during stream and riparian recovery (Minshall et al. 1989; Lawrence & Minshall 1994; Benda et al. 2003). Damaging effects from postfire logging in riparian areas can persist for many decades because of the loss of dead trees that would normally become incorporated into stream channels and forest floors over several decades or more (Lyon 1984; May & Gresswell 2003). Similarly, logging large trees from upslope areas that are prone to landslides would also reduce, over time, the recruitment of large wood to riparian and aquatic ecosystems.

Based on the need to preserve important ecological functions associated with trees and large wood following fire, Beschta et al. (1995) recommend that salvage logging should leave at least 50% of standing dead trees in each diameter class. They also indicate that proportional retention is needed because of the important graded inputs that a mix of large wood contributes to streams over the extended postfire recovery period (Lyon 1984; Minshall et al. 1989). Furthermore, R.L.B. et al. (unpublished report) recommend no harvest of live trees within burn perimeters or of dead trees >51 cm dbh or older than 150 years. Henjum et al. (1994) similarly recommended retention of trees >51 cm dbh or >150 years

old and cessation of logging in late-successional forests. These recommendations emphasize the importance of retaining the oldest and largest trees, both live and dead, in postfire environments.

Postfire salvage logging has sometimes been justified on the assumption that >50% crown scorch results in tree mortality. However, trees within low- and mid-elevation forests of the western United States possess a suite of adaptations that facilitate fire survival (Kauffman 1990). Stephens and Finney (2000) found that the probability of conifer mortality is low when the percentage of the crown scorch was <60%. For trees ≥ 50 cm dbh, they determined that the probability of mortality of ponderosa pine, incense cedar, and white fir was <40% when crown scorch was as high as 80%. The multiple ecological roles of large trees and their high probability of survival support the need to retain them in burned areas.

Postfire salvage logging, based primarily on economic values, typically removes only the largest trees and, by reducing total fuel loads, can supposedly reduce the severity of a subsequent fire. The principal fuels that carry wildland fire are not large trees, however, but finer fuels such as grasses, shrubs, and tree foliage. With regard to future fires, perhaps a more important concern of postfire logging is its influence on fuel composition, particle-size distribution, and site microclimate (i.e., creating warmer, drier, and windier conditions; Sexton 1998). The harvest of green trees increases fine fuels (activity fuels) even though the mass of large wood has decreased (Brown 1980). If similar shifts in fuel composition (and loads) occur on salvage logged sites, they could increase the potential future fire intensity and rate of spread of these sites over the short term. Few, if any, studies have quantified the effects of salvage logging on fuel loads (McIver & Starr 2000).

Postfire salvage logging also affects plant species composition and forest succession through changes in microclimate and mechanical damage to regenerating plants and soils. Even where salvage logging occurred in winter over approximately 60 cm of snow, logged areas had significantly lower understory biomass, species richness, species diversity, growth, and survival of both tree and shrub species (Stuart et al. 1993; Sexton 1998). Such logging can also have detrimental effects on the microhabitats of organisms associated with recovery (e.g., soil microbes) (Borchers & Perry 1990) and early successional vegetation.

Both ground-based yarding systems (tractors and skidders) and, to a lesser degree, cable systems can cause significant soil disturbance and compaction. Such practices should be prohibited in burned areas whenever they are likely to accelerate onsite erosion. Logging may be suitable where accelerated soil erosion and increased soil compaction are unlikely to occur and where there will be no impairment of hydrologic and soil biological integrity. Helicopter logging and cable yarding systems (particu-

larly those providing partial or full suspension) that use existing roads and landings also may be appropriate in some areas because they produce smaller impacts on surface runoff and sediment production. Salvage logging generally should be prohibited on sensitive sites, however, including riparian areas, moderately or severely burned areas, fragile soils, steep slopes, roadless areas, watersheds where sedimentation is already a problem, where significant impacts to early successional vegetation may occur, and sites where accelerated surface erosion or accelerated mass soil erosion are likely to occur.

Prohibiting New Road Construction

In the western United States, roads represent a persistent cause of watershed degradation (U.S. Department of Agriculture Forest Service 1993, 2000; Henjum et al. 1994) and a major cause of the reduced abundance and range of native salmonids (Quigley & Arbelbide 1997; Kessler et al. 2001). Accelerated short- and long-term sediment production from roads is of particular concern in most watersheds because it exacerbates the effects of severe fires on soils, aquatic habitats, and water quality (CWWR 1996; U.S. Department of Agriculture Forest Service 2000).

Accelerated surface erosion from roads is typically greatest within the first years following construction, although in most situations sediment production remains elevated over the life of a road (Furniss et al. 1991; Ketcheson & Megahan 1996). Thus, even "temporary" roads can have enduring effects on aquatic systems. Similarly, major reconstruction of unused roads can increase erosion for several years and potentially reverse reductions in sediment yields that occurred with disuse (Potyondy et al. 1991). Where roads are unpaved or insufficiently surfaced with erosion-resistant aggregate, sediment production typically increases with increased vehicular usage (Reid & Dunne 1984).

Elevated sedimentation can adversely affect aquatic biota (Young et al. 1991) and inhibit pool development (Quigley & Arbelbide 1997; Buffington et al. 2002). In depositional environments, elevated sedimentation can widen channels (Dose & Roper 1994). Either of these situations—shallower or wider channels—can contribute to increased water-temperature maxima (Bartholow 2000).

It is perhaps widely accepted that "best management practices" (BMPs) can reduce damage to aquatic environments from roads. Time trends in aquatic habitat indicators indicate, however, that BMPs fail to protect salmonid habitats from cumulative degradation by roads and logging (Espinosa et al. 1997). Ziemer and Lisle (1993) note a lack of reliable data showing that BMPs are cumulatively effective in protecting aquatic resources from damage. Although the location, design, construction, and maintenance of roads may have improved over the years, many tens of thousands of kilometers of roads remain on public

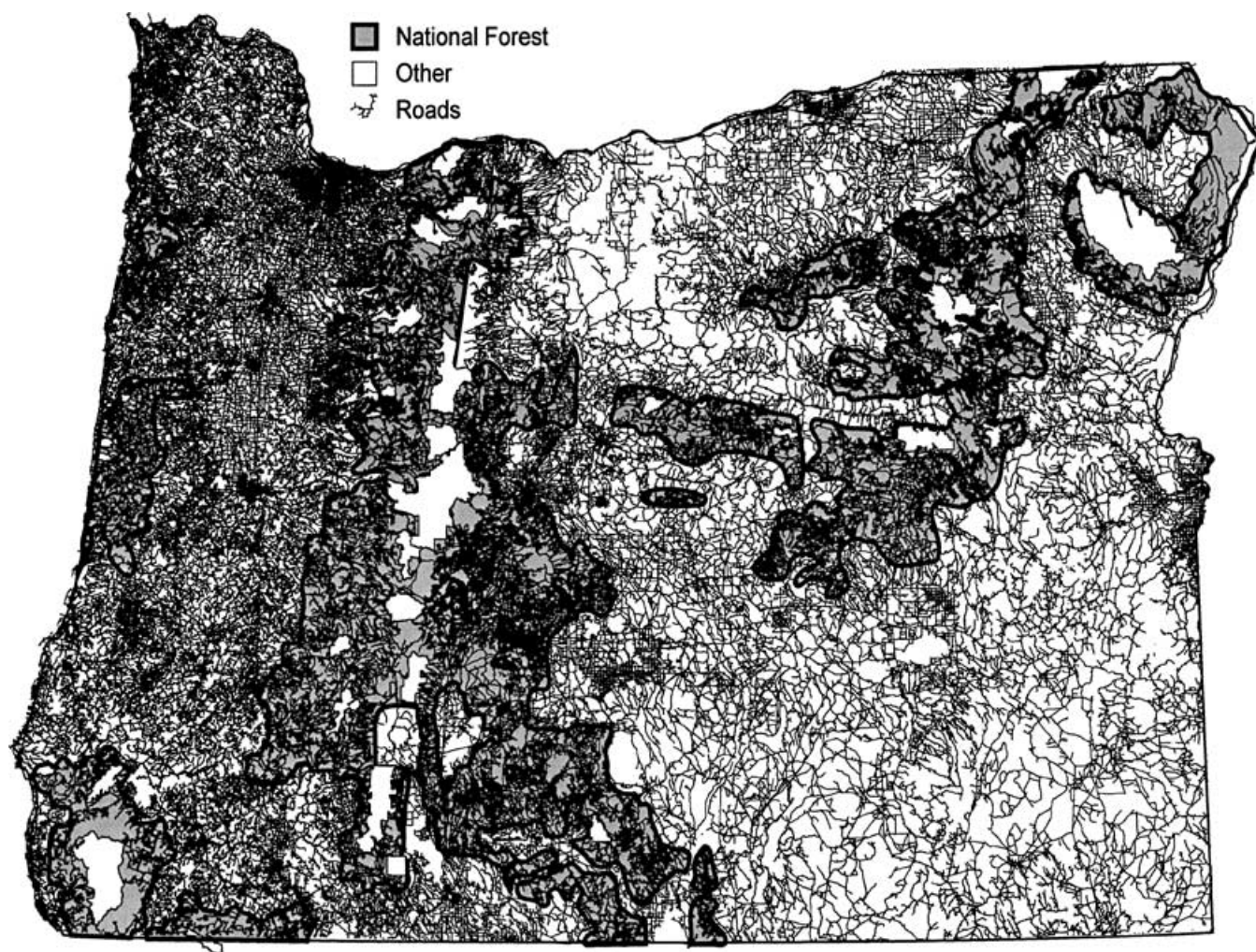


Figure 2. Road densities on public lands managed by the U.S. Department of Agriculture Forest Service and other lands in Oregon (source: Oregon Natural Resources Council, Portland).

and private lands that were constructed with relatively little concern for their environmental consequences (Fig. 2). Until problem “legacy roads” are improved (e.g., surfaced, stabilized, obliterated), they will continue to degrade water quality and aquatic systems for many years. Furthermore, the assumption that road obliteration or BMPs will offset the negative impacts of new road and landing construction and use is unsound because road construction has immediate negative impacts and the benefits of obliteration accrue slowly.

Finally, road and landing construction is expensive and can siphon limited funds away from effective restoration measures, such as obliteration and maintenance. The backlog in maintenance of U.S. Forest Service roads has been estimated to be several billion dollars (U.S. Department of Agriculture Forest Service 2000), and road construction inevitably adds to this seemingly insurmountable backlog. For these reasons, the construction and reconstruction of roads and landings is not consistent with postfire ecosystem restoration.

Research Needs: Social, Ecological, and Economic Issues

In recent years, fire suppression costs for U.S. federal agencies have averaged in excess of \$500 million annually. Given expenditures of this magnitude and the desire by land-management agencies to capture economic benefits from burned areas via salvage logging, the need increases for research to answer a wide range of questions to guide postfire management decisions. Of particular importance is a need to address the consequences—social, ecological, and economic—of various postfire treatments. For example, few studies have rigorously addressed the short- and long-term ecological effects of systematically dispensing nonindigenous species across burned landscapes. Similarly, there is limited scientific literature quantifying changes in sediment yield following postfire salvage logging. A wide range of postfire treatments is often implemented following fire to reduce erosion and runoff, but their effectiveness remains largely unknown

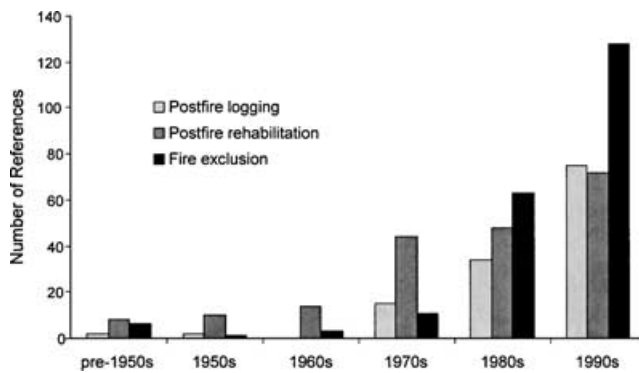


Figure 3. Frequency distribution of publication dates for fire-related publications, by decade, from three literature reviews: postfire logging (McIver & Star 2000), postfire rehabilitation (Robichaud et al. 2000), and fire exclusion (Keane et al. 2002).

(Robichaud et al. 2000), and rigorous research is scarce. Similarly, relatively few large areas have been allowed to recover without major intervention after fire, limiting the availability of “control” areas in ecological research. This is a particularly acute need in low-elevation ponderosa pine forests. Although research productivity on diverse fire and postfire issues (Fig. 3) has increased in recent years, the complexity and controversy surrounding many of these issues indicates the need for carefully focused research programs. We strongly encourage public land-management agencies to significantly invest in interdisciplinary research that directly addresses important issues and concerns associated with wildland fire, postfire salvage logging, and other postfire treatments. Until additional research provides different information, an ecologically based approach to postfire restoration is in order.

Conclusions

Based on our review of the research and from the perspective of ecosystem restoration, several promising approaches to postfire management exist, including full protection of soils, road and fireline restoration, retention of large trees, and nurture of natural recovery processes. Some of these approaches are likely to be even more effective if undertaken proactively before a fire. Conversely, available information indicates that the following postfire activities are not likely to be consistent with ecosystem restoration: seeding non-native species, livestock grazing, installation of instream structures, ground-based logging and soil disruption, removal of large trees, road and landing construction, and logging of ecologically sensitive areas including roadless areas, riparian areas, and areas with moderate to severe burns. Postfire land-use decisions obviously occur in a very challenging environment for the general public and for managers of the nation's public

lands. Although we understand the need and desire for society to obtain products of economic value from forested landscapes, the current body of research indicates that the loss of ecosystem services that can result from post-fire treatments is significant.

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Adapting to Climate Change on Western Public Lands: Addressing the Ecological Effects of Domestic, Wild, and Feral Ungulates

Robert L. Beschta · Debra L. Donahue · Dominick A. DellaSala ·
Jonathan J. Rhodes · James R. Karr · Mary H. O'Brien ·
Thomas L. Fleischner · Cindy Deacon Williams

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Abstract Climate change affects public land ecosystems and services throughout the American West and these effects are projected to intensify. Even if greenhouse gas emissions are reduced, adaptation strategies for public lands are needed to reduce anthropogenic stressors of terrestrial and aquatic ecosystems and to help native species and ecosystems survive in an altered environment. Historical and contemporary livestock production—the most widespread and long-running commercial use of public

lands—can alter vegetation, soils, hydrology, and wildlife species composition and abundances in ways that exacerbate the effects of climate change on these resources. Excess abundance of native ungulates (e.g., deer or elk) and feral horses and burros add to these impacts. Although many of these consequences have been studied for decades, the ongoing and impending effects of ungulates in a changing climate require new management strategies for limiting their threats to the long-term supply of ecosystem services on public lands. Removing or reducing livestock across large areas of public land would alleviate a widely recognized and long-term stressor and make these lands less susceptible to the effects of climate change. Where livestock use continues, or where significant densities of wild or feral ungulates occur, management should carefully document the ecological, social, and economic consequences (both costs and benefits) to better ensure management that minimizes ungulate impacts to plant and animal communities, soils, and water resources. Reestablishing apex predators in large, contiguous areas of public land may help mitigate any adverse ecological effects of wild ungulates.

R. L. Beschta (✉)
Department of Forest Ecosystems and Society, Oregon State
University, Corvallis, OR 97331, USA
e-mail: robert.beschta@oregonstate.edu

D. L. Donahue
College of Law, University of Wyoming, Department 3035,
1000 East University Avenue, Laramie, WY 82071, USA

D. A. DellaSala
Geos Institute, 84 Fourth Street, Ashland, OR 97520, USA

J. J. Rhodes
Planeto Azul Hydrology, P.O. Box 15286, Portland, OR 97293,
USA

J. R. Karr
190 Cascadia Loop, Sequim, WA 98382, USA

M. H. O'Brien
Grand Canyon Trust, HC 64 Box 2604, Castle Valley, UT
84532, USA

T. L. Fleischner
Environmental Studies, Prescott College, 220 Grove Avenue,
Prescott, AZ 86301, USA

C. Deacon Williams
Environmental Consultants, 4393 Pioneer Road, Medford, OR
97501, USA

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Introduction

During the 20th century, the average global surface temperature increased at a rate greater than in any of the previous nine centuries; future increases in the United States (US) are likely to exceed the global average (IPCC 2007a; Karl and others 2009). In the western US, where most public lands are found, climate change is predicted to

intensify even if greenhouse gas emissions are reduced dramatically (IPCC 2007b). Climate-related changes can not only affect public-land ecosystems directly, but may exacerbate the aggregate effects of non-climatic stressors, such as habitat modification and pollution caused by logging, mining, grazing, roads, water diversions, and recreation (Root and others 2003; CEQ 2010; Barnosky and others 2012).

One effective means of ameliorating the effects of climate change on ecosystems is to reduce environmental stressors under management control, such as land and water uses (Julius and others 2008; Heller and Zavaleta 2009; Prato 2011). Public lands in the American West provide important opportunities to implement such a strategy for three reasons: (1) despite a history of degradation, public lands still offer the best available opportunities for ecosystem restoration (CWWR 1996; FS and BLM 1997; Karr 2004); (2) two-thirds of the runoff in the West originates on public lands (Coggins and others 2007); and (3) ecosystem protection and restoration are consistent with laws governing public lands. To be effective, restoration measures should address management practices that prevent public lands from providing the full array of ecosystem services and/or are likely to accentuate the effects of climate change (Hunter and others 2010). Although federal land managers have recently begun considering how to adapt to and mitigate potential climate-related impacts (e.g., GAO 2007; Furniss and others 2009; CEQ 2010; Peterson and others 2011), they have not addressed the combined effects of climate change and ungulates (hooved mammals) on ecosystems.

Climate change and ungulates, singly and in concert, influence ecosystems at the most fundamental levels by affecting soils and hydrologic processes. These effects, in turn, influence many other ecosystem components and processes—nutrient and energy cycles; reproduction, survival, and abundance of terrestrial and aquatic species; and community structure and composition. Moreover, by altering so many factors crucial to ecosystem functioning, the combined effects of a changing climate and ungulate use can affect biodiversity at scales ranging from species to ecosystems (FS 2007) and limit the capability of large areas to supply ecosystem services (Christensen and others 1996; MEA 2005b).

In this paper, we explore the likely ecological consequences of climate change and ungulate use, individually and in combination, on public lands in the American West. Three general categories of large herbivores are considered: livestock (largely cattle [*Bos taurus*] and sheep [*Ovis aries*]), native ungulates (deer [*Odocoileus* spp.] and elk [*Cervus* spp.]), and feral ungulates (horses [*Equus caballus*] and burros [*E. asinus*]). Based on this assessment, we propose first-order recommendations to decrease these

consequences by reducing ungulate effects that can be directly managed.

Climate Change in the Western US

Anticipated changes in atmospheric carbon dioxide (CO₂), temperature, and precipitation (IPCC 2007a) are likely to have major repercussions for upland plant communities in western ecosystems (e.g., Backlund and others 2008), eventually affecting the distribution of major vegetation types. Deserts in the southwestern US, for example, will expand to the north and east, and in elevation (Karl and others 2009). Studies in southeastern Arizona have already attributed dramatic shifts in species composition and plant and animal populations to climate-driven changes (Brown and others 1997). Thus, climate-induced changes are already accelerating the ongoing loss of biodiversity in the American West (Thomas and others 2004).

Future decreases in soil moisture and vegetative cover due to elevated temperatures will reduce soil stability (Karl and others 2009). Wind erosion is likely to increase dramatically in some ecosystems such as the Colorado Plateau (Munson and others 2011) because biological soil crusts—a complex mosaic of algae, lichens, mosses, microfungi, cyanobacteria, and other bacteria—may be less drought tolerant than many desert vascular plant species (Belnap and others 2006). Higher air temperatures may also lead to elevated surface-level concentrations of ozone (Karl and others 2009), which can reduce the capacity of vegetation to grow under elevated CO₂ levels and sequester carbon (Karnosky and others 2003).

Air temperature increases and altered precipitation regimes will affect wildfire behavior and interact with insect outbreaks (Joyce and others 2009). In recent decades, climate change appears to have increased the length of the fire season and the area annually burned in some western forest types (Westerling and others 2006; ITF 2011). Climate induced increases in wildfire occurrence may aggravate the expansion of cheatgrass (*Bromus tectorum*), an exotic annual that has invaded millions of hectares of sagebrush (*Artemisia* spp.) steppe, a widespread yet threatened ecosystem. In turn, elevated wildfire occurrence facilitates the conversion of sagebrush and other native shrub-perennial grass communities to those dominated by alien grasses (D'Antonio and Vitousek 1992; Brooks 2008), resulting in habitat loss for imperiled greater sage-grouse (*Centrocercus urophasianus*) and other sagebrush-dependent species (Welch 2005). The US Fish and Wildlife Service (FWS 2010) recently concluded climate change effects can exacerbate many of the multiple threats to sagebrush habitats, including wildfire, invasive plants, and heavy ungulate use. In addition, the combined effects

of increased air temperatures, more frequent fires, and elevated CO₂ levels apparently provide some invasive species with a competitive advantage (Karl and others 2009).

By the mid-21st century, Bates and others (2008) indicate that warming in western mountains is very likely to cause large decreases in snowpack, earlier snowmelt, more winter rain events, increased peak winter flows and flooding, and reduced summer flows. Annual runoff is predicted to decrease by 10–30 % in mid-latitude western North America by 2050 (Milly and others 2005) and up to 40 % in Arizona (Milly and others 2008; ITF 2011). Drought periods are expected to become more frequent and longer throughout the West (Bates and others 2008). Summertime decreases in streamflow (Luce and Holden 2009) and increased water temperatures already have been documented for some western rivers (Kaushal and others 2010; Isaak and others 2012).

Snowmelt supplies about 60–80 % of the water in major western river basins (the Columbia, Missouri, and Colorado Rivers) and is the primary water supply for about 70 million people (Pederson and others 2011). Contemporary and future declines in snow accumulations and runoff (Mote and others 2005; Pederson and others 2011) are an important concern because current water supplies, particularly during low-flow periods, are already inadequate to satisfy demands over much of the western US (Piechota and others 2004; Bates and others 2008).

High water temperatures, acknowledged as one of the most prevalent water quality problems in the West, will likely be further elevated and may render one-third of the current coldwater fish habitat in the Pacific Northwest unsuitable by this century's end (Karl and others 2009). Resulting impacts on salmonids include increases in virulence of disease, loss of suitable habitat, and mortality as well as increased competition and predation by warmwater species (EPA 1999). Increased water temperatures and changes in snowmelt timing can also affect amphibians adversely (Field and others 2007). In sum, climate change will have increasingly significant effects on public-land terrestrial and aquatic ecosystems, including plant and animal communities, soils, hydrologic processes, and water quality.

Ungulate Effects and Climate Change Synergies

Climate change in the western US is expected to amplify “combinations of biotic and abiotic stresses that compromise the vigor of ecosystems—leading to increased extent and severity of disturbances” (Joyce and others 2008, p. 16). Of the various land management stressors affecting western public lands, ungulate use is the most widespread

(Fig. 1). Domestic livestock annually utilize over 70 % of lands managed by the Bureau of Land Management (BLM) and US Forest Service (FS). Many public lands are also used by wild ungulates and/or feral horses and burros, which are at high densities in some areas. Because ungulate groups can have different effects, we discuss them individually.

Livestock

History and Current Status

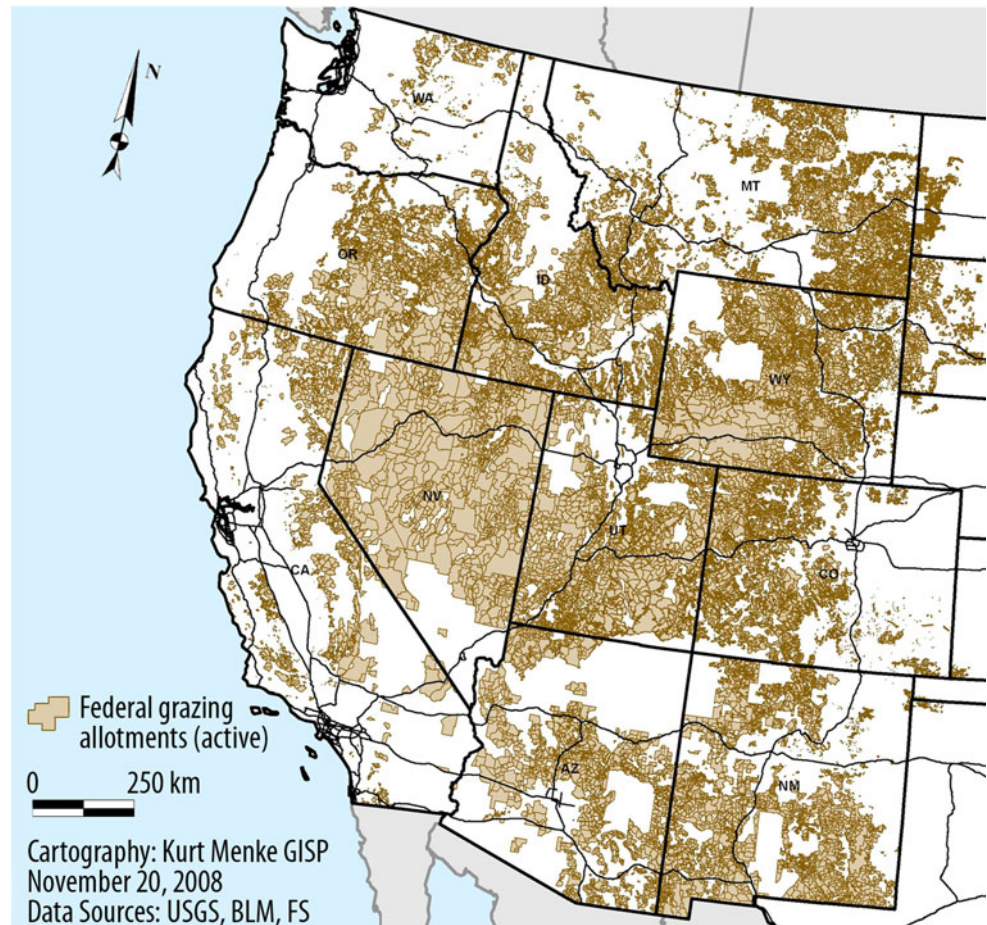
Livestock were introduced to North America in the mid-sixteenth century, with a massive influx from the mid-1800s through early 1900s (Worster 1992). The deleterious effects of livestock—including herbivory of both herbaceous and woody plants and trampling of vegetation, soils, and streambanks—prompted federal regulation of grazing on western national forests beginning in the 1890s (Fleischner 2010). Later, the 1934 Taylor Grazing Act was enacted “to stop injury to the public grazing lands by preventing overgrazing and soil deterioration” on lands subsequently administered by the BLM.

Total livestock use of federal lands in eleven contiguous western states today is nearly 9 million animal unit months (AUMs, where one AUM represents forage use by a cow and calf pair, one horse, or five sheep for one month) (Fig. 2a). Permitted livestock use occurs on nearly one million square kilometers of public land annually, including 560,000 km² managed by the BLM, 370,000 km² by the FS, 6,000 km² by the National Park Service (NPS), and 3,000 km² by the US Fish and Wildlife Service (FWS).

Livestock use affects a far greater proportion of BLM and FS lands than do roads, timber harvest, and wildfires combined (Fig. 3). Yet attempts to mitigate the pervasive effects of livestock have been minor compared with those aimed at reducing threats to ecosystem diversity and productivity that these other land uses pose. For example, much effort is often directed at preventing and controlling wildfires since they can cause significant property damage and social impacts. On an annual basis, however, wildfires affect a much smaller portion of public land than livestock grazing (Fig. 3) and they can also result in ecosystem benefits (Rhodes and Baker 2008; Swanson and others 2011).

The site-specific impacts of livestock use vary as a function of many factors (e.g., livestock species and density, periods of rest or non-use, local plant communities, soil conditions). Nevertheless, extensive reviews of published research generally indicate that livestock have had numerous and widespread negative effects to western ecosystems (Love 1959; Blackburn 1984; Fleischner 1994; Belsky and others 1999; Kauffman and Pyke 2001; Asner

Fig. 1 Areas of public-lands livestock grazing managed by federal agencies in the western US (adapted from Salvo 2009)



and others 2004; Steinfeld and others 2006; Thornton and Herrero 2010). Moreover, public-land range conditions have generally worsened in recent decades (CWWR 1996, Donahue 2007), perhaps due to the reduced productivity of these lands caused by past grazing in conjunction with a changing climate (FWS 2010, p. 13,941, citing Knick and Hanser 2011).

Plant and Animal Communities

Livestock use effects, exacerbated by climate change, often have severe impacts on upland plant communities. For example, many former grasslands in the Southwest are now dominated by one or a few woody shrub species, such as creosote bush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*), with little herbaceous cover (Grover and Musick 1990; Asner and others 2004; but see Allington and Valone 2010). Other areas severely affected include the northern Great Basin and interior Columbia River Basin (Middleton and Thomas 1997). Livestock effects have also contributed to severe degradation of sagebrush-grass ecosystems (Connelly and others 2004; FWS 2010) and widespread desertification, particularly in the Southwest (Asner and others 2004; Karl and others

2009). Even absent desertification, light to moderate grazing intensities can promote woody species encroachment in semiarid and mesic environments (Asner and others 2004, p. 287). Nearly two decades ago, many public-land ecosystems, including native shrub steppe in Oregon and Washington, sagebrush steppe in the Intermountain West, and riparian plant communities, were considered threatened, endangered, or critically endangered (Noss and others 1995).

Simplified plant communities combine with loss of vegetation mosaics across landscapes to affect pollinators, birds, small mammals, amphibians, wild ungulates, and other native wildlife (Bock and others 1993; Fleischner 1994; Saab and others 1995; Ohmart 1996). Ohmart and Anderson (1986) suggested that livestock grazing may be the major factor negatively affecting wildlife in eleven western states. Such effects will compound the problems of adaptation of these ecosystems to the dynamics of climate change (Joyce and others 2008, 2009). Currently, the widespread and ongoing declines of many North American bird populations that use grassland and grass-shrub habitats affected by grazing are “on track to become a prominent wildlife conservation crisis of the 21st century” (Brennan and Kuvlesky 2005, p. 1).

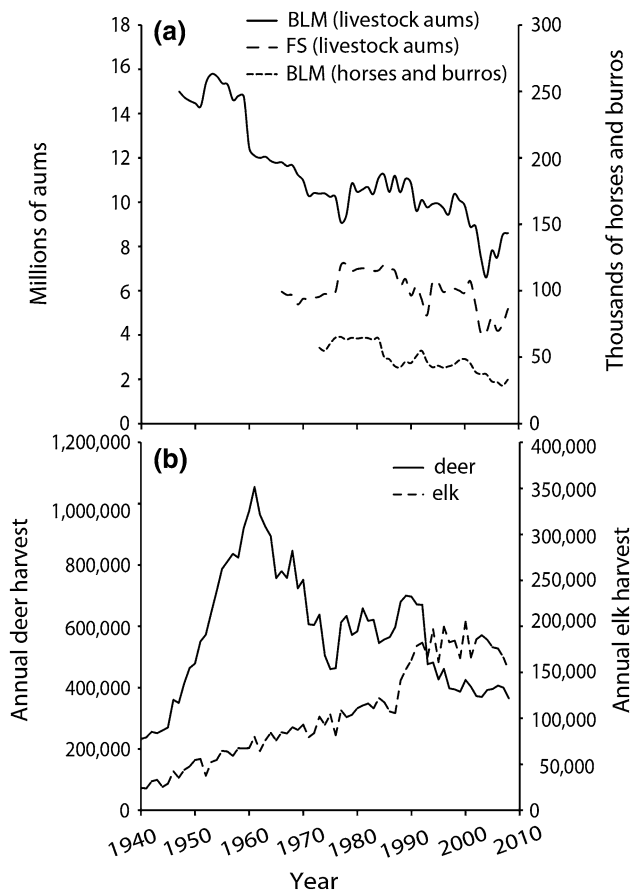


Fig. 2 **a** Bureau of Land Management (BLM) and US Forest Service (FS) grazing use in animal unit months (AUMs) and number of feral horses and burros on BLM lands, and **b** annual harvest of deer and elk by hunters, for eleven western states. *Data sources* **a** BLM grazing and number of horses and burros reported annually in Public Land Statistics; FS grazing reported annually in Grazing Statistical Summary; **b** deer and elk harvest records from individual state wildlife management agencies

Soils and Biological Soil Crusts

Livestock grazing and trampling can damage or eliminate biological soil crusts characteristic of many arid and semiarid regions (Belnap and Lange 2003; Asner and others 2004). These complex crusts are important for fertility, soil stability, and hydrology (Belnap and Lange 2003). In arid and semiarid regions they provide the major barrier against wind erosion and dust emission (Munson and others 2011). Currently, the majority of dust emissions in North America originate in the Great Basin, Colorado Plateau, and Mojave and Sonoran Deserts, areas that are predominantly public lands and have been grazed for nearly 150 years. Elevated sedimentation in western alpine lakes over this period has also been linked to increased aeolian deposition stemming from land uses, particularly those associated with livestock grazing (Neff and others 2008).

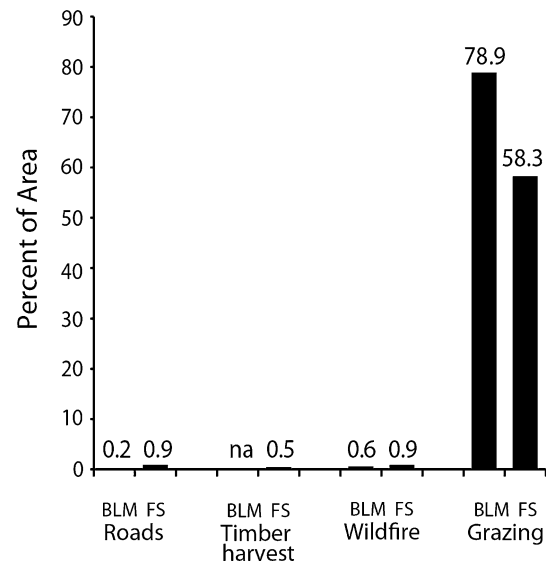


Fig. 3 Percent of Bureau of Land Management (BLM) and US Forest Service (FS) lands in eleven western states that are occupied by roads or are affected annually by timber harvest, wildfire, and grazing. *Data sources* Roads, BLM (2009) and FS, Washington Office; Timber harvest (2003–09), FS, Washington Office; Wildfire (2003–09), National Interagency Fire Center, Missoula, Montana; Grazing, BLM (2009) and GAO (2005). “na” = not available

If livestock use on public lands continues at current levels, its interaction with anticipated changes in climate will likely worsen soil erosion, dust generation, and stream pollution. Soils whose moisture retention capacity has been reduced will undergo further drying by warming temperatures and/or drought and become even more susceptible to wind erosion (Sankey and others 2009). Increased aeolian deposition on snowpack will hasten runoff, accentuating climate-induced hydrological changes on many public lands (Neff and others 2008). Warmer temperatures will likely trigger increased fire occurrence, causing further reductions in cover and composition of biological soil crusts (Belnap and others 2006), as well as vascular plants (Munson and others 2011). In some forest types, where livestock grazing has contributed to altered fire regimes and forest structure (Belsky and Blumenthal 1997; Fleischner 2010), climate change will likely worsen these effects.

Water and Riparian Resources

Although riparian areas occupy only 1–2 % of the West’s diverse landscapes, they are highly productive and ecologically valuable due to the vital terrestrial habitats they provide and their importance to aquatic ecosystems (Kauffman and others 2001; NRC 2002; Fleischner 2010). Healthy riparian plant communities provide important corridors for the movement of plant and animal species

(Peterson and others 2011). Such communities are also crucial for maintaining water quality, food webs, and channel morphology vital to high-quality habitats for fish and other aquatic organisms in the face of climate change. For example, well-vegetated streambanks not only shade streams but also help to maintain relatively narrow and stable channels, attributes essential for preventing increased stream temperatures that negatively affect salmonids and other aquatic organisms (Sedell and Beschta 1991; Kondolf and others 1996; Beschta 1997); maintaining cool stream temperatures is becoming even more important with climate change (Isaak and others 2012). Riparian vegetation is also crucial for providing seasonal fluxes of organic matter and invertebrates to streams (Baxter and others 2005). Nevertheless, in 1994 the BLM and FS reported that western riparian areas were in their worst condition in history, and livestock use—typically concentrated in these areas—was the chief cause (BLM and FS 1994).

Livestock grazing has numerous consequences for hydrologic processes and water resources. Livestock can have profound effects on soils, including their productivity, infiltration, and water storage, and these properties drive many other ecosystem changes. Soil compaction from livestock has been identified as an extensive problem on public lands (CWWR 1996; FS and BLM 1997). Such compaction is inevitable because the hoof of a 450-kg cow exerts more than five times the pressure of heavy earth-moving machinery (Cowley 2002). Soil compaction significantly reduces infiltration rates and the ability of soils to store water, both of which affect runoff processes (Branson and others 1981; Blackburn 1984). Compaction of wet meadow soils by livestock can significantly decrease soil water storage (Kauffman and others 2004), thus contributing to reduced summer base flows. Concomitantly, decreases in infiltration and soil water storage of compacted soils during periods of high-intensity rainfall contribute to increased surface runoff and soil erosion (Branson and others 1981). These fundamental alterations in hydrologic processes from livestock use are likely to be exacerbated by climate change.

The combined effects of elevated soil loss and compaction caused by grazing reduce soil productivity, further compromising the capability of grazed areas to support native plant communities (CWWR 1996; FS and BLM 1997). Erosion triggered by livestock use continues to represent a major source of sediment, nutrients, and pathogens in western streams (WSWC 1989; EPA 2009). Conversely, the absence of grazing results in increased litter accumulation, which can reduce runoff and erosion and retard desertification (Asner and others 2004).

Historical and contemporary effects of livestock grazing and trampling along stream channels can destabilize

streambanks, thus contributing to widened and/or incised channels (NRC 2002). Accelerated streambank erosion and channel incision are pervasive on western public lands used by livestock (Fig. 4). Stream incision contributes to desiccation of floodplains and wet meadows, loss of flood-water detention storage, and reductions in baseflow (Ponce and Lindquist 1990; Trimble and Mendel 1995). Grazing and trampling of riparian plant communities also contribute to elevated water temperatures—directly, by reducing stream shading and, indirectly, by damaging streambanks and increasing channel widths (NRC 2002). Livestock use of riparian plant communities can also decrease the availability of food and construction materials for keystone species such as beaver (*Castor canadensis*).

Livestock effects and climate change can interact in various ways with often negative consequences for aquatic species and their habitats. In the eleven ecoregions encompassing western public lands (excluding coastal regions and Alaska), about 175 taxa of freshwater fish are considered imperiled (threatened, endangered, vulnerable, possibly extinct, or extinct) due to habitat-related causes (Jelks and others 2008, p. 377; GS and AFS 2011). Increased sedimentation and warmer stream temperatures associated with livestock grazing have contributed significantly to the long-term decline in abundance and distribution and loss of native salmonids, which are imperiled throughout the West (Rhodes and others 1994; Jelks and others 2008).

Water developments and diversions for livestock are common on public lands (Connelly and others 2004). For example, approximately 3,700 km of pipeline and 2,300 water developments were installed on just 17 % of the BLM's land base from 1961 to 1999 in support of livestock operations (Rich and others 2005). Such developments can reduce streamflows thus contributing to warmer stream temperatures and reduced fish habitat, both serious problems for native coldwater fish (Platts 1991; Richter and others 1997). Reduced flows and higher temperatures are also risk factors for many terrestrial and aquatic vertebrates (Wilcove and others 1998). Water developments can also create mosquito (e.g., *Culex tarsalis*) breeding habitat, potentially facilitating the spread of West Nile virus, which poses a significant threat to sage grouse (FWS 2010). Such developments also tend to concentrate livestock and other ungulate use, thus locally intensifying grazing and trampling impacts.

Greenhouse Gas Emissions and Energy Balances

Livestock production impacts energy and carbon cycles and globally contributes an estimated 18 % to the total anthropogenic greenhouse gas (GHG) emissions (Steinfeld and others 2006). How public-land livestock contribute to



Fig. 4 Examples of long-term grazing impacts from livestock, unless otherwise noted: **a** bare soil, loss of understory vegetation, and lack of aspen recruitment (i.e., growth of seedlings/sprouts into tall saplings and trees) (Bureau of Land Management, Idaho), **b** bare soil, lack of ground cover, lack of aspen recruitment and channel incision (US Forest Service, Idaho), **c** conversion of a perennial stream to an intermittent stream due to grazing of riparian vegetation and subsequent channel incision; channel continues to erode during runoff events (Bureau of Land Management, Utah), **d** incised and

widening stream due to loss of streamside vegetation and bank collapse from trampling (Bureau of Land Management, Wyoming), **e** incised and widening stream due to loss of streamside vegetation and bank collapse from trampling (US Forest Service, Oregon), and **f** actively eroding streambank from the loss of streamside vegetation due to several decades of excessive herbivory by elk and, more recently, bison (National Park Service, Wyoming). Photographs **a** J Carter, **b** G Wuerthner, **c** and **d** J Carter, **e** and **f** R Beschta

these effects has received little study. Nevertheless, livestock grazing and trampling can reduce the capacity of rangeland vegetation and soils to sequester carbon and contribute to the loss of above- and below-ground carbon pools (e.g., Lal 2001b; Bowker and others 2012).

Lal (2001a) indicated that heavy grazing over the long-term may have adverse impacts on soil organic carbon content, especially for soils of low inherent fertility. Although Gill (2007) found that grazing over 100 years or longer in subalpine areas on the Wasatch Plateau in central

Utah had no significant impacts on total soil carbon, results of the study suggest that “if temperatures warm and summer precipitation increases as is anticipated, [soils in grazed areas] may become net sources of CO₂ to the atmosphere” (Gill 2007, p. 88). Furthermore, limited soil aeration in soils compacted by livestock can stimulate production of methane, and emissions of nitrous oxide under shrub canopies may be twice the levels in nearby grasslands (Asner and others 2004). Both of these are potent GHGs.

Reduced plant and litter cover from livestock use can increase the albedo (reflectance) of land surfaces, thereby altering radiation energy balances (Balling and others 1998). In addition, widespread airborne dust generated by livestock is likely to increase with the drying effects of climate change. Air-borne dust influences atmospheric radiation balances as well as accelerating melt rates when deposited on seasonal snowpacks and glaciers (Neff and others 2008).

Other Livestock Effects

Livestock urine and feces add nitrogen to soils, which may favor nonnative species (BLM 2005), and can lead to loss of both organic and inorganic nitrogen in increased runoff (Asner and others 2004). Organic nitrogen is also lost via increased trace-gas flux and vegetation removal by grazers (Asner and others 2004). Reduced soil nitrogen is problematic in western landscapes because nitrogen is an important limiting nutrient in most arid-land soils (Fleischner 2010).

Managing livestock on public lands also involves extensive fence systems. Between 1962 and 1997, over 51,000 km of fence were constructed on BLM lands with resident sage-grouse populations (FWS 2010). Such fences can significantly impact this wildlife species. For example, 146 sage-grouse died in less than three years from collisions with fences along a 7.6-km BLM range fence in Wyoming (FWS 2010). Fences can also restrict the movements of wild ungulates and increase the risk of injury and death by entanglement or impalement (Harrington and Conover 2006; FWS 2010). Fences and roads for livestock access can fragment and isolate segments of natural ecological mosaics thus influencing the capability of wildlife to adapt to a changing climate.

Some have posited that managed cattle grazing might play a role in maintaining ecosystem structure in shortgrass steppe ecosystems of the US, if it can mimic grazing by native bison (*Bison bison*) (Milchunas and others 1998). But most public lands lie to the west of the Great Plains, where bison distribution and effects were limited or nonexistent; livestock use (particularly cattle) on these lands exert disturbances without evolutionary parallel (Milchunas and Lauenroth 1993; MEA 2005a).

Feral Horses and Burros

Feral horses and burros occupy large areas of public land in the western US. For example, feral horses are found in ten western states and feral burros occur in five of these states, largely in the Mojave and Sonoran Deserts and the Great Basin (Abella 2008; FWS 2010). About half of these horses and burros are in Nevada (Coggins and others 2007), of which 90 % are on BLM lands. Horse numbers peaked at perhaps two million in the early 1900s, but had plummeted to about 17,000 by 1971, when protective legislation (Wild, Free-Ranging Horses and Burros Act [WFRHBA]) was passed (Coggins and others 2007). Protection resulted in increased populations and today some 40,000 feral horses and burros utilize ~ 130,000 km² of BLM and FS lands (DOI-OIG 2010; Gorte and others 2010). Currently, feral horse numbers are doubling every four years (DOI-OIG 2010); burro populations can also increase rapidly (Abella 2008). Unlike wild ungulates, feral equines cannot be hunted and, unlike livestock, they are not regulated by permit. Nor are their numbers controlled effectively by existing predators. Accordingly, the BLM periodically removes animals from herd areas; the NPS also has undertaken burro control efforts (Abella 2008).

In sage grouse habitat, high numbers of feral horses reduce vegetative cover and plant diversity, fragment shrub canopies, alter soil characteristics, and increase the abundance of invasive species, thus reducing the quality and quantity of habitat (Beever and others 2003; FWS 2010). Horses can crop plants close to the ground, impeding the recovery of affected vegetation. Feral burros also have had a substantial impact on Sonoran Desert vegetation, reducing the density and canopy cover of nearly all species (Hanley and Brady 1977). Although burro impacts in the Mojave Desert may not be as clear, perennial grasses and other preferred forage species likely require protection from grazing in burro-inhabited areas if revegetation efforts are to be successful (Abella 2008).

Wild Ungulates

Extensive harvesting of wild (native) ungulates, such as elk and deer, and the decimation of large predator populations (e.g., gray wolf [*Canis lupus*], grizzly bear [*Ursus arctos*], and cougar [*Puma concolor*]) was common during early EuroAmerican settlement of the western US. With continued predator control in the early 1900s and increased protection of game species by state agencies, however, wild ungulate populations began to increase in many areas. Although only 70,000 elk inhabited the western US in the early 1900s (Graves and Nelson 1919), annual harvest data indicate that elk abundance has increased greatly since the about the 1940s (Fig. 2b), due in part to the loss of apex

predators (Allen 1974; Mackie and others 1998). Today, approximately one million elk (Karnopp 2008) and unknown numbers of deer inhabit the western US where they often share public lands with livestock.

Because wild ungulates typically occur more diffusely across a landscape than livestock, their presence might be expected to cause minimal long-term impacts to vegetation. Where wild ungulates are concentrated, however, their browsing can have substantial impacts. For example, sagebrush vigor can be reduced resulting in decreased cover or mortality (FWS 2010). Heavy browsing effects have also been documented on other palatable woody shrubs, as well as deciduous trees such as aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), and maple (*Acer* sp.) (Beschta and Ripple 2009).

Predator control practices that intensified following the introduction of domestic livestock in the western US resulted in the extirpation of apex predators or reduced their numbers below ecologically effective densities (Soulé and others 2003, 2005), causing important cascading effects in western ecosystems (Beschta and Ripple 2009). Following removal of large predators on the Kaibab Plateau in the early 20th century, for example, an irruption of mule deer (*O. hemionus*) led to extensive over-browsing of aspen, other deciduous woody plants, and conifers; deterioration of range conditions; and the eventual crash of the deer population (Binkley and others 2006). In the absence of apex predators, wild ungulate populations can significantly limit recruitment of woody browse species, contribute to shifts in abundance and distribution of many wildlife species (Berger and others 2001; Weisberg and Coughenour 2003), and can alter streambanks and riparian communities that strongly influence channel morphology and aquatic conditions (Beschta and Ripple 2012). Numerous studies support the conclusion that disruptions of trophic cascades due to the decline of apex predators constitute a threat to biodiversity for which the best management solution is likely the restoration of effective predation regimes (Estes and others 2011).

Ungulate Herbivory and Disturbance Regimes

Across the western US, ecosystems evolved with and were sustained by local and regional disturbances, such as fluctuating weather patterns, fire, disease, insect infestation, herbivory by wild ungulates and other organisms, and hunting by apex predators. Chronic disturbances with relatively transient effects, such as frequent, low-severity fires and seasonal moisture regime fluctuations, helped maintain native plant community composition and structure. Relatively abrupt, or acute, natural disturbances, such as insect outbreaks or severe fires were also important for the

maintenance of ecosystems and native species diversity (Beschta and others 2004; Swanson and others 2011). Livestock use and/or an overabundance of feral or wild ungulates can, however, greatly alter ecosystem response to disturbance and can degrade affected systems. For example, high levels of herbivory over a period of years, by either domestic or wild ungulates, can effectively prevent aspen sprouts from growing into tall saplings or trees as well as reduce the diversity of understory species (Shepherd and others 2001; Dwire and others 2007; Beschta and Ripple 2009).

Natural floods provide another illustration of how ungulates can alter the ecological role of disturbances. High flows are normally important for maintaining riparian plant communities through the deposition of nutrients, organic matter, and sediment on streambanks and floodplains, and for enhancing habitat diversity of aquatic and riparian ecosystems (CWWR 1996). Ungulate effects on the structure and composition of riparian plant communities (e.g., Platts 1991; Chadde and Kay 1996), however, can drastically alter the outcome of these hydrologic disturbances by diminishing streambank stability and severing linkages between high flows and the maintenance of streamside plant communities. As a result, accelerated erosion of streambanks and floodplains, channel incision, and the occurrence of high instream sediment loads may become increasingly common during periods of high flows (Trimble and Mendel 1995). Similar effects have been found in systems where large predators have been displaced or extirpated (Beschta and Ripple 2012). In general, high levels of ungulate use can essentially uncouple typical ecosystem responses to chronic or acute disturbances, thus greatly limiting the capacity of these systems to provide a full array of ecosystem services during a changing climate.

The combined effects of ungulates (domestic, wild, and feral) and a changing climate present a pervasive set of stressors on public lands, which are significantly different from those encountered during the evolutionary history of the region's native species. The intersection of these stressors is setting the stage for fundamental and unprecedented changes to forest, arid, and semi-arid landscapes in the western US (Table 1) and increasing the likelihood of alternative states. Thus, public-land management needs to focus on restoring and maintaining structure, function, and integrity of ecosystems to improve their resilience to climate change (Rieman and Isaak 2010).

Federal Law and Policy

Federal laws guide the use and management of public-land resources. Some laws are specific to a given agency (e.g., the BLM's Taylor Grazing Act of 1934 and the FS's

Table 1 Generalized climate change effects, heavy ungulate use effects, and their combined effects as stressors to terrestrial and aquatic ecosystems in the western United States

Climate change effects	Ungulate use effects	Combined effects
Increased drought frequency and duration	Altered upland plant and animal communities	Reduced habitat and food-web support; loss of mesic and hydric plants, reduced biodiversity
Increased air temperatures, decreased snowpack accumulation, earlier snowmelt	Compacted soils, decreased infiltration, increased surface runoff	Reduced soil moisture for plants, reduced productivity, reductions in summer low flows, degraded aquatic habitat
Increased variability in timing and magnitude of precipitation events	Decreased biotic crusts and litter cover, increased surface erosion	Accelerated soil and nutrient loss, increased sedimentation
Warmer and drier in the summer	Reduced riparian vegetation, loss of shade, increased stream width	Increased stream temperatures, increased stress on cold-water fish and aquatic organisms
Increased variability in runoff	Reduced root strength of riparian plants, trampled streambanks, streambank erosion	Accelerated streambank erosion and increased sedimentation, degraded water quality and aquatic habitats
Increased variability in runoff	Incised stream channels	Degraded aquatic habitats, hydrologically disconnected floodplains, reduced low flows

National Forest Management Act [NFMA] of 1976), whereas others cross agency boundaries (e.g., Endangered Species Act [ESA] of 1973; Clean Water Act [CWA] of 1972). A common mission of federal land management agencies is “to sustain the health, diversity, and productivity of public lands” (GAO 2007, p. 12). Further, each of these agencies has ample authority and responsibility to adjust management to respond to climate change (GAO 2007) and other stressors.

The FS and BLM are directed to maintain and improve the condition of the public rangelands so that they become as productive as feasible for all rangeland values. As defined, “range condition” encompasses factors such as soil quality, forage values, wildlife habitat, watershed and plant communities, and the present state of vegetation of a range site in relation to the potential plant community for that site (Public Rangelands Improvement Act of 1978). BLM lands and national forests must be managed for sustained yield of a wide array of multiple uses, values, and ecosystem services, including wildlife and fish, watershed, recreation, timber, and range. Relevant statutes call for management that meets societal needs, without impairing the productivity of the land or the quality of the environment, and which considers the “relative values” of the various resources, not necessarily the combination of uses that will give the greatest economic return or the greatest unit output (Multiple-Use Sustained-Yield Act of 1960; Federal Land Policy and Management Act of 1976 [FLPMA]).

FLPMA directs the BLM to “take any action necessary to prevent unnecessary or undue degradation” of the public lands. Under NFMA, FS management must provide for diversity of plant and animal communities based on the suitability and capability of the specific land area. FLPMA also authorizes both agencies to “cancel, suspend, or

modify” grazing permits and to determine that “grazing uses should be discontinued (either temporarily or permanently) on certain lands.” FLPMA explicitly recognizes the BLM’s authority (with congressional oversight) to “totally eliminate” grazing from large areas (> 405 km²) of public lands. These authorities are reinforced by law providing that grazing permits are not property rights (*Public Lands Council v. Babbitt* 2000).

While federal agencies have primary authority to manage federal public lands and thus wildlife *habitats* on these lands, states retain primary management authority over resident *wildlife*, unless preempted, as by the WFRHBA or ESA (*Kleppe v. New Mexico* 1976). Under WFRHBA, wild, free-roaming horses and burros (i.e., feral) by law have been declared “wildlife” and an integral part of the natural system of the public lands where they are to be managed in a manner that is designed to achieve and maintain a thriving natural ecological balance.

Restoring Ungulate-Altered Ecosystems

Because livestock use is so widespread on public lands in the American West, management actions directed at ecological restoration (e.g., livestock removal, substantial reductions in numbers or length of season, extended or regular periods of rest) need to be accomplished at landscape scales. Such approaches, often referred to as passive restoration, are generally the most ecologically effective and economically efficient for recovering altered ecosystems because they address the root causes of degradation and allow natural recovery processes to operate (Kauffman and others 1997; Rieman and Isaak 2010). Furthermore, reducing the impact of current stressors is a “no regrets” adaptation strategy that could be taken now to help enhance



Fig. 5 Examples of riparian and stream recovery in the western United States after the removal of livestock grazing: Hart Mountain National Antelope Refuge, Oregon, in **a** October 1989 and **b** September 2010 after 18 years of livestock removal; Strawberry River, Utah, in **c** August 2002 after 13 years of livestock removal and **d** July 2003 illustrating improved streambank protection and riparian productivity as beaver reoccupy this river system; and San Pedro River, Arizona in **e** June 1987 and **f** June 1991 after 4 years of livestock removal. Photographs **a** Fish and Wildlife Service, Hart Mountain National Antelope Refuge, **b** J Rhodes, **c** and **d** US Forest Service, Uintah National Forest, **e** and **f** Bureau of Land Management, San Pedro Riparian National Conservation Area

ecosystem resilience to climate change (Joyce and others 2008). This strategy is especially relevant to western ecosystems because removing or significantly reducing the cause of degradation (e.g., excessive ungulate use) is likely to be considerably more effective over the long term, in both costs and approach, than active treatments aimed at specific ecosystem components (e.g., controlling invasive plants) (BLM 2005). Furthermore, the possibility that passive restoration measures may not accomplish all ecological goals is an insufficient reason for *not* removing or reducing stressors at landscape scales.

For many areas of the American West, particularly riparian areas and other areas of high biodiversity, significantly reducing or eliminating ungulate stressors should, over time, result in the recovery of self-sustaining and ecologically robust ecosystems (Kauffman and others 1997; Floyd and others 2003; Allington and Valone 2010; Fig. 5). Indeed, various studies and reviews have concluded that the most effective way to restore riparian areas and aquatic systems is to exclude livestock either temporarily (with subsequent changed management) or long-term (e.g., Platts 1991; BLM and FS 1994; Dobkin and others

1998; NRC 2002; Seavy and others 2009; Fleischner 2010). Recovering channel form and riparian soils and vegetation by reducing ungulate impacts is also a viable management tool for increasing summer baseflows (Ponce and Lindquist 1990; Rhodes and others 1994).

In severely degraded areas, initiating recovery may require active measures in addition to the removal/reduction of stressors. For example, where native seed banks have been depleted, reestablishing missing species may require planting seeds or propagules from adjacent areas or refugia (e.g., Welch 2005). While active restoration approaches in herbivory-degraded landscapes may have some utility, such projects are often small in scope, expensive, and unlikely to be self-sustaining; some can cause unanticipated negative effects (Kauffman and others 1997). Furthermore, if ungulate grazing effects continue, any benefits from active restoration are likely to be transient and limited. Therefore, addressing the underlying causes of degradation should be the first priority for effectively restoring altered public-land ecosystems.

The ecological effectiveness and low cost of wide-scale reduction in ungulate use for restoring public-land ecosystems, coupled with the scarcity of restoration resources, provide a forceful case for minimizing ungulate impacts. Other conservation measures are unlikely to make as great a contribution to ameliorating landscape-scale effects from climate change or to do so at such a low fiscal cost. As Isaak and others (2012, p. 514) noted with regard to the impacts of climate change on widely-imperiled salmonids: "...conservation projects are likely to greatly exceed available resources, so strategic prioritization schemes are essential."

Although restoration of desertified lands was once thought unlikely, recovery in the form of significant increases in perennial grass cover has recently been reported at several such sites around the world where livestock have been absent for more than 20 years (Floyd and others 2003; Allington and Valone 2010; Peters and others 2011). At a desertified site in Arizona that had been ungrazed for 39 years, infiltration rates were significantly (24 %) higher (compared to grazed areas) and nutrient levels were elevated in the bare ground, inter-shrub areas (Allington and Valone 2010). The change in vegetative structure also affected other taxa (e.g., increased small mammal diversity) where grazing had been excluded (Valone and others 2002). The notion that regime shifts caused by grazing are irreversible (e.g., Bestelmeyer and others 2004) may be due to the relative paucity of large-scale, ungulate-degraded systems where grazing has been halted for sufficiently long periods for recovery to occur.

Removing domestic livestock from large areas of public lands, or otherwise significantly reducing their impacts, is consistent with six of the seven approaches recommended

for ecosystem adaptation to climate change (Julius and others 2008, pp. 1-3). Specifically, removing livestock would (1) protect key ecosystem features (e.g., soil properties, riparian areas); (2) reduce anthropogenic stressors; (3) ensure representation (i.e., protect a variety of forms of a species or ecosystem); (4) ensure replication (i.e., protect more than one example of each ecosystem or population); (5) help restore ecosystems; and (6) protect refugia (i.e., areas that can serve as sources of "seed" for recovery or as destinations for climate-sensitive migrants). Although improved livestock management practices are being adopted on some public lands, such efforts have not been widely implemented. Public land managers have rarely used their authority to implement landscape-scale rest from livestock use, lowered frequency of use, or multi-stakeholder planning for innovative grazing systems to reduce impacts.

While our findings are largely focused on adaptation strategies for western landscapes, reducing ungulate impacts and restoring degraded plant and soil systems may also assist in mitigating any ongoing or future changes in regional energy and carbon cycles that contribute to global climate change. Simply removing livestock can increase soil carbon sequestration since grasslands with the greatest potential for increasing soil carbon storage are those that have been depleted in the past by poor management (Wu and others 2008, citing Jones and Donnelly 2004). Riparian area restoration can also enhance carbon sequestration (Flynn and others 2009).

Socioeconomic Considerations

A comprehensive assessment of the socioeconomic effects of changes in ungulate management on public lands is beyond the scope of this paper. However, herein we identify a few of the *general* costs and benefits associated with implementing our recommendations (see next section), particularly with regard to domestic livestock grazing. The socioeconomic effects of altering ungulate management on public lands will ultimately depend on the type, magnitude, and location of changes undertaken by federal and state agencies.

Ranching is a contemporary and historically significant aspect of the rural West's social fabric. Yet, ranchers' stated preferences in response to grazing policy changes are as diverse as the ranchers themselves, and include intensifying, extensifying, diversifying, or selling their operations (Genter and Tanaka 2002). Surveys indicate that most ranchers are motivated more by amenity and lifestyle attributes than by profits (Torell and others 2001, Genter and Tanaka 2002). Indeed, economic returns from ranching are lower than any other investments with similar risk

(Torrell and others 2001) and public-land grazing's contributions to income and jobs in the West are relatively small fractions of the region's totals (BLM and FS 1994; Power 1996).

If livestock grazing on public lands were discontinued or curtailed significantly, some operations would see reduced incomes and ranch values, some rural communities would experience negative economic impacts, and the social fabric of those communities could be altered (Genter and Tanaka 2002). But for most rural economies, and the West in general, the economic impacts of managing public lands to emphasize environmental amenities would be relatively minor to modestly positive (Mathews and others 2002). Other economic effects could include savings to the US Treasury because federal grazing fees on BLM and FS lands cover only about one-sixth of the agencies' administration costs (Vincent 2012). Most significantly, improved ecosystem function would lead to enhanced ecosystem services, with broad economic benefits. Various studies have documented that the economic values of other public-land resources (e.g., water, timber, recreation, and wilderness) are many times larger than that of grazing (Haynes and others 1997; Laitos and Carr 1999; Patterson and Coelho 2009).

Facilitating adaptation to climate change will require changes in the management of public-land ecosystems impacted by ungulates. *How* ungulate management policy changes should be accomplished is a matter for the agencies, the public, and others. The recommendations and conclusions presented in the following section are based solely on ecological considerations and the federal agencies' legal authority and obligations.

Recommendations

We propose that large areas of BLM and FS lands should become free of use by livestock and feral ungulates (Table 2) to help initiate and speed the recovery of affected ecosystems as well as provide benchmarks or controls for assessing the effects of "grazing versus no-grazing" at significant spatial scales under a changing climate. Further, large areas of livestock exclusion allow for understanding potential recovery foregone in areas where livestock grazing is continued (Bock and others 1993).

While lowering grazing pressure rather than discontinuing use might be effective in some circumstances, public land managers need to rigorously assess whether such use is compatible with the maintenance or recovery of ecosystem attributes such as soils, watershed hydrology, and native plant and animal communities. In such cases, the contemporary status of at least some of the key attributes and their rates of change should be carefully

Table 2 Priority areas for permanently removing livestock and feral ungulates from Bureau of Land Management and US Forest Service lands to reduce or eliminate their detrimental ecological effects

Watersheds and other large areas that contain a variety of ecotypes to ensure that major ecological and societal benefits of more resilient and healthy ecosystems on public lands will occur in the face of climate change
Areas where ungulate effects extend beyond the immediate site (e.g., wetlands and riparian areas impact many wildlife species and ecosystem services with cascading implications beyond the area grazed)
Localized areas that are easily damaged by ungulates, either inherently (e.g., biological crusts or erodible soils) or as the result of a temporary condition (e.g., recent fire or flood disturbances, or degraded from previous management and thus fragile during a recovery period).
Rare ecosystem types (e.g., perched wetlands) or locations with imperiled species (e.g., aspen stands and understory plant communities, endemic species with limited range), including fish and wildlife species adversely affected by grazing and at-risk and/or listed under the ESA
Non-use areas (i.e., ungrazed by livestock) or exclosures embedded within larger areas where livestock grazing continues. Such non-use areas should be located in representative ecotypes so that actual rates of recovery (in the absence of grazing impacts) can be assessed relative to resource trend and condition data in adjacent areas that continue to be grazed
Areas where the combined effects of livestock, wild ungulates, and feral ungulates are causing significant ecological impacts

monitored to ascertain whether continued use is consistent with ecological recovery, particularly as the climate shifts (e.g., Karr and Rossano 2001, Karr 2004; LaPaix and others 2009). To the extent possible, assessments of recovering areas should be compared to similar measurements in reference areas (i.e., areas exhibiting high ecological integrity) or areas where ungulate impacts had earlier been removed or minimized (Angermeier and Karr 1994; Dobkin and others 1998). Such comparisons are crucial if scientists and managers are to confirm whether managed systems are attaining restoration goals and to determine needs for intervention, such as reintroducing previously extirpated species. Unfortunately, testing for impacts of livestock use at landscape scales is hampered by the lack of large, ungrazed areas in the western US (e.g., Floyd and others 2003; FWS 2010).

Shifting the burden of proof for continuing, rather than significantly reducing or eliminating ungulate grazing is warranted due to the extensive body of evidence on ecosystem impacts caused by ungulates (i.e., consumers) and the added ecosystem stress caused by climate change. As Estes and others (2011, p. 306) recommended: "[T]he burden of proof [should] be shifted to show, for any ecosystem, that consumers do (or did) not exert strong cascading effects" (see also Henjum and others 1994; Kondolf 1994; Rhodes and others 1994). Current livestock or feral

ungulate use should continue only where stocking rates, frequency, and timing can be demonstrated, in comparison with landscape-scale reference areas, exclosures, or other appropriate non-use areas, to be compatible with maintaining or recovering key ecological functions and native species complexes. Furthermore, such use should be allowed only when monitoring is adequate to determine the effects of continued grazing in comparison to areas without grazing.

Where wild native ungulates, such as elk or deer, have degraded plant communities through excessive herbivory (e.g., long-term suppression of woody browse species [Weisberg and Coughenour 2003; Beschta and Ripple 2009; Ripple and others 2010]), state wildlife agencies and federal land managers need to cooperate in controlling or reducing those impacts. A potentially important tool for restoring ecosystems degraded by excessive ungulate herbivory is reintroduction or recolonization of apex predators. In areas of public land that are sufficiently large and contain suitable habitat, allowing apex predators to become established at ecologically effective densities (Soulé and others 2003, 2005) could help regulate the behavior and density of wild ungulate populations, aiding the recovery of degraded ecosystems (Miller and others 2001; Ripple and others 2010; Estes and others 2011). Ending government predator control programs and reintroducing predators will have fewer conflicts with livestock grazing where the latter has been discontinued in large, contiguous public-land areas. However, the extent to which large predators might also help control populations of feral horses and burros is not known.

Additionally, we recommend removing livestock and feral ungulates from national parks, monuments, wilderness areas, and wildlife refuges wherever possible and managing wild ungulates to minimize their potential to adversely affect soil, water, vegetation, and wildlife populations or impair ecological processes. Where key large predators are absent or unable to attain ecologically functional densities, federal agencies should coordinate with state wildlife agencies in managing wild ungulate populations to prevent excessive effects of these large herbivores on native plant and animal communities.

Conclusions

Average global temperatures are increasing and precipitation regimes changing at greater rates than at any time in recent centuries. Contemporary trends are expected to continue and intensify for decades, even if comprehensive mitigations regarding climate change are implemented immediately. The inevitability of these trends requires adaptation to climate change as a central planning goal on federal lands.

Historical and on-going ungulate use has affected soils, vegetation, wildlife, and water resources on vast expanses of public forests, shrublands, and grasslands across the American West in ways that are likely to accentuate any climate impacts on these resources. Although the effects of ungulate use vary across landscapes, this variability is more a matter of degree than type.

If effective adaptations to the adverse effects of climate change are to be accomplished on western public lands, large-scale reductions or cessation of ecosystem stressors associated with ungulate use are crucial. Federal and state land management agencies should seek and make wide use of opportunities to reduce significant ungulate impacts in order to facilitate ecosystem recovery and improve resiliency. Such actions represent the most effective and extensive means for helping maintain or improve the ecological integrity of western landscapes and for the continued provision of valuable ecosystem services during a changing climate.

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EDITED BY

Alfredo Di Filippo,
University of Tuscia, Italy

REVIEWED BY

Roel Brien, University of Leeds, United Kingdom
Jeffrey Stenzel, University of California, Merced, United States

*CORRESPONDENCE

Richard A. Birdsey
✉ rbirdsey@woodwellclimate.org

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

Richard A. Birdsey^{1*}, Dominick A. DellaSala²,
Wayne S. Walker¹, Seth R. Gorelik¹, Garrett Rose³ and
Carolyn E. Ramírez³

¹Woodwell Climate Research Center, Falmouth, MA, United States, ²The Wild Heritage, A Project of Earth Island Institute, Berkeley, CA, United States, ³Natural Resources Defense Council, Inc., Washington, DC, United States

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 (CO₂) emissions and increasing CO₂ 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.

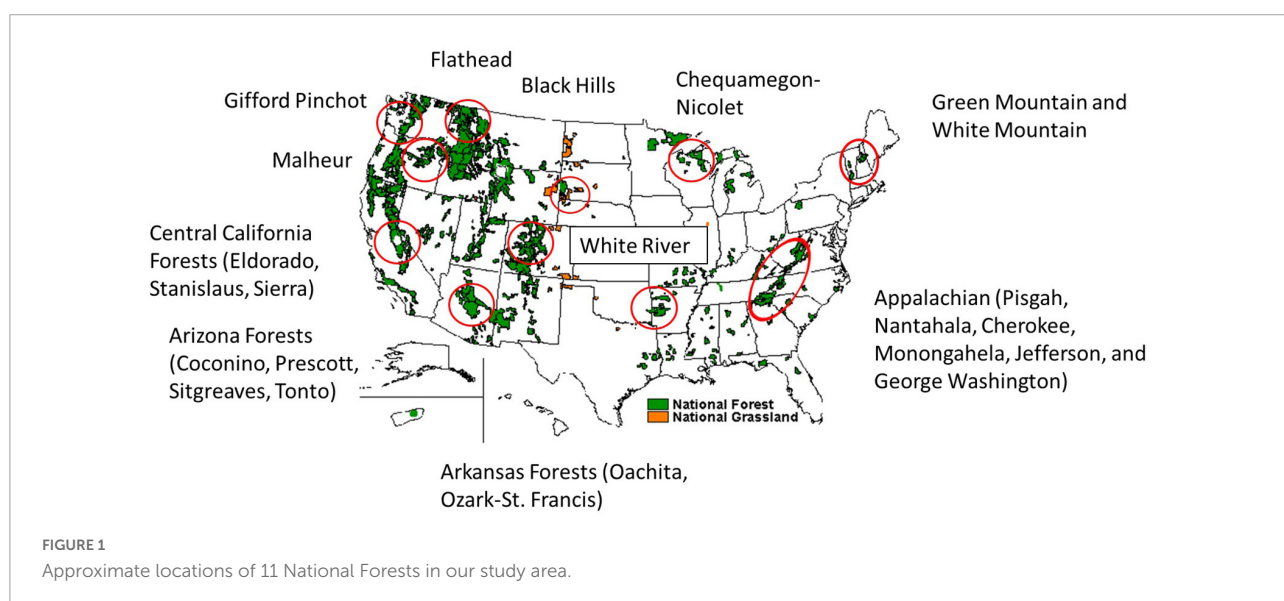
ecosystem is fully covered by leaf area—i.e., tree canopy closure reaches 100%. After this age, NPP either stays constant or declines gradually, depending on tree species composition, and other environmental factors such as nutrient availability (Kutsch et al., 2009; He et al., 2012). Previous analyses 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



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

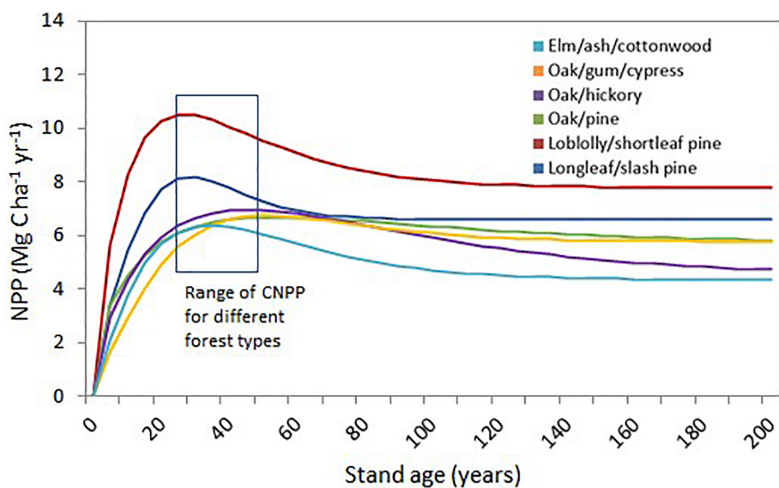


FIGURE 2
Net primary productivity (NPP) for selected forest types in the South (He et al., 2012). Culmination of NPP (CNPP) occurs at the stand age having the greatest annual increment rate, typically at or just after the tree canopy closes. Younger stands are those with ages less than CNPP. Older stands 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.
¹Stand structural stage is classified based on the relative basal area of canopy stems in various size classes.
²Forest maturity model based on three spatial data layers of forest cover, height, and above-ground living biomass for all landownerships.
³Based 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) $\text{Mg ha}^{-1}\text{yr}^{-1}$. 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 $4.0 \text{ MgC ha}^{-1}\text{yr}^{-1}$, 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

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](#).

the carbon stocks in larger trees in mature forests for each national forest, highlighted in yellow in the example table ([Supplementary Table 3](#)).

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		2,102,766		72.5	44.4

¹With 95% confidence.²Calculated 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](#); [Hurt 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 CO₂) for analyses of climate mitigation potential by the forest sector to reduce emissions or remove atmospheric CO₂. 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; Griscorn 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/>.

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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.

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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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Article

Forest Management, Barred Owls, and Wildfire in Northern Spotted Owl Territories

Monica L. Bond ^{1,*} , Tonja Y. Chi ² , Curtis M. Bradley ³ and Dominick A. DellaSala ⁴

¹ Wild Nature Institute, 15 North Main Street #208, Concord, NH 03301, USA

² Independent Researcher, PO Box 10022, South Lake Tahoe, CA 91158, USA

³ Center for Biological Diversity, PO Box 710, Tucson, AZ 85701, USA

⁴ Wild Heritage, Earth Island Institute, PO Box 9451, Berkeley, CA 94709, USA

* Correspondence: monica@wildnatureinstitute.org

Abstract: The Northern Spotted Owl (*Strix occidentalis caurina*) (NSO) was listed as federally threatened in 1992 due to widespread logging of its old-growth forest habitat. The NSO recovery plan in 2011 elevated competition with Barred Owls (*Strix varia*) (BO) and wildfires as primary NSO threats based partly on the assumption that severely burned forests were no longer NSO nesting and roosting habitat. We quantified amount of logging before and/or after wildfire and opportunistic detections of BOs within two home range scales (0.8 and 2.09 km) at 105 NSO sites that experienced severe wildfire from 2000–2017. Logging affected 87% of severely burned NSO sites, with BO recorded at 22% of burned-and-logged sites. Most (60%) severely burned NSO sites had evidence of logging both before and after fires while only 12% of severely burned sites had no logging or BO detections, indicating rarity of NSO territories subjected to severe fire without the compounding stressors of logging and invasive BOs. We recommend changes to NSO habitat modeling that assume nesting and roosting habitat is no longer viable if severely burned, and to the U.S. Fish and Wildlife Service’s practice of granting incidental take permits for NSOs in logging operations within severely burned owl sites.

Keywords: logging; severe fire; *Strix occidentalis*; thinning; threatened species



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1. Introduction

The U.S. Endangered Species Act (ESA) developed a formal process for listing a species at risk of extinction based on “listing factors.” Listing factors may act individually or in concert and are difficult to untangle when multiple interacting factors are involved in population declines, as often the case with imperiled species. The Northern Spotted Owl (NSO; *Strix occidentalis caurina*; Figure 1) is a territorial, monogamous, nocturnal raptor that primarily inhabits late-successional coniferous forests in the Pacific Northwest of the U.S. and southwest British Columbia [1]. Adults are territorial, have large home ranges, and have high fidelity to roosting and breeding sites [1,2]. Spotted Owls select forests that contain a high density of large conifers, high canopy cover, multiple canopy layers, numerous large snags, understory shrubs and hardwoods, and downed woody debris [1–3]. These conditions provide the owl with shade for hiding and thermoregulating, structures for nesting and roosting, and habitat for its primary prey, including northern flying squirrels (*Glaucomys sabrinus*), dusky-footed woodrats (*Neotoma fuscipes*), mice (*Peromyscus* spp.), pocket gophers (*Thomomys* spp.), and red tree voles (*Phenacomys longicaudus*) [1–3]. Elimination or degradation of older, structurally complex forests is associated with reduced site occupancy and reproduction failures of NSO [4].



Figure 1. Northern Spotted Owl (NSO) nest site with young in a severely burned undisclosed location (photograph Courtesy of Maya Khosla with permission).

The NSO was listed under the ESA as a federally threatened species in 1992 due primarily to adverse modification of older forest habitat by logging and inadequate regulatory mechanisms to prevent the owl's extinction [5–7]. The 2011 NSO recovery plan expanded on the primary listing factors by including threats from competitive exclusion by Barred Owls (BO; *Strix varia*) and habitat alteration by severe wildfires [4].

There is evidence that ongoing old forest habitat loss together with BOs are the main factors behind continued NSO declines [8–11]. However, whether wildfire is also a driver of NSO population declines is equivocal [12–14] because the few empirical wildfire studies of this subspecies are confounded by the additional stressor of logging (e.g., [15,16]). Spotted Owl territories are often compromised by pre- and post-fire logging that can obscure effects of severe fire on site occupancy [17,18]. Recent large-scale analyses of NSO demography and occupancy dynamics have used habitat covariates that made no distinction between logging and wildfire [9–11], rather these factors are lumped together as hectares of 'disturbance' and reductions in the amount of 'nesting-roosting habitat'.

Studies of wildfire effects on the related California Spotted Owl (*S. o. occidentalis*) have found that the presence of relatively large severely burned patches in a breeding site that was not consistently inhabited, was occupied mostly by single owls, and/or was unproductive before fire was associated with the loss of occupancy in that site after fire, but this was not evident in sites that were consistently occupied by pairs and reproductive owls before fire [19–21]. Formal meta-analyses that combined effect sizes of different studies showed no statistically significant negative influence of severe fire on site occupancy by Spotted Owls and in some cases significant positive effects on foraging and reproduction [12,13], whereas post-fire salvage logging has a demonstrated negative effect on occupancy [17,18]. Additionally, older forests where Spotted Owls live, as well as unmanaged forests in general, were less likely to burn severely [22,23]. Nevertheless, logging (before and after fire) continues to be proposed in wildfire risk reduction efforts and for "restoring forests" in NSO habitat [24] despite: (1) documented adverse effects of logging on NSO site occupancy and habitat use [4,25]; (2) questionable efficacy of logging on reducing severe fires driven mainly by extreme fire weather [26,27]; and (3) damage that post-fire salvage logging causes to post-fire tree regrowth [28] and forest ecosystems generally [29].

The main objective of our study was to determine the extent to which logging activities before and/or after wildfire routinely compound the stresses of wildfire and BO on the

federally threatened NSO. We assessed the annual amount of pre- and post-fire logging, and whether BOs were detected within 105 NSO sites affected by severe wildfire in forests managed by the USDA Forest Service (USFS) throughout the range of the subspecies over an 18-year period (2000–2017). We quantified the cumulative site- and year-specific amount of logging in the USFS-designated core home range area of 0.8 km radius and provincial home range area of 2.09 km radius around each site center [4]. We also quantified the cumulative amount of severe fire at both spatial scales, as well as whether BOs were opportunistically detected during surveys for NSOs. Our findings may help managers understand the extent of forest management activities in NSO sites that were affected by wildfire and BOs. This information is useful when quantifying anthropogenic disturbances and adjusting recovery actions for the NSO.

2. Materials and Methods

2.1. Study Area

Our study area incorporated portions of five national forests throughout the geographic range of the NSO (Okanagan-Wenatchee in Washington, Deschutes and Umpqua in Oregon, and Klamath and Six Rivers in California; Figure 2). On National Forest System lands, the USFS establishes a permanent alpha-numeric ‘activity center’ to represent a known NSO territory and delineates for management purposes a ‘core home range’ of 0.8 km radius and a ‘provincial home range’ of 2.09 km radius around the center of NSO detections, as per the interim guidelines of the U.S. Fish and Wildlife Service (USFWS) [4]. We requested field survey data from the USFS Region 6 for all historical NSO activity centers (hereafter, ‘sites’) that had experienced fire from 2000–2017. Our final sample included data from all the NSO sites having core or provincial home range areas that intersected with severe fire and logging (or no logging) either before or after fire, or both. We also quantified whether BOs had been opportunistically detected at the site during NSO surveys at any point during the 18-year study period. This offered contrasting gradients of stressors, enabling us to quantify the relative prevalence of the three effects in known NSO sites that experienced severe wildfire.

2.2. NSO Survey Data and Site Characteristics

We used a combination of the original NSO field survey forms, summary reports, and the California Natural Diversity DataBase (CNDDB: <https://wildlife.ca.gov/Data/CNDDB/Spotted-Owl-Info>; accessed on 10 August 2022) to plot geographic locations of nests, young, daytime roosts, and nighttime detections. The detections were then used to determine the ‘center’ of the site each year and to quantify forest attributes around that center.

NSO locations were digitized from the records provided for each year of the study and assembled into a GIS database. For each year that an NSO site was surveyed, the site was assigned a single core location at the geographic mean of all observations, around which we drew the core and provincial home ranges for geospatial analysis and quantification of environmental covariates. We based the center of the site on the highest status and most biologically significant NSO detection, in the following descending order of importance: (1) location of active nest; (2) location of juvenile owlets; (3) centroid of daytime roosts of adult pairs; (4) centroid of daytime roosts of single adults; (5) centroid of nighttime detections; and finally, (6) old site center location. For sites without a known nest location and where NSOs were recorded in multiple locations within one year, we assigned a point at the geographic mean of the locations. This geospatial analysis was repeated for each year of the study as the amount of severe wildfire and logging within the home range circles changed over time, and as the owls might have shifted their location(s) within the site. We quantified covariate values for each year for each NSO site as: (1) area of initial conifer forest cover in 2001; (2) year-specific area of logging in conifer forest (including commercial thinning, clearcuts, and post-fire salvage); and (3) year-specific area of severe wildfire in

conifer forest. We presented annual estimates of logging and severe fire within each spatial scale (0.8 km radius and 2.09 km radius) cumulatively.

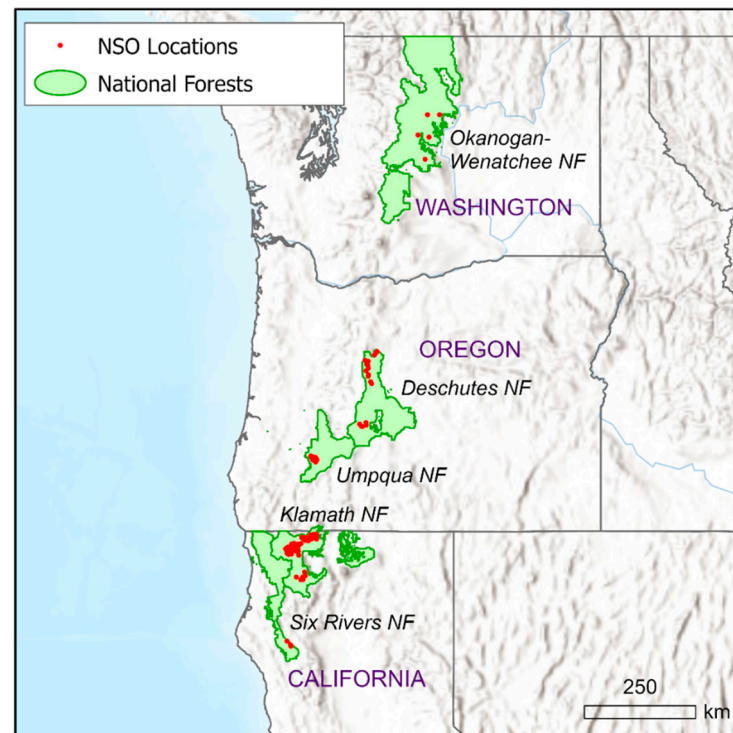


Figure 2. Study area showing the location of severely burned Northern Spotted Owl sites in five national forests where information on logging, wildfires, and Barred Owls was available from 2000–2017.

To define initial forest cover, we used the Existing Vegetation Type dataset from LANDFIRE version 1.0.5 (LANDFIRE, *public communication*, <http://www.landfire.gov>; accessed on 10 August 2022). We chose this version of LANDFIRE because it employed satellite imagery from 2001, which is nearest to the beginning of our study period. The EVT data layer represents the current distribution of the terrestrial ecological systems classification developed by NatureServe for the western hemisphere. EVT cover was reclassified into conifer and non-conifer using the “System Group Physiology” attribute and intersected with our home range circles for each year.

2.3. Logging Type and Severe Wildfire

We used three datasets to determine severely burned NSO sites that underwent some type of logging during the study period via the Forest Service Activity System (FACTS) (<https://data.fs.usda.gov/geodata/edw/datasets.php>; accessed on 10 August 2022): ‘Timber Harvests’ dataset, representing areas clearcut and thinned; pre-commercial thinning activities within the ‘Silviculture Timber Stand Improvement’ dataset; and thinning and cutting activities within the ‘Hazardous Fuel Treatment Reduction’ dataset. These logged areas were combined for each specific year of the study and then intersected with our home range circles for the year of the logging.

For determining high severity fire in conifer forests for each year of our study, we used the Monitoring Trends in Burn Severity project (MTBS, *public communication*, <http://www.mtbs.gov>; accessed on 10 August 2022). MTBS is a U.S. Department of Interior and USDA-sponsored program designed to consistently map burn severity and perimeters using satellite imagery across all lands of the United States. We used the burn severity mosaics that represented a composite of all the individual fires that occurred in each year of our study and are classified by a MTBS analyst into 5 different categories: unburned

and unburned to low burn severity, low burn severity, moderate burn severity, high burn severity, and increased greenness. These categories are typically based on values of the Differenced Normalized Burn Ratio (dNBR). The fires in our study were reclassified into two categories: high burn severity and not high burn severity. High severity areas were then intersected with the home range circles for the year of the fire. Figure 3 provides two examples of NSO provincial home range areas and the intersecting conifer forest, severe fire, and logging covariates.

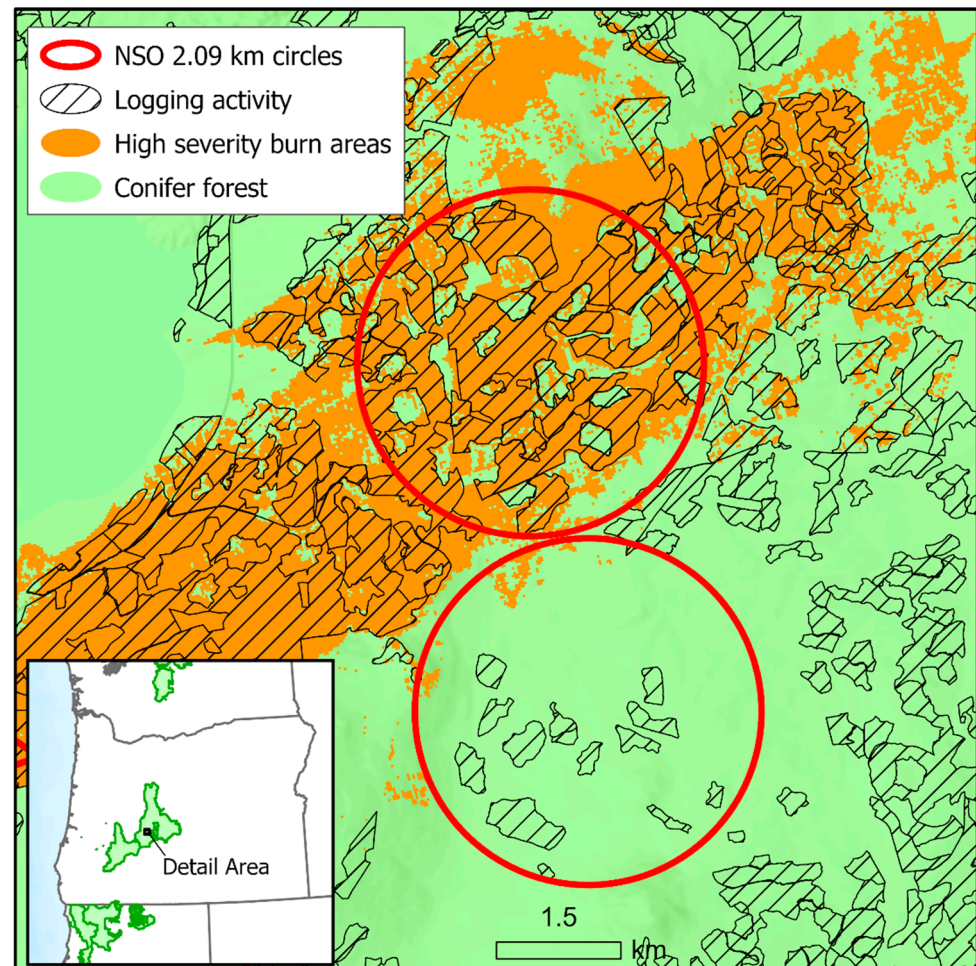


Figure 3. Examples of two Northern Spotted Owl provincial home range areas and the intersecting conifer forest, severe fire, and logging covariates.

3. Results

3.1. NSO Sample Size and Distribution

We identified 105 severely burned NSO sites obtained from the Okanagan-Wenatchee National Forest ($n = 5$); the Deschutes ($n = 18$) and the Umpqua National Forests ($n = 14$); and the Six Rivers ($n = 3$) and the Klamath National Forests ($n = 65$) (Figure 2). Data for all 105 NSO sites included national forest location, proportion of conifer forest and cumulative logged area, amount of severe wildfire in the core and provincial home ranges, whether the site was logged and/or BOs detected, the number of times the site was logged, and the type of logging (pre-fire and/or post-fire) (Online Supplemental Table S1).

3.2. NSO Site Characteristics and Degree of Logging

The mean proportion of the NSO core home range comprised of conifer forest was 0.89 (SD = 0.14, range = 0.28–1.00, $n = 105$) and the mean proportion of the provincial home range that was conifer forest was 0.86 (SE = 0.14, range = 0.34–1.00, $n = 105$). The

vast majority (87%) of burned sites (91 of 105) were affected by logging, while only 12% of burned sites (13 of 105) had no logging or BO detections during the 18-year period (Figure 4). That is, just 13 NSO sites experienced severe fire only; 1 severely burned site had BO detections and no logging; 68 sites had both severe fire and logging; and all three effects (BO, logging, severe fire) were present in 23 NSO sites.

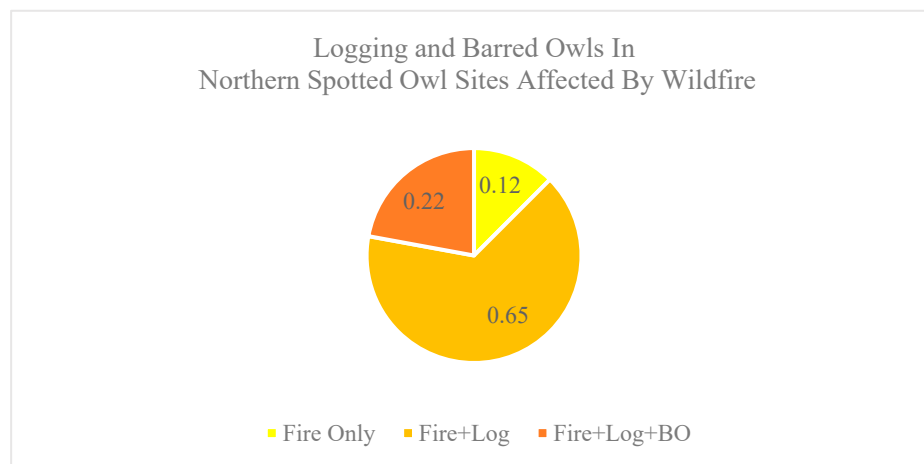


Figure 4. Proportion of Northern Spotted Owl sites that experienced severe wildfire and were not logged (fire only); that were also logged (fire + log), and that were logged and Barred Owls were detected (fire + log + BO).

We further quantified whether the 91 logged sites were subjected to pre-fire logging only, post-fire logging only, or both pre- and post-fire logging. The majority ($n = 63$, 60%) of NSO sites were logged both before and after fire, followed by those logged only after fire ($n = 15$, 14%) and sites logged only before fire ($n = 13$, 12%) (Online Supplemental Table S1). At both the core and provincial home range scales, most NSO sites were logged multiple times. Within the 0.8 km circle logged sites, NSO experienced a mean of 2.3 logging entries (SD = 1.3, maximum = 8 times). Within the 2.09 km circle sites, logged NSO sites experienced a mean of 4.9 logging entries (SD = 2.7, maximum = 14 times). The mean amount of conifer forest in the 0.8 km home range cores that was logged within our sample of NSO sites (including sites that were not logged) was 27 ha (SD = 32.8 ha) with a maximum of 174.8 ha logged within the core area. The mean amount of logging in conifer forests within the 2.09 km provincial home range (including unlogged sites) was 171.8 ha (SD = 152.1 ha) with a maximum of 965 ha logged in the provincial area.

Examples of actual (pre- and post-fire) and proposed logging activities within NSO sites are provided in Figure 5.



Figure 5. Cont.

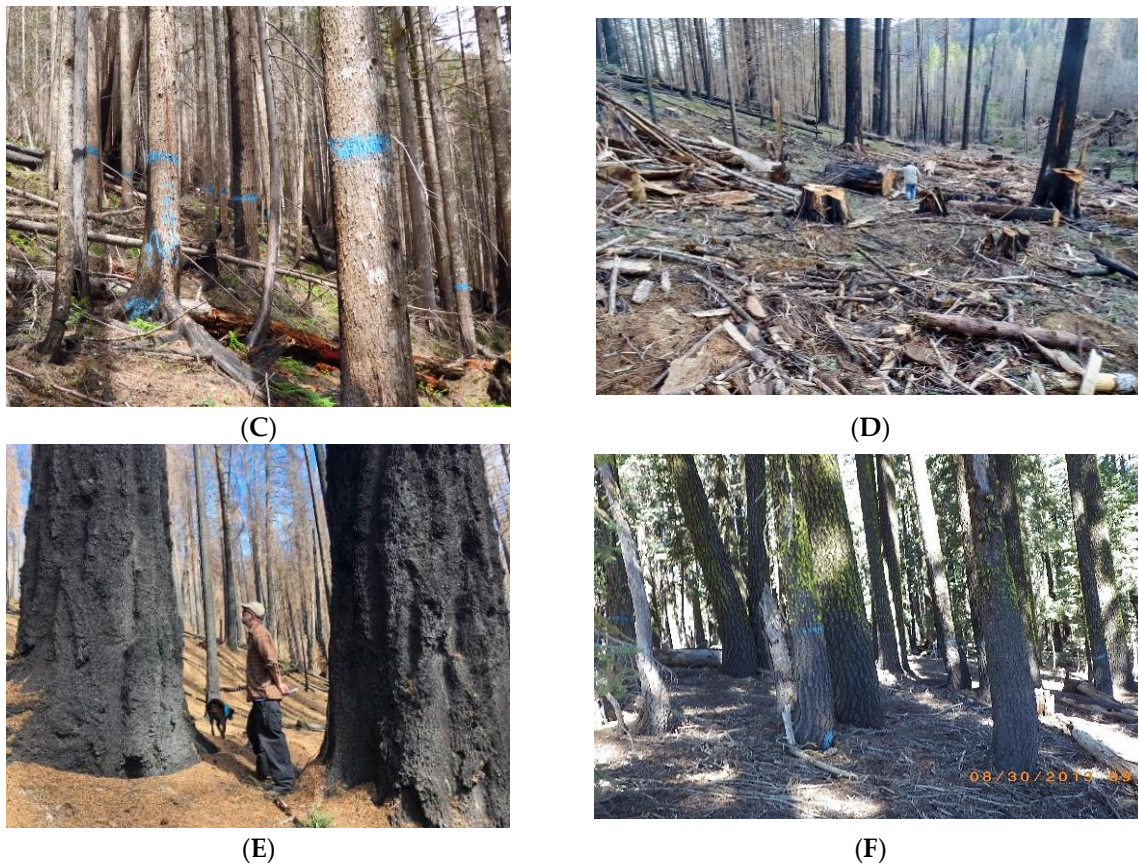


Figure 5. (A) Bureau of Land Management’s Picket West timber sale in NSO Critical Habitat in Oregon where fuel treatments will reduce overstory canopy closure to 40% (photograph Courtesy of Luke Ruediger). (B) Trees marked for logging in the Pilgrim project on California’s Shasta-Trinity National Forest in NSO occupied territories (photograph Courtesy of Doug Bevington). (C) Downey Creek timber sale in the Darrington Ranger District of the Mt. Baker-Snoqualmie National Forest in California showing large trees to be removed within a Late Successional Reserve (LSR) where fire occurred (photograph Courtesy of Kathy Johnson). (D) Post-fire logging within NSO core areas on the Bureau of Land Management’s Roseburg District in Oregon (photograph Courtesy of Francis Eatherington). (E) Seiad-Horse post-fire timber sale within an LSR on the Klamath National Forest in California (photograph Courtesy of George Sexton). (F) Trees marked for logging in an occupied NSO activity center in the Smokey project on the Mendocino National Forest in California (photograph Courtesy of Monica Bond). All photographs are with permission from their copyright owners.

4. Discussion

We enumerated the amount of logging and severe fire at two spatial scales, the NSO core home range and the provincial home range, as well as the presence of BOs, in 105 NSO sites that had experienced severe wildfire in conifer forests on USFS lands from 2000–2017. By quantifying the simultaneous extent of these three primary stressors (logging, severe fire, BO) within NSO core and provincial home ranges, we showed that logging was the predominant stressor in 87% of NSO sites that also experienced severe fire, with the additional stressor of BO at 22% of the burned-and-logged sites. Most (60%) of the NSO sites had evidence of logging (clearcuts, commercial thin, fuels reduction) both before and after severe fires. Only 12% of severely burned sites had no logging or BO detections during the 18-year study period, indicating the rarity of NSO territories subjected to severe fire without the compounding effects of multiple logging entries and invasive BOs.

An interesting finding was that of 14 sites that experienced wildfire but were not logged at any point during the 18-year period, only 1 site (8%) also had BOs recorded. Of the sites that were logged either before or after fire, or both before and after, 23 sites

(34%) had BOs detected. This result agrees with previous research demonstrating low use of severely burned forests by BOs [30] and offers some support for the hypothesis that logging facilitates invasions of BOs into NSO sites [31,32]. Conversely, NSO territories with relatively high proportions of suitable NSO habitat (unlogged) may be better capable of withstanding BO competition [32]. However, one caveat to our study is that BOs were only recorded opportunistically when detected during NSO surveys, so true prevalence of BOs may be underestimated.

The USFS claims that severe wildfire is a major cause of NSO territory abandonment and has constructed habitat suitability models that assume severely burned areas are no longer nesting or roosting habitat [33] (also see <https://www.fs.usda.gov/rmrs/science-spotlights/severe-fire-good-or-bad-spotted-owls>; accessed on 26 April 2022). Based on this assumption, the agency applies for ‘incidental take’ permits under section 7 of the ESA to log and presumably kill or harass any NSOs in designated Critical Habitat, Late-Successional Reserves, and NSO activity centers (known territories) following severe fires where logging is most often proposed [14]. Take permits are routinely granted by the USFWS, who also assumes severely burned sites are no longer nesting or roosting habitat. In these situations, competing hypotheses are seldom addressed nor are habitat suitability models validated. We note that despite assertions by federal agencies and some researchers that logging for fire risk reduction is mostly about small trees (e.g., [34]) in Spotted Owl territories and elsewhere [27], fuels reduction logging most often removes large trees to pay for the costs of thinning (see Figure 5A–F). This can impact critical NSO habitat by reducing canopy closure below recommended thresholds (e.g., 60% canopy overstory; Figure 5) while altering ground cover that supports NSO prey species [35].

Logging, and to some extent BOs, are stressors that can be managed [36]. It remains an area of active research and debate as to whether severe fires can be reduced through certain forms of logging (e.g., thinning), particularly as the recent increase in megafires is attributed to extreme fire weather associated with climate change that is overriding efforts to reduce flammable vegetation via thinning [26,27,37,38]. Further, the extent to which severe fire is a major threat to Spotted Owls is often biased by the tendency for federal agencies and some researchers to falsely attribute abandonment by Spotted Owls in severely burned sites to fire alone [39] even though logging is usually present on those sites [12,13,17,18].

Our findings support the need to validate NSO habitat modeling assumptions and adjust incidental take permits that are routinely granted by the USFWS based on the assumption that severe fire is no longer NSO habitat. For instance, the Klamath National Forest in 2016 proposed to clearcut 2720 ha of severely burned NSO sites within Late-Successional Reserves under the Northwest Forest Plan based on the assumption that they were no longer suitable NSO habitat. The USFWS [40] proceeded to grant the USFS an incidental take permit to harm, kill, or harass 74 adult NSOs and 12–29 juveniles, concluding that logging would not trigger a range-wide jeopardy decision because the sites were assumed to no longer provide suitable habitat. With the recent uptick in wildfires within the range of the NSO [41], ongoing NSO incidental take under the assumption that severely burned forest patches are no longer NSO habitat could indeed trigger cumulative effects resulting in a future jeopardy decision. This could otherwise be avoided by validating NSO habitat models based on our findings and prohibiting incidental take permits in severely burned NSO sites.

5. Conclusions and Management Recommendations

Recovery Action 8 in the NSO Recovery Plan [4] (p. III-40) suggests “analyz[ing] exiting data on [NSO] occupancy pre- and post-fire and establish a consistent database to track owl occupancy response to fires across the dry Cascades provinces”. We note that in our study NSO survey forms lacked a standardized data reporting protocol, resulting in many survey forms where activity center numbers or specific site coordinates were missing; hence the need for consistency in reporting. Moreover, our findings point to the need for

federal agencies responsible for the recovery of the NSO (USFWS) and the management of its habitat (USFS) to adjust recovery actions to better quantify and address two of the principal interacting NSO stressors—logging and BOs—that complicate severe fire effects on NSOs as well as agency efforts (e.g., thinning) to reduce fire intensity based on this assumption. Odion et al. [35] used a transition state model to conclude thinning at the scale proposed in the 2011 NSO recovery plan would result in 3.4 to 6.0 times more NSO habitat loss than severe wildfire over a 40-year timeline that was similarly demonstrated by Raphael et al. [42]. That is to say, the main treatment type on National Forest lands to lower fire intensity in NSO sites may actually be causing more habitat degradation than severe wildfires, especially when results of NSO site occupancy are conflicted by pre- and post-fire logging.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13101730/s1>, Table S1: Table of cumulative amounts of logging, wildfire, and BO detections.

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Multifunctionality and biodiversity: Ecosystem services in temperate rainforests of the Pacific Northwest, USA



Patric Brandt^{a,b,*}, David J. Abson^c, Dominick A. DellaSala^d, Robert Feller^b, Henrik von Wehrden^{b,c}

^a Karlsruhe Institute of Technology, Institute of Meteorology and Climate - Atmospheric Environmental Research, Kreuzeckbahnstraße 19, 82467 Garmisch-Partenkirchen, Germany

^b Leuphana University Lüneburg, Centre for Methods & Institute of Ecology, Faculty of Sustainability, Scharnhorststr. 1, 21335 Lüneburg, Germany

^c Leuphana University Lüneburg, FuturES Research Center, Scharnhorststr. 1, 21335 Lüneburg, Germany

^d Geos Institute, 84–4th St., Ashland, OR 97520, USA

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ABSTRACT

Forests produce a myriad of ecosystem related benefits known as ecosystem services. Maximizing the provision of single goods may lead to the overexploitation of ecosystems that negatively affects biodiversity and causes ecosystem degradation. We analyzed the temperate rainforest region of the Pacific Northwest, which offers a multitude of ecosystem services and harbors unique biodiversity, to investigate linkages and trade-offs between ecosystem services and biodiversity. We mapped nine actual and potential ecosystem services, grouped into provision, supporting, regulating and cultural ecosystem service categories, as well as species richness of four taxonomic groups (mammals, birds, trees, and amphibians). We analyzed linkages and tradeoffs between ecosystem services, their overall diversity, and species richness as well as different levels of taxon diversity. We also tested if ecosystem service categories, in addition to climate and land cover parameters, could indicate species richness. We found significant positive linkages between ecosystem service diversity and species richness of all considered taxa. The provision of the majority of ecosystem services was higher in areas of high taxon diversity, indicating both positive relationships and slight trade-offs in maximizing single ecosystem services. In general, ecosystem service categories were a comparable indicator of species richness as climate. Our findings show that multifunctionality largely coincides with high levels of biodiversity within the study region. Hence, an integrative ecosystem management approach that incorporates ecosystem services and biodiversity concerns is needed to both provide diverse ecosystem benefits and conserve biological diversity.

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1. Introduction

Ecosystem services and biodiversity conservation have become the two dominant, and potentially conflicting (Bullock et al., 2011; Marrs et al., 2007; McShane et al., 2011) management aims in conservation science during the last decades. Ecosystem services are the numerous benefits people directly or indirectly appropriate from the functioning of ecological systems and provide the foundations for human well-being (Daily, 1997; Nelson et al., 2009). The ecosystem services concept combines resource use, ecosystem management – including adaptation to impacts of driving forces such as land use and climate change – and the valuation of nature (Maskell et al., 2013), making it a key concept that bridges social and ecological systems (Carpenter et al., 2009). Biodiversity is vital for maintaining ecosystem processes and functioning (Duffy, 2009; Hector and Bagchi, 2007). Its loss has been shown to cause ecosystem degradation (Hooper et al., 2012). Hence, biodiversity

is seen as essential requirement for the provisioning of ecosystem services (Diaz et al., 2006). Here it should be noted that as well as an instrumental value related to the provision of ecosystem services, the conservation of biodiversity is also a normative goal in its own right (Mace et al., 2012). Biodiversity conservation is therefore not solely contingent on the instrumental contribution to human well-being it may provide.

The increasing number of studies on the functional relationships between biodiversity and ecosystem services reveal mostly positive patterns (Gamfeldt et al., 2013; Hector and Bagchi, 2007; Maskell et al., 2013). However, many of these diversity-ecosystem services studies focus on a single facet of diversity such as one species group and a single ecosystem service, such as primary productivity (Costanza et al., 2007), pest control (Simon et al., 2010) or agricultural yields (Di Falco and Chavas, 2006). Managing an ecosystem for a single ecosystem service is potentially problematic as it may result in trade-offs in terms of associated biodiversity (Ingram et al., 2012; Ridder, 2008; Rodriguez et al., 2006) and thereby compromises conservation efforts. The interplay between the provision of multiple ecosystem services and biodiversity

* Corresponding author. Tel.: +49 4131 677 1571.

E-mail address: patricbrandt@gmx.de (P. Brandt).

represents an important knowledge gap (Geijzenborffer and Roche, 2013; Sircely and Naem, 2012), potentially limiting our ability to effectively manage multifunctional landscapes for both ecosystem services provision and biodiversity conservation.

In this regard, it becomes vital to analyze ecosystems that are managed for diverse societal needs. Multifunctional ecosystems offer several services simultaneously to satisfy social, cultural, economic and environmental demands (O'Farrell et al., 2010). Hence, a diverse set of ecosystem services needs to be considered when assessing the relations between biodiversity conservation and ecosystem service provision in multifunctional ecosystems (Chan et al., 2006; Tallis and Polasky, 2009). This includes services that cannot be straightforwardly linked to specific ecosystem functions such as cultural services (Hernandez-Morcillo et al., 2013). Potential synergies between ecosystem services and biodiversity are expected, though they might vary across ecosystems and depend on the specific ecosystem services and aspects of biodiversity taken into consideration (Mace et al., 2012).

Forests are of immense global importance in delivering a myriad of benefits to humanity (Bonan, 2008; FAO, 2010; Schwenk et al., 2012). In particular, temperate rainforests represent an ecologically complex, unique ecosystem with high biodiversity importance, subjected to multiple human demands. We analyzed a region along the Pacific coastline of North America harboring the world's largest remaining extents of temperate rainforests (DellaSala, 2011). While currently offering a broad range of goods and services such as salmon (*Oncorhynchus* spp.), timber, water regulation and recreation, these rainforests are threatened by climate and land use changes (DellaSala, 2011; Fitzgerald et al., 2011).

We addressed three key questions to investigate linkages and trade-offs between ecosystem services and biodiversity across the temperate rainforest region of the Pacific Northwest: (1) How is ecosystem service diversity related to species richness across different taxonomic groups? (2) How are ecosystem services and their diversity linked to different diversity levels of the considered taxa? (3) In order to untangle the interrelations among the environment, ecosystem services and species richness we tested if the provision of ecosystem services, grouped by the millennium ecosystem service assessment (MA) categories, alongside environmental variables such as climate and land cover, indicate species richness. Here, we did not seek to explain the functional relations between biodiversity and ecosystem services categories. Rather, we described the patterns (Shmueli, 2010) between the types of ecosystem services provided, their diversity and biodiversity across the temperate rainforest region of the Pacific Northwest and discussed the implications of these patterns for multifunctional landscape management and conservation at a regional scale.

Recent studies focusing on the relationship between ecosystem services and biodiversity have taken a functional perspective and mostly considered limited ecosystem service categories such as provisioning or regulating services (e.g. Balvanera et al., 2006; Costanza et al., 2007; Schwenk et al., 2012) and single species groups such as plant species (e.g. Gamfeldt et al., 2013; Maskell et al., 2013; Tilman et al., 2012). By involving multiple taxa and multiple ecosystem services including supporting and cultural services, we aim to identify more comprehensive patterns relating ecosystem services to biodiversity.

Here we note that the direct quantification of ecosystem services is often problematic and that there might be considerable differences between the ecosystem services that potentially flow from a given ecosystem and the actual services that are appropriated at a given point in time. For example, timber harvest is an indicator for the appropriation of timber but provides limited information regarding the capacity of a given system to sustainably provide timber. Similarly it can be argued that benefits received

(i.e. the direct quantification of services) from physically appropriated goods such as timber must be related to how those physical goods contribute to human well-being (Fischer et al., 2009). Given the importance of both the actual appropriation and the potential capacity to supply ecosystem services and the difficulty in directly and accurately quantifying multiple ecosystem services across large spatial and temporal extents, we focus on the mapping of proxy datasets that indicate nine important potential and actual ecosystem services within the temperate rainforest region of the Pacific Northwest. The following proxy data for ecosystem services were modeled: timber harvest, salmon abundance, deer hunting, net primary productivity, carbon storage in vegetation, organic matter in soil, forest importance for drinking water supply, landscape aesthetics, and park visitation. These proxies for ecosystem services were grouped into the MA categories of provision, supporting, regulating, and cultural ecosystem services (MA, 2005). Biodiversity was quantified in terms of spatially explicit species richness data for higher taxa, including mammals, birds, trees and amphibians. Diversity metrics were derived for ecosystem services and the higher taxa. Subsequently, we computed univariate models to reveal the patterns between ecosystem service diversity and species richness. Potential and actual ecosystem services and their diversity were linked to the higher taxon diversity. Multivariate direct gradient analyses were performed to assess if the MA ecosystem service categories are able to indicate species richness in interaction with and untangled from environmental variables such as climate and land cover.

2. Materials and methods

2.1. Study area

The study area was based on the original coastal temperate rainforest extent of the Pacific Northwest region (DellaSala, 2011) that shows an overall high proportion of forest coverage. All US counties that intersect the original coastal rainforest extent, including a buffer of 15 km, were incorporated into the study area of 325,614 km². This broad extent was chosen to ensure that climate and land cover gradients are well represented. Due to limited data availability, coastal rainforest regions located in British Columbia and Alaska were excluded from our analyses. All metrics related to species richness, ecosystem services and environmental data were mapped at a resolution of approximately 8 × 8 km – 3997 grid cells in total. It is important to note that the study extent, while dominated by forests, encompasses a spatially heterogeneous matrix of different land uses that in turn create spatially heterogeneous patterns of ecosystem service provision and biodiversity. The study extent comprised 55% forest, 33% scrub and grassland, 7% cultivated areas and 5% developed/urban regions. Public lands in this region are managed under the Northwest Forest Plan that governs ecosystem management and biodiversity conservation (DellaSala and Williams, 2006). However, non-federal landowners frequently focus on timber management as the primary ecosystem service. ARCGIS 10.1 was used for all geo-processing work.

2.2. Ecosystem service data

The proxy data used refer either to the actual goods or services people appropriate from nature, known as 'ecosystem services', or to the capacity of the ecosystem to deliver those goods and services to society, conceptualized here as 'potential ecosystem services' (Vira and Adams, 2009). The data were based on physical occurrence of actual and potential ecosystem services, rather than the monetary or non-monetary values associated with those services.

All data were gathered from publically available datasets, further processed and linked to spatial data or were readily available in a spatially explicit format. We compiled GIS-layers indicating the nine potential and actual ecosystem services, which were also grouped into MA categories – i.e. provisioning, regulating, supporting, and cultural ecosystem services (MA, 2005). Detailed descriptions of the datasets and data sources can be found in the online appendix (Online appendix, Table A1).

2.2.1. Provisioning services

2.2.1.1. Timber harvest. Timber is one of the most prominent resources derived from forest ecosystems and has been intensively harvested from temperate rainforests in this region. This layer depicts the total volume of timber harvested in 2010 measured in thousands of board feet. Derived tabular data are based on the county level.

2.2.1.2. Salmon abundance. Salmon are an important economic and food resource for the entire coastal rainforest region in North America and they are the key for trophic dynamics and energy transfer (DellaSala, 2011). The salmon abundance data are based on observed (1998–2005) and modeled data at the watershed level (Pinsky et al., 2009). Watershed based data were normalized and then converted into gridded data.

2.2.1.3. Deer hunting. Hunting has been taking place for millennia across the coastal temperate rainforest region of North America (Schoonmaker et al., 1997). Hence, hunting can be considered as a traditional source of local food resources. This layer indicates overall deer hunting successes for 2010 measured in counted deer kills. Census data are obtained and mapped based on hunting management units defined by State Departments of Fish & Wildlife.

2.2.2. Supporting services

2.2.2.1. Net primary productivity. The Pacific coastal rainforests belong to the most productive ecosystems worldwide (DellaSala, 2011), and primary productivity is a key ecological function from which many other, directly used, ecosystem services flow. Gridded information on NPP is derived from NASA's MODIS satellite data in a 10 km² grid cell resolution based on monthly values averaged for 2010 in gC m⁻² day⁻¹.

2.2.3. Regulating services

2.2.3.1. Carbon storage in vegetation. The storage of atmospheric carbon in biomass is essential to climate regulation and climate change mitigation. The coastal temperate rainforests in North America show high carbon densities compared to other forest ecosystems (DellaSala, 2011; Woodbury et al., 2007). Gridded data show total mean carbon content in vegetation for 1961–1990 and originate from outputs of the MC1 dynamic vegetation model (Bachelet et al., 2001a,b) in an 8.8 km² grid cell resolution.

2.2.3.2. Organic matter in soil. Organic matter strongly influences soil properties such as water retention, erodibility and fertility (Ontl and Schulte, 2012). Furthermore, soil represents a large carbon pool. The sequestration of atmospheric carbon in soil organic matter contributes to climate change mitigation (Lal, 2004). The data used indicates the total content of organic matter in soil expressed as percent by weight of the 2 mm soil fraction at the watershed level.

2.2.3.3. Forest importance for drinking water supply. Forests are known to serve as important regulators of drinking water, particularly in this region (DellaSala et al., 2011). This layer combines precipitation intensity, proportion of forests and population density per watershed and was derived from the USDA 'forests to faucets'

dataset (Barnes et al., 2009). We used these data as proxy for water regulation (Todd and Weidner, 2010).

2.2.4. Cultural services

2.2.4.1. Landscape aesthetics. The possibility to experience landscapes that are largely undisturbed by human pressure is usually accepted as a great benefit that ecological systems may offer in terms of recreation (Gobster et al., 2007). The compiled dataset consists of several spatial layers related to infrastructure such as roads, railroads and settlements, and natural elements such as lakes, rivers and forests that are undisturbed by human influences. All layers were weighted according to their naturalness. Terrain roughness was incorporated as proxy for physical landscape heterogeneity. Each layer was weighted either positively or negatively except for terrain roughness that was weighted based on three states, low roughness as negative, medium roughness as neutral and high roughness as positive. The resulted 'landscape aesthetics' layer is considered as a potential ecosystem service since the quantification of the actual cultural values associated with the landscapes of the study region was beyond the scope of our analysis.

2.2.4.2. Park visitation. State and national parks represent essential recreation areas in the US (Daniel et al., 2012), facilitating environmental education and sustainable tourism. We mapped the tabular park visitation data for 2010 on state and national parks, derived from the PAD-US protected area database (v. 1.2). Subsequently spatial data were aggregated on county level since most of the state parks do not match the working resolution and hence would not have been visible for the analyses. We used this dataset as proxy for the provision of space for recreation and cultural experiences.

All data based on unequally sized areas were normalized based on area. Thus, every layer refers to equal area units. For further analyses all potential and actual ecosystem service layers were transformed to a standardized scale based on their maximum values (Raudsepp-Hearne et al., 2010). Hence, all ecosystem service values range between 0 and 1.

2.3. Species data

Spatially explicit species richness data for higher taxa, including mammals (between 1 and 85 species recorded), birds (88–223 species), trees (1–50 species) and amphibians (2–38 species) were obtained as gridded layer from several resources (Online appendix, Table A2). For tree species, we compiled a richness layer through aggregating range polygon data (Little, 1978). Selected species groups represent major parts of the overall species diversity that exists across the Pacific coastal temperate rainforests and contain numerous species of economic, cultural and conservation importance. Reptiles, as a further terrestrial vertebrate group, were not included into the analyses since they are not well represented, nor particularly abundant, across the Pacific coastal temperate rainforests compared to other regions of their occurrence (Böhm et al., 2013).

2.4. Applied statistical approaches

All statistical analyses were undertaken using R 2.15, including the packages 'raster' (v. 2.1.12) for handling spatial data, 'car' (v. 2.0.16) for building generalized linear models (GLMs), 'spdep' (v. 0.5.56) for correcting autocorrelation patterns, 'vegan' (v. 2.0.6) to obtain diversity indices and to perform principal component analyses (PCAs) as well as redundancy analyses (RDAs).

2.4.1. Simpson diversity metrics

Diversity metrics were derived by using the Simpson diversity index for potential and actual ecosystem services (Raudsepp-Hearne et al., 2010) and higher taxa ranging between 0 (low diversity) and 1 (high diversity). The Simpson index is illustrated by the following formula:

$$D = 1 - \sum_{i=1}^R p_i^2$$

R is the richness of taxa/ecosystem services and p_i is the proportion of abundances for the i th taxon/ecosystem service.

The Simpson diversity measure takes abundances into account and equals the probability that two entities taken at random from the dataset represent the same type (Simpson, 1949). The Simpson diversity of higher taxonomic groups was used as biodiversity metric that is comparable to the Simpson diversity of ecosystem services. A color map was compiled illustrating the degree of spatial correspondence between the diversity metrics across the study area.

2.4.2. Univariate linkage modeling: ecosystem service diversity – species richness

In order to model the relationship between ecosystem service diversity and species richness, we chose a univariate model approach using GLMs (Crawley, 2007). Due to the non-normalized distribution of model residuals, we opted for GLMs with Poisson error structure. Species richness data were selected as dependent variables and ecosystem service diversity as independent variable since Poisson-GLMs require real count data. Hence, we follow a descriptive approach rather than explaining the causal relationship between biodiversity and ecosystem services. GLMs also included quadratic terms and were reduced based on the Akaike information criterion (AIC), to avoid overfitting (Sakamoto et al., 1986). Since model residuals revealed patterns of spatial autocorrelation, we applied spatial eigenvector filtering to incorporate spatial autocorrelation structures (Dray et al., 2006; Griffith and Peres-Neto, 2006). Spatial eigenvectors are derived from a neighborhood matrix spanning a distance of 100 km, which was chosen due to highest spatial autocorrelation values within that distance. The number of incorporated spatial eigenvectors was based on Moran's I significance values for each GLM. Eigenvectors were included until they exceeded a significant Moran's I value ($p < 0.05$).

2.4.3. Ordination techniques: ecosystem service categories, land cover and climate – species richness

A multivariate direct gradient analysis was applied to investigate the proportion of species richness variances captured by potential as well as actual ecosystem services grouped into the MA categories and environmental variables. Initial analyses of data distribution and gradient lengths showed that linear models are a correct general assumption for our data. Hence we used a PCA to reduce multicollinearity inherent to the climatic parameters applied and a partially constrained RDA as overall multivariate model (Legendre and Legendre, 2012) to partition the explained variance of four different variable groups, such as potential and actual ecosystem services for each MA category, 'climate', 'land cover' and 'geography'. Species richness data from the considered taxonomic groups served as response variables and were subjected to Hellinger transformations as proposed for analyzing heterogeneous community datasets (Legendre and Gallagher, 2001). Climatic data were derived by performing a PCA, including 19 BIOCLIM variables that were obtained as downscaled spatial grids in a 2.5 arc-min resolution (Hijmans et al., 2005). The PCA scores from the first two principal components were extracted and subsequently used as 'climate' variable group for the RDAs (Hanspach et al., 2011). Land cover data were derived from the USGS land use survey 2006 comprising 16 land cover classes, including developed, forested, cultivated, wetland, herbaceous, scrubland and barren land cover types at a grid cell resolution of 30 meters. The original dataset was spatially downscaled to match the working resolution. To account for spatial autocorrelation effects, we defined latitude and longitude as a further variable group named 'geography'.

3. Results

3.1. Ecosystem service diversity and species richness

The compiled spatial layers of potential as well as actual ecosystem services, the derived Simpson diversity metrics of the considered taxa and ecosystem services varied across the study area (Fig. 1). The diversity of taxa and the diversity of ecosystem services were highly correlated, indicated by Spearman's $\rho = 0.719$ ($p < 0.001$). Species richness maps for mammals, birds, trees and amphibians are shown in online appendix (Fig. A1).

Ecosystem service diversity showed significant positive interactions with the richness of mammal, bird, tree, and amphibian

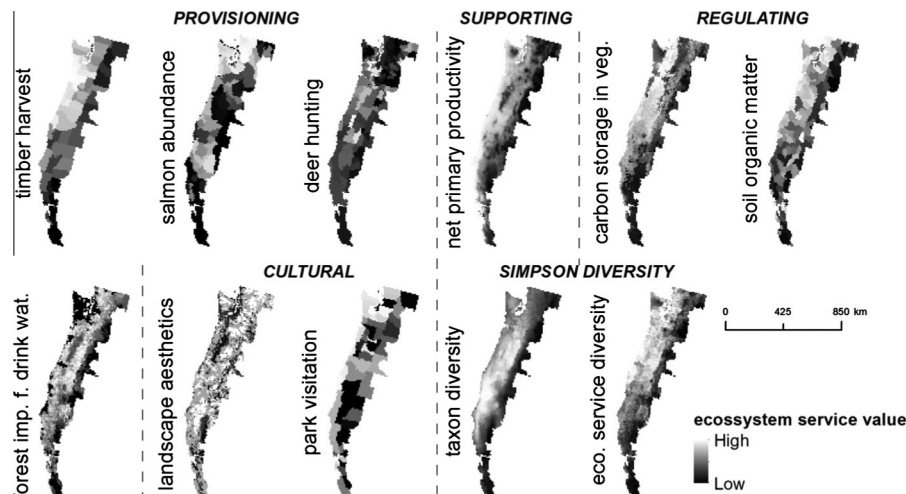


Fig. 1. Spatial distribution of nine potential and actual ecosystem services as well as the Simpson diversity of considered taxa and ecosystem services across the coastal temperate rainforest region of the Pacific Northwest, USA.

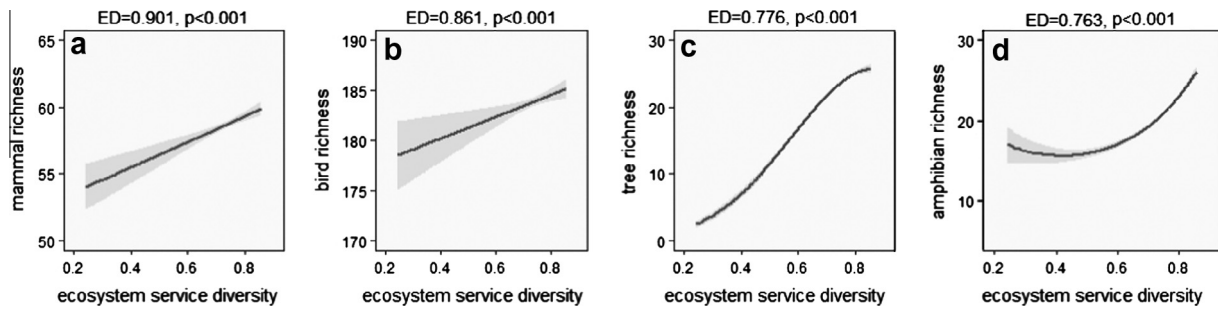


Fig. 2. GLM results for linkages between ecosystem service diversity and mammal, bird, tree, and amphibian richness. Incorporated spatial eigenvectors were kept at mean level. Light gray areas indicate the 95% confidence intervals of prediction errors (ED = explained deviance).

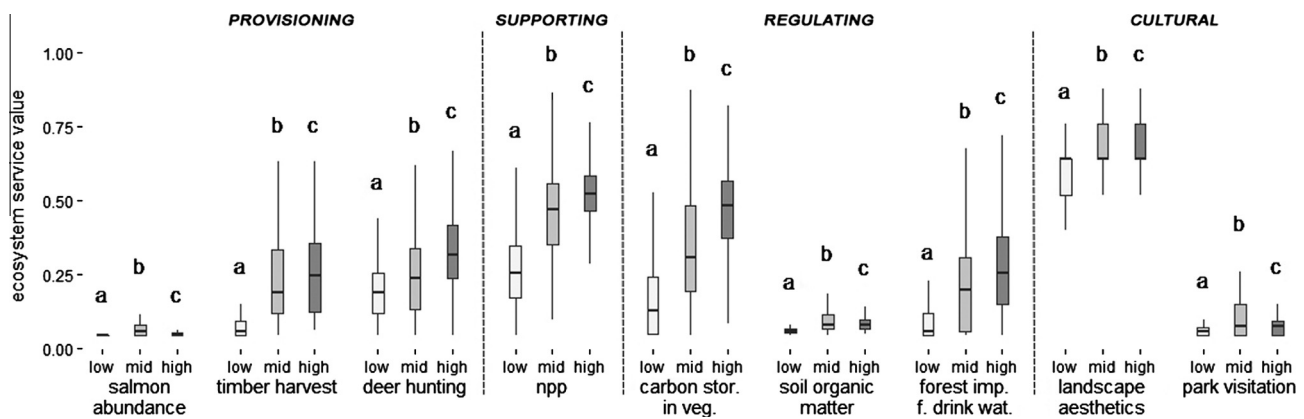


Fig. 3. Potential and actual ecosystem services for three levels of overall Simpson diversity of considered taxa (low = 0.335–0.514, mid = 0.514–0.573, high = 0.573–0.634). Grouping maintained equal sample sizes within each level. A Wilcoxon rank sum test was performed to assess the mean differences between Simpson diversity levels ($p < 0.001$). P -values were Bonferroni corrected to account for multiple testing.

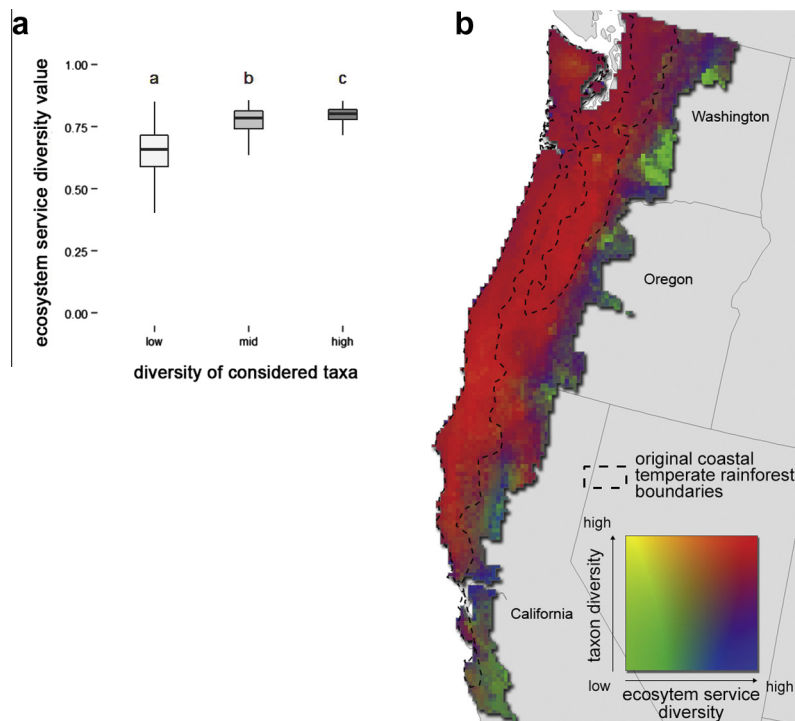


Fig. 4. (a) Ecosystem service diversity for three levels of overall Simpson diversity of the four considered taxonomic groups (low = 0.335–0.514, mid = 0.514–0.573, high = 0.573–0.634). Grouping maintained equal sample sizes within each level. A Wilcoxon rank sum test was performed to assess the mean differences between Simpson diversity levels ($p < 0.001$). P -values were Bonferroni corrected to account for multiple testing. (b) Spatial correspondence between ecosystem service diversity and diversity of considered taxa. Mapped pixel colors were assigned based on a RGB color space defined by ecosystem service diversity on the x-axis and diversity of four considered taxa on the y-axis.

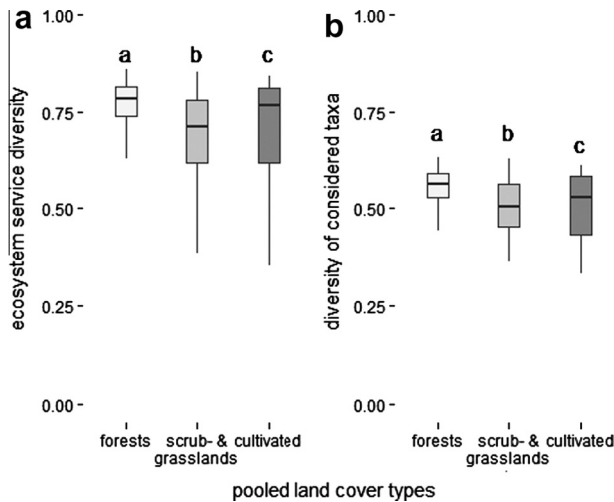


Fig. 5. Ecosystem service diversity (a) and diversity of considered taxa (b) for three pooled land cover types: forests, scrub- and grasslands, and cultivated areas. Developed land cover types were excluded due to minor relevance for the provisioning of analyzed ecosystem services.

species (Fig. 2, $p < 0.001$). Mammal and bird species richness increased linearly with higher ecosystem service diversity (Fig. 2a and b), tree richness showed a sigmoidal relationship indicating a saturation effect of tree species richness at the highest levels of ecosystem service diversity (Fig. 2c). Amphibian richness increased steeply with elevated ecosystem service diversity (Fig. 2d). The GLM on mammal richness had the highest model fit expressed as explained deviance (ED = 0.901), the model that considered amphibian richness the lowest (ED = 0.763).

3.2. Ecosystem services and taxon diversity

Higher values of ecosystem services were related to higher levels of the overall Simpson taxon diversity for most of the applied potential and actual ecosystem services across all MA categories (Fig. 3). However, salmon abundance, soil organic matter and park visitation differed from that pattern, indicating trade-offs between maxima of single ecosystem services and diversity of involved taxa. No pronounced ecosystem service gradient could be detected based on a PCA, including all modeled ecosystem services (not shown). The first two PCA axes together explained 46% of the overall variance.

Higher ecosystem service diversity was significantly linked to elevated taxon diversity (Fig. 4a, $p < 0.001$). However, less pronounced differences between medium and high levels of taxon diversity suggested a nonlinear relationship resulting in a saturation effect for ecosystem service diversity in areas of high taxon diversity. High spatial correspondence between ecosystem service diversity and the diversity of included taxa was shown within coastal temperate rainforest regions throughout most of the Pacific Northwest (Fig. 4b).

3.3. Ecosystem service categories as indicators for species richness

To assess both the distribution of ecosystem service diversity and the diversity of higher taxa for major land cover types, we pooled the detailed land cover types into three groups, namely, 'forests', 'scrub- and grasslands', and 'cultivated areas'. Highest diversity values for ecosystem services as well as considered taxa were significantly higher for forests (Fig. 5a and b, $p < 0.05$). Groups differed significantly as assessed through a one-way analysis of

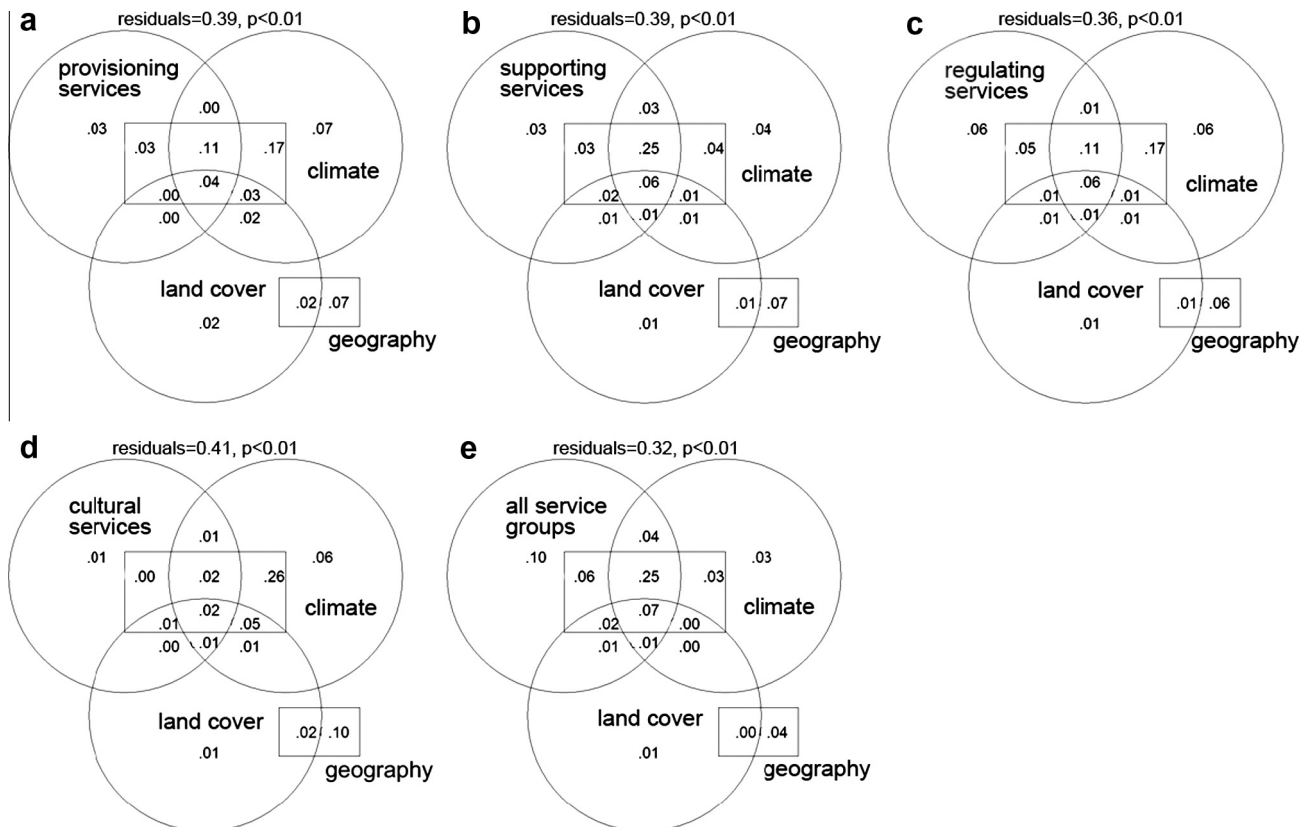


Fig. 6. RDA variance partitioning results for species richness including mammals, birds, trees and amphibians separately indicated by different ecosystem service categories: (a) provisioning, (b) supporting, (c) regulating, (d) cultural and (e) all potential and actual ecosystem services, climate, land cover (circles) and geography (rectangle). Displayed values show captured variances as adjusted R^2 for all single (non-overlapping parts of circles and the rectangle) and combined effects (overlapping parts of circles and the rectangle).

variance and a subsequent paired *t*-test ($p < 0.05$). *P*-values were Bonferroni corrected to account for multiple testing.

Constrained RDAs revealed that ecosystem service categories significantly indicated species richness in a comparable magnitude of land cover and climate (Fig. 6, $p < 0.001$). Among the RDAs that were fitted with single ecosystem service categories, the RDA with regulating services showed the lowest model error (Fig. 6c, residuals = 0.36) and the one that included cultural services the highest error (Fig. 6d, residuals = 0.41). The RDA incorporating the entire set of potential and actual ecosystem services as variable group showed the lowest model error among all RDAs (Fig. 6e, residuals = 0.32). However, for the majority of RDAs the climatic space was, after geography, the variable group that captured most of the species richness variances. This reflected both the prevailing climatic gradient that shapes diversity patterns across the temperate rainforests of the Pacific Northwest and an inherent autocorrelation pattern. Focusing on interactions between variable groups the climate-geography interactions showed the strongest effects followed by the ecosystem service category–climate interactions.

4. Discussion

4.1. Ecosystem service diversity and species richness

We found broad, positive relationships between ecosystem service diversity and species richness. Such a pattern confirms the findings of Egoh et al. (2009) who illustrated a spatial congruency between ecosystem services and biological diversity in South Africa. No trade-offs were observed in our study between ecosystem service diversity and species richness. Other studies reported both trade-offs and concordances between ecosystem service hotspots and biodiversity or its conservation (Chan et al., 2006; Turner et al., 2007). Our results clearly show that high levels of biodiversity are found in areas that provide diverse actual and potential ecosystem services across the coastal temperate rainforest region of the Pacific Northwest. This pattern was also apparent when all considered taxa were combined to one diversity index, particularly within the original coastal temperate rainforest boundaries. Though, some minor areas showed a contrasting pattern of low biodiversity but high ecosystem service diversity. These scattered areas were mostly distributed at the inland edges of our study region indicating transition zones to other ecosystems that might start to harbor different species inventories not included in our study.

Saturation effects were revealed for tree species and overall taxon diversity suggesting that further ecosystem service increases in regions of highly diverse ecosystem service provision coincide with marginally higher biodiversity levels. This might relate to redundancies of present species in terms of the necessary ecosystem functions that are required to maintain considered ecosystem services (Duffy, 2009; Hector and Bagchi, 2007). Notwithstanding, including more services and thus more ecosystem functions would probably incorporate more biodiversity needed to sustain these functions (Gamfeldt et al., 2008). Moreover, biodiversity reduces the vulnerability of ecosystems to disturbances, serving both as a backup for functional degradation and to ensure diverse and fast responses to perturbations hence improving overall ecosystem resilience (Mori et al., 2013).

4.2. Ecosystem services and their diversity for different levels of taxon diversity

The majority of our results indicate positive relationships between single ecosystem services included and the overall diversity of the considered taxa. Similar patterns are found in recent studies (Balvanera et al., 2006; Schneiders et al., 2012), in particular for

productivity and biodiversity (Gamfeldt et al., 2013; Tilman et al., 2012) – though Costanza et al. (2007) found a temperature dependent relationship. The relation between timber harvest and taxon diversity was most surprising and probably, in part, resulted from a scale artifact inherent to the data used. It is important to note here that the established relationships do not imply causality. Yet, intense forest management is usually considered to have negative impacts on biodiversity (Bengtsson et al., 2000). The data used in our study did not include any information on how the forests are managed for timber harvest on a local scale. Hence, it is beyond the scope of our analyses to assess the effects of forest practices on biodiversity patterns.

Despite the largely positive patterns found, a few trade-offs were noticeable in our results. Salmon abundance, soil organic matter and park visitation were highest in areas with moderate levels of taxon diversity. Non-supporting patterns or trade-offs among ecosystem services are postulated (Bennett et al., 2009) and reported on a regional (Raudsepp-Hearne et al., 2010), continental (Haines-Young et al., 2012) and global scale (Naidoo et al., 2008). Though, in our case, no clear trade-offs among the studied ecosystem services could be detected.

4.3. Ecosystem service categories as indicators for species richness

Both, ecosystem service diversity and taxon diversity were highest in forested extents within the study region. Although the differences among land cover types were only marginal, it suggests that forests provide conditions most suited for supplying ecosystem services and biodiversity.

Using a multivariate approach, including the nine actual and potential ecosystem services grouped into MA categories as well as environmental variables showed that the different MA ecosystem service categories indicated species richness of the four different taxa in a comparable magnitude to climate and land cover. The capability of all ecosystem service categories, in interaction with climate, to indicate species richness illustrates that a management focusing on multiple ecosystem-based benefits and the current climatic conditions are synergistic for both ecosystem services and biodiversity. These findings support the idea that the ecosystem service approach could be used to monitor and manage biodiversity (Egoh et al., 2009). However, cultural services showed an overall weak link, probably due to the most indirect relationship to richness for instance compared to the considered regulating ecosystem services. Nevertheless, the management of ecosystems based on providing a diversity of ecosystem services might have co-benefits in terms of biodiversity conservation.

4.4. Ecosystem service approach and multifunctional ecosystems

Temperate rainforests of the Pacific Northwest simultaneously offer a multitude of ecosystem-based benefits. We were able to show that such a multifunctional ecosystem might serve as indicator of biodiversity and its conservation while delivering important goods and services to society. Our results are restricted to one region and spatial scale as well as one point in time. Thus, extrapolating these results to other regions featuring different ecosystem properties and species should be done with considerable caution. However, high biodiversity levels in multifunctional landscapes also have been shown before for areas with heterogeneous land use or agricultural regions (O'Farrell et al., 2010; Schneiders et al., 2012; Sircely and Naem, 2012). Managing for multiple ecosystem services may also create conditions for higher levels of biodiversity. Given the co-occurrence of biodiversity and diverse ecosystem service provision, we suggest that biodiversity conservation should be integrated into the management of

multifunctional ecosystems and not only take place in areas explicitly designated for conservation.

4.5. Threats to ecosystem services and biodiversity: land use and climate change

North America's temperate rainforests are fragmented by logging, road building, and other human disturbances (DellaSala, 2011). Coinciding biodiversity loss and the degradation of ecosystem functions are expected due to habitat fragmentation and increasing land use intensity (Foley et al., 2005). However, sustainable trajectories of land use changes and restoration efforts have been positively linked to ecosystem service provision and biodiversity conservation (Nelson et al., 2009; Rey Benayas et al., 2009).

Ecosystem services in this region are threatened by a changing climate regime and projected vegetation shifts in Western North America (Wang et al., 2012). Dominant tree species and vegetation types in our study area are predicted to shift substantially until the end of the 21st century (Coops and Waring, 2011; Gonzalez et al., 2010; McKenney et al., 2007), probably detrimentally affecting both current ecosystem service and biodiversity patterns. Hence, an adaptive ecosystem management approach is needed to mitigate estimated impacts.

5. Conclusions

Our results confirm that multifunctional landscapes, here largely covered by temperate rainforests, co-occur with high levels of biodiversity. Thus, the management of ecosystem services should not substitute, but rather incorporate, biodiversity conservation since the two concepts are interdependently related through maintaining the functioning of ecosystems on the one hand and the management for goods and services on the other hand (Ingram et al., 2012; Mace et al., 2012). Based on our results, we derive the following management and research recommendations for the coastal temperate rainforest region across the Pacific Northwest.

1. The concepts of ecosystem services and biodiversity are not only linked, they act in concert. Based on our analysis, an integrative approach of ecosystem management that incorporates both ecosystem services and biodiversity is indeed beneficial in providing goods and services to society while maintaining biodiversity. We therefore support the perspective that multifunctional ecosystems should become a key for sustainable ecosystem management in this region, particularly in a way that optimizes land-use and strives for compatibility in management among different ecosystem services.
2. Our findings generally show that land managers who are interested in the provisioning of diverse ecosystem services are also able to maintain biodiversity. For instance, large landscape level management efforts inherent to the Northwest Forest Plan (DellaSala and Williams, 2006) represent approaches in which ecosystem management and biodiversity conservation on public lands are capable to produce multiple ecosystem benefits and, hence, help to maintain multifunctionality.
3. Research at finer spatial scales, incorporating time series data and information on how local forest management practices determine possible relationships between timber harvest, other ecosystem services and biodiversity would be useful for our study region. Standardized surveys and sampling protocols are required and data on socio-economical dynamics and ecosystem service valuations should be linked to assess the compatibility of (potentially competing) provisioning ecosystem services at the local and regional scale. Scenario driven analyses

(Carpenter et al., 2006; Nelson et al., 2009) that consider climate and land-use changes are necessary since they may offer valuable insights about possible future trajectories of biodiversity and ecosystem service patterns in this region.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.12.003>.

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FIRST RECORD OF THE NORTHERN SPOTTED OWL NESTING IN FOREST BURNED AT THE HIGHEST LEVEL OF SEVERITY

TONJA Y. CHI, 597 Maple Avenue, Campbell, California 95008;
tonja_chi@hotmail.com

ABSTRACT: An instance of the Northern Spotted Owl (*Strix occidentalis caurina*) nesting successfully in severely burned forest indicates that under some circumstances, such habitat may indeed provide the species suitable habitat. Current forest-management approaches treat wildfire as the primary cause of habitat loss for both the Northern and California (*S. o. occidentalis*) Spotted Owls. Assumptions that severely burned forest does not provide any viable nesting or roosting habitat for these Spotted Owl subspecies has resulted in substantial post-fire logging and removal of burned trees throughout both owls' ranges. In addition, forest management intended to prevent severe fires may entail thinning of unburned Spotted Owl habitat to reduce tree density and potential fuel loads. In the Mendocino National Forest of western Glenn County, California, I followed a pair of Northern Spotted Owls nesting and roosting deep within a large patch of severely burned forest two years after a fire, in a stand with no post-fire salvage logging, pre-fire thinning, fuels reduction, or attempts at restoration. A pair of Spotted Owls had used this location consistently since 1990, and the territory remained occupied with owls roosting and nesting successfully in 2022, despite 73% of the territory burning at high severity in 2020.

Under the Federal Endangered Species Act, the United States Fish and Wildlife Service (USFWS) designated the Northern Spotted Owl (*Strix occidentalis caurina*) a threatened subspecies in 1990 (USFWS 1990). Despite 25 years of this designation the subspecies has continued to decline precipitously throughout its range. In 2020, the USFWS reexamined the Northern Spotted Owl's vulnerability to extinction and confirmed severe and significant downward population trends, with declines of 32–77% since the early 1990s (USFWS 2019). The USFWS (2020) concluded that an elevating the owl's status from "threatened" to "endangered" was "warranted but precluded," meaning that although the Northern Spotted Owl met the requirements to be designated "endangered," the agency lacked the resources to take action at that time. The USFWS (2019) recognized the primary threats to the Northern Spotted Owl as competition with the Barred Owl (*Strix varia*), past and present habitat loss from timber management, and stated that "the primary loss of habitat is due to wildfire." Although the USFWS (2019) briefly mentioned post-fire logging, the agency failed to consider loss of potential *Strix occidentalis* habitat caused by logging of severely burned forest because such burned forest is not recognized as suitable habitat for the Spotted Owl's nesting or roosting. Here I document the successful nesting and roosting by a pair of Northern Spotted Owls in a large severely burned patch of forest, which indicates not only that such burned areas need closer examination, as they may offer breeding Spotted Owls viable habitat, but that the practice of logging severely burned forest should be reevaluated.

The Spotted Owl is recognized as having high site fidelity to established territories that meet fundamental biological needs and may remain in a terri-

tory even after a fire (Lee and Bond 2015). Although the Spotted Owl activity center I monitored was not surveyed every year, records such as those available through the California Natural Diversity DataBase (CNDDDB: <https://wildlife.ca.gov/Data/CNDDDB/Spotted-Owl-Info>; accessed on 20 February 2024) attest to stable long-term occupancy of this site (confirmed occupancy: 1977, 1980, 1982, 1990, 1992, 2002, 2006, 2008, 2021, 2022; confirmed reproductive success: 1980, 1990, 1992, 2002, 2008, 2022). In 2020 this entire Northern Spotted Owl activity center was burned in the August Complex Fire at high severity, typically defined as 76–100% mortality of the basal area of trees (USDA 2021b). In 2022, two years following the August Complex Fire, I returned to this site and confirmed Northern Spotted Owls nesting and roosting more than 1.5 km from the edge, within the deep interior of a 4500-ha swath of severely burned forest where 100% of the trees within at least 50 m of the nest and roost trees were killed. This may be the first report of a Northern Spotted Owl nest located in a large severely burned patch of mixed conifer forest.

The recent increase of wildfire in the Spotted Owl's habitat raises the question of the relationship between fire and the owl's habitat use over both the short and long term (CDFW 2016, Lesmeister et al. 2018, USFWS 2019). This increase raises concern for loss of high-quality nesting and roosting habitat, the scarcity of which has historically limited the number of Spotted Owl territories. Although the increase of fire has created more opportunity for study of the relationship between the Spotted Owl and burned forest (Clark et al. 2013, Rockweit et al. 2017, Bond et al. 2022), there remains little conclusive information about effects of fire *only*, unencumbered by logging pre- or post-fire (Bond et al. 2022, Hanson et al. 2021).

Most studies reporting fire to have negative effects on the Spotted Owl have not been able to distinguish between the effects of fire itself versus those of post-fire logging (Hanson et al. 2021). The few studies that have separated the two effects have shown that the effects of fires of mixed levels of severity are neutral or positive, while those of post-fire logging are consistently negative (Lee 2020, Hanson et al. 2021). The Northern Spotted Owl's use of severely burned forest has not been investigated, yet in the absence of published evidence such forest has been broadly assumed to be unsuitable for nesting or roosting habitat. Implicit in this assumption is the inference that the owl nests and roosts only in habitat traditionally considered suitable.

The Northern Spotted Owl's traditional nesting and roosting habitats in unburned forests of northwestern California are well documented, being characterized by structural complexity, decadent features, old conifers of large diameter, high basal area of live trees, trees of mixed ages, a multi-storied canopy, a high percentage of canopy cover, and coarse downed woody debris (Blakesley et al. 1992, Folliard et al. 2000, LaHaye and Gutiérrez 1999). With little information on how Spotted Owls respond to wildfire, these characteristics of unburned forest have been assumed to be the same requirements the owl needs to nest and roost in burned forests, fostering the idea that forests burned at high severity are unsuitable habitat (USFWS 2019). However, widespread assumptions that *Strix occidentalis* does not use burned habitats are inconclusive and untested because of widespread logging of severely burned forests, including those encompassing Northern Spotted Owl territories

(Bond et al. 2022). As reported by many (Brown 2008, Lee et al. 2013, Hanson et al. 2018) and statistically supported by other research (Bond et al. 2009, Clark 2007, Clark et al. 2011, 2013), *Strix occidentalis* avoids areas logged after fire. Whether Spotted Owls may nest or roost within severely burned areas that have not been logged after the fire, however, has not been investigated.

Many studies of the California Spotted Owl's relationship with wildfire have been similarly faced with the challenge of isolating the effects of wildfire from those of other factors. California Spotted Owl studies able to distinguish between these factors have found fire to be either neutral or slightly positive for territorial occupancy and survival (Bond et al. 2002, Roberts et al. 2011, Lee et al. 2012, Lee and Bond 2015, Hanson et al. 2018, Schofield et al. 2020). Studies that failed to document post-fire logging and distinguish between behavioral responses to post-fire logging versus severe fire (Comfort et al. 2016, Jones et al. 2016, 2020, Rockweit et al. 2017) may also have failed to recognize the ecological role such burned forests may play in the Spotted Owl's biology.

METHODS

Study Area

The Mendocino National Forest is located in northwestern California on the inland eastern spur of the northern California's Coast Range. It is about 320 km north of San Francisco and 195 km northwest of Sacramento. My observations took place at elevations from 1425 to 1460 m in Glenn County, on a west-facing slope within a patch burned at high severity in the 417,898-ha August Complex Fire of 2020. The fire burned hot through this entire area, including a 40-ha "late-successional reserve" composed of mature mixed coniferous forest. The reserve was surrounded by early- to mid-successional forest heavily logged in the mid-1980s, when approximately 85 ha of forest was removed. Draining into Butte Creek on a moderate slope are multiple year-round and ephemeral waterways.

Spotted Owl Surveys

In May and June 2002, my Spotted Owl surveys followed the protocol specified by the USFWS (1992), whereas those in May and June 2022 adhered to the updated "Protocol for Surveying Proposed Management Activities that May Impact Northern Spotted Owls" (USFWS 2012). All observations and data for each field visit were recorded and compiled on individual field outing forms with attached United States Geologic Survey (USGS) topographic 7.5-minute quadrangle maps, showing coordinates obtained from a hand-held Garmin GPS unit (global positioning system).

RESULTS

In 2002, I was one of a two-person team documenting a pair of Northern Spotted Owls with two successfully fledged young in the Mendocino National Forest. The habitat within the core area (within 1126 m of the nest) consisted of traditional nesting/roosting habitat in late-successional forest.

In 2022, after the area burned in the August Complex Fire of 2020, I located

a Northern Spotted Owl nest ~325 m downslope and west of the nest used in 2002 and identified several of the male's day-roost sites. The Northern Spotted Owl nest and roosts were >1300 m from the perimeter of a ~4500-ha patch burned at high severity (Figures 1–4). The nest contained three nestlings, of which two successfully fledged (Figure 2). It was situated in a cavity within a Douglas fir (*Pseudotsuga menziesii*) tree (diameter at breast height 105.5 cm) that was fire-scorched and moribund (Figure 1). The nest tree and some others in the same stand were not immediately killed by the fire but subsequently died between 2021 and 2022, as dead needles remained on branches. The nest tree stood approximately 30 m tall, with the south-facing nest cavity approximately two-thirds up the trunk, midway up a ~30° west-facing slope. The nearest live tree was ≥50 m north of the nest along a large perennial creek. In addition, I observed the male roosting by day on two separate days in burned snags ~38 m southwest and ~33 m southeast of the nest (Figure 3). Concentrated accumulations of recent whitewash and pellets indicating routine owl use lay around the trunks of many other burned trees within 40 m of the nest tree and throughout the burned stand. Chew marks observed on feather shafts found on the ground ~30 m south of the nest tree implied mammalian predation of the third chick.

The severity of the fire in these owls' home range, based on the USGS's Monitoring Trends in Burn Severity Project (www.mtbs.gov; accessed on 13 March 2024), is shown in Figures 4a and 4b. Within the home range (radius 2092 m), the severity of the fire was 73% high, 20% moderate, 6% low, and 1% unburned.

DISCUSSION

For the California Spotted Owl, Lee and Bond (2015) found an 87% probability of a pair occupying a previously identified territory even when 100% of the 121-ha activity center had been burned severely. Though I found no previous records of Spotted Owls nesting in such burned forest, my results here add to those of Lee and Bond (2015) regarding the California Spotted Owl. Mine may be the first documentation of the Northern Spotted Owl nesting within severely burned forest, but the findings of Lee and Bond (2015) with the California Spotted Owl imply that nesting under such conditions is unlikely an isolated event. The lack of previous documentation of Northern Spotted Owl nests inside large patches of forest burned at high severity may reflect the very high proportion of such areas that are logged shortly after wildfires (Bond et al. 2022), as well as the long-standing assumption by land managers and Spotted Owl survey crews that severely burned forest is not suitable for Spotted Owl nesting or occupancy (USFWS 2019). This assumption may lead to nest-site surveys within the few large severely burned patches that are not largely clearcut soon after the fire being inadequate or lacking (Bond et al. 2022).

The 2022 Northern Spotted Owl nest that I documented in the area burned in the August Complex Fire had three nestlings, of which two fledged successfully (Figure 2). Spotted Owls typically rear one or two young and have been rarely known to fledge three in any given season (Bond et al. 2013). Thus a brood of three offspring suggests that this severely burned forest provided

NORTHERN SPOTTED OWL NESTING IN SEVERELY BURNED FOREST



FIGURE 1. Northern Spotted Owl cavity nest in mixed conifer forest severely burned in the 2020 August Complex Fire, Mendocino National Forest, 1 June 2022.

Photo by Maya Khosla



FIGURE 2. Adult Northern Spotted Owl with two fledglings in mixed conifer forest severely burned in the 2020 August Complex Fire, Mendocino National Forest, 3 July 2022.

Photo by Tonja Chi



FIGURE 3. A northeast-facing view of two roost trees (indicated by yellow arrows) of a male Northern Spotted Owl in mixed conifer forest severely burned in the 2020 August Complex Fire, Mendocino National Forest, 19 May 2022.

Photo by Tonja Chi

prey sufficient to support a brood of at least typical size (Bond et al. 2013). Lee (2020) found that Spotted Owl productivity increased as the proportion of the pair's territory burned severely increased. Examples of increased prey abundance resulting in increased brood sizes and larger clutches are common in other raptor species, for example, the Great Horned Owl (*Bubo virginianus*;

NORTHERN SPOTTED OWL NESTING IN SEVERELY BURNED FOREST

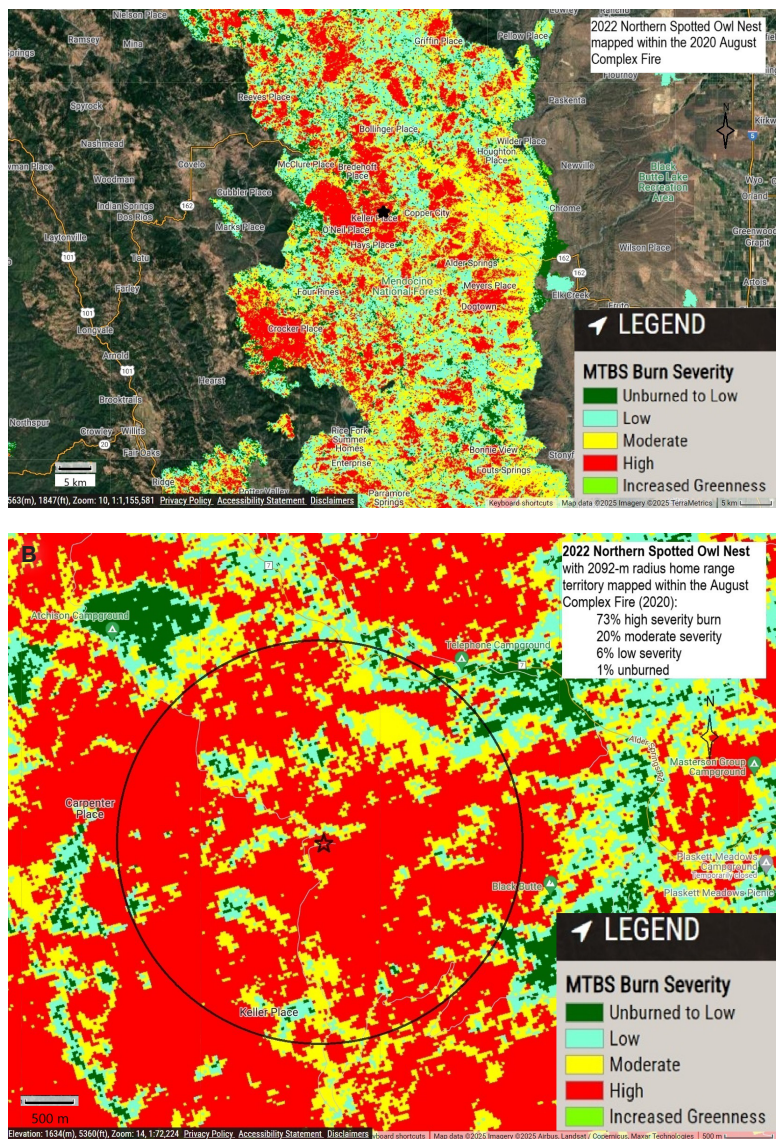


FIGURE 4. Location of Northern Spotted Owl nest (black star), plotted on a map of levels of fire severity in areas burned in the August Complex Fire of 2020. Fire-severity data obtained from the Monitoring Trends in Burn Severity Project of the USGS (2024). (A) The southern half of the 2020 August Complex Fire, Mendocino National Forest. (B) Closer view, showing a radius of 2092 m around the nest, defining the pair's home range or activity center (indicated black circle).

Reynolds et al. 2021), Eurasian Eagle Owl (*Bubo bubo*; Hadad et al. 2024), Tengmalm's or Boreal Owl (*Aegolius funereus*; Korpimäki 1990), and Eurasian Kestrel (*Falco tinnunculus*; Korpimäki and Wiehn 1998).

My surveys in 2022 were a response to the Mendocino National Forest's proposal, in the wake of the August Complex Fire, to salvage-log 306 ha (Plaskett-Keller Phase I Project) around the Northern Spotted Owl nest I found active. This proposal would have resulted in the removal of one quarter of the burned forest within 2.1 km of the nest or one quarter of the 1372-ha territory. The project's environmental assessment (USDA 2021a) also specified logging much of the severely burned forest in two other Northern Spotted Owl activity centers. The following excerpt from the proposal is a common example of the assumptions have been frequently applied to severely burned forest: "All three of these [activity centers] have the most habitat loss from fire. Nesting and roosting habitat has been greatly diminished, and new nests are not expected to occur in these activity centers" (USDA 2021a). The Northern Spotted Owls I observed were roosting (Figures 2 and 3) and nesting (Figure 1) in a long-established territory deep within the perimeter of the August Complex Fire in which tree mortality two years after the fire was 100% (Figure 4a).

SUMMARY

A successful Northern Spotted Owl nest located in a patch of severely burned forest suggests an unrecognized value to such burned forest—it may be not only beneficial but essential to Spotted Owls after a wildfire. Currently, this habitat is regularly undervalued, overlooked, and routinely removed, be the forest federally, state, or privately owned (Bond et al. 2022). This finding of a successful Spotted Owl nest within a large patch of severely burned forest introduces a new dialog to evaluation of the species' use of burned landscapes. It emphasizes the need for further research into such use, as well as a need for establishment of new protections of such sites from post-fire logging. It appears that the high-quality conditions for nesting and roosting observed at this site in 2002 (unmanaged from 2002 to 2022) persisted in a different form after the territory burned in 2020.

Most public lands on which the Spotted Owl has been studied have a long history of management and timber harvest, with national parks being the exception. This emphasis on logged forest has likely led to the habitat at a large percentage of study sites being complex and heterogeneous, a baseline variable not considered when different regions are compared. Schofield et al. (2020), who studied the Spotted Owl in areas burned at mixed levels of severity within national parks protected from logging, compared their results to those of other studies conducted in wildfire-burned and managed forests. They surmised that pre-fire forest structure was likely paramount to the legacy of post-fire habitat conditions the owls need. My findings, in a stand of high-quality habitat pre-fire, demonstrate that severely burned forest can not only provide nesting and roosting habitat for Northern Spotted Owl but may supply an enhanced food abundance, allowing for an increase in fecundity, as indicated by Lee (2020). This finding suggests not only the need to increase protection of severely burned forest but also protection of the

habitat's structural complexity pre-fire, essential for resilience in maintaining habitat value for *Strix occidentalis* post-fire. It further highlights pre- and post-fire forest conditions as aspects of *Strix occidentalis* territories that must be protected to slow the continuing loss and degradation of Northern Spotted Owl habitat, identified as a top contributing factor to the Northern Spotted Owl's population decline range wide (USFWS 2019).

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Research Article

Relationship Between Wildfire, Salvage Logging, and Occupancy of Nesting Territories by Northern Spotted Owls

DARREN A. CLARK,¹ Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

ROBERT G. ANTHONY, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

LAWRENCE S. ANDREWS, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

ABSTRACT The northern spotted owl (*Strix occidentalis caurina*) is one of the most intensively studied raptors in the world; however, little is known about the impacts of wildfire on the subspecies and how they use recently burned areas. Three large-scale wildfires in southwest Oregon provided an opportunity to investigate the short-term impacts of wildfire and salvage logging on site occupancy of spotted owls. We used Program MARK to develop single-species, multiple-season models of site occupancy using data collected during demographic surveys of spotted owl territories. In our first analysis, we compared occupancy dynamics of spotted owl nesting territories before (1992–2002) and after the Timbered Rock burn (2003–2006) to a reference area in the south Cascade Mountains that was not affected recently by wildfire. We found that the South Cascades had greater colonization probabilities than Timbered Rock before and after wildfire ($\hat{\beta} = 1.31$, 95% CI = 0.60–2.03), and colonization probabilities declined over time at both areas ($\hat{\beta} = -0.06$, 95% CI = -0.12 to 0.00). Extinction probabilities were greater at South Cascades than at Timbered Rock prior to the burn ($\hat{\beta} = 0.69$, 95% CI = 0.23–2.62); however, Timbered Rock had greater extinction probabilities following wildfire ($\hat{\beta} = 1.46$, 95% CI = 0.29–2.62). The Timbered Rock and South Cascades study areas had similar patterns in site occupancy prior to the Timbered Rock burn (1992–2001). Furthermore, Timbered Rock had a 64% reduction in site occupancy following wildfire (2003–2006) in contrast to a 25% reduction in site occupancy at South Cascades during the same time period. This suggested that the combined effects of habitat disturbances due to wildfire and subsequent salvage logging on private lands negatively affected site occupancy by spotted owls. In our second analysis, we investigated the relationship between wildfire, salvage logging, and occupancy of spotted owl territories at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006. Extinction probabilities increased as the combined area of early seral forests, high severity burn, and salvage logging increased within the core nesting areas ($\hat{\beta} = 1.88$, 95% CI = 0.10–3.66). We were unable to identify any relationships between initial occupancy or colonization probabilities and the habitat covariates that we considered in our analysis where the β coefficient did not overlap zero. We concluded that site occupancy of spotted owl nesting territories declined in the short-term following wildfire, and habitat modification and loss due to past timber harvest, high severity fire, and salvage logging jointly contributed to declines in site occupancy. © 2013 The Wildlife Society.

KEY WORDS colonization, extinction, northern spotted owl, occupancy, salvage logging, site occupancy, southwest Oregon, *Strix occidentalis caurina*, wildfire.

Northern spotted owls (*Strix occidentalis caurina*, hereafter spotted owl) are a medium sized, forest-dwelling owl with high levels of mate and site fidelity (Forsman et al. 1984, 2002; Thomas et al. 1990; Zimmerman et al. 2007). Nesting territories of spotted owls have greater proportions of mature and older forest than surrounding landscapes (Ripple et al. 1991, 1997; Meyer et al. 1998; Swindle et al. 1999). Forest

stands used by spotted owls have large proportions of downed woody debris and snags, high canopy cover and high structural diversity (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). The features that provide structural complexity within spotted owl habitat also serve as ladder fuels that increase the likelihood of stand-replacing wildfire (Agee 1993, Wright and Agee 2004). As a result, forest stands that provide favorable habitat conditions for spotted owls within dry forest ecosystems are at risk of stand-replacing wildfire (Agee 1993, Agee et al. 2000). Presently, wildfire is the leading cause of spotted owl habitat modification on

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¹E-mail: darren.clark@oregonstate.edu

federally administered lands, and the rate of habitat modification due to wildfire within dry forest ecosystems has exceeded predictions (Davis and Lint 2005). Consequently, the viability of owl populations in dry forests has been questioned (Spies et al. 2006), and wildfire has been identified as a threat to the persistence of spotted owls occupying dry forest ecosystems (U.S. Fish and Wildlife Service [USFWS] 2011).

Despite the perceived threat of wildfire, little is known about the effects of wildfire on spotted owls, and the hypothesized effects come from research conducted in unburned landscapes. Numerous studies have documented that spotted owl survival, reproduction (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), and territory occupancy (Blakesley et al. 2005, Dugger et al. 2011) were positively associated with increased amounts of late-successional forest within their core use areas or home range. Furthermore, owl territories with large reductions in the amount of older forest will have low reproduction or be abandoned (Bart and Forsman 1992, Bart 1995). These studies suggest that loss of older forests negatively affects spotted owls; however, the response of spotted owls to high severity fire and subsequent harvest of dead standing trees is unknown. Conversely, survival rates of spotted owls were greater at territories that were not entirely composed of late-successional forests (Franklin et al. 2000, Olson et al. 2004), which suggests that spotted owls may be adapted to natural disturbances such as wildfire that create a mosaic of forest conditions. Territory occupancy and nest success of spotted owls decreased as the amount of the territory composed of clear-cuts increased (Thraill et al. 1998), which suggests widespread post-fire salvage logging may negatively affect spotted owls.

The few studies that have been conducted on spotted owls in burned landscapes have provided equivocal results regarding the effects of wildfire on the species. Lack of consensus between studies may be owing to the confounding effects of salvage logging, the short-term nature of studies, small sample sizes from which to draw inference, treating the effect of fire as a binomial variable (i.e., burned or unburned), or potentially different responses of the 3 subspecies of spotted owls to wildfire. Radio-marked northern and California spotted owls (*Strix occidentalis occidentalis*) used forest stands that burned with low to high severities (Clark 2007, Bond et al. 2009); however, survival rates of radio-marked northern spotted owls occupying a burned area that was subsequently salvage logged were less than others reported throughout the subspecies' range (Clark et al. 2011). Conversely, short-term (<1 yr) survival rates of northern, Mexican (*Strix occidentalis lucida*), and California spotted owls in burned landscapes that were not subjected to post-fire salvage logging were similar to annual survival rates (Bond et al. 2002). The number of reproductive spotted owl pairs and the number of occupied spotted owl territories declined 1 year post-fire on the eastern slope of the Washington Cascade Range (Gaines et al. 1997); however, only 6 territories were surveyed in this study, 1 of which had a large amount of stand-replacing fire. Other studies indicate low and moderate severity burns may have

minimal impacts on spotted owls. Territory occupancy of Mexican spotted owls in burned areas was similar to unburned areas (Jenness et al. 2004). Probability of territory occupancy for California spotted owls in the Sierra Nevada Mountains of California were similar between randomly selected burned and unburned sites (Roberts et al. 2011).

Because spotted owls are territorial and have high site fidelity (Forsman et al. 2002, Zimmerman et al. 2007), occupancy of nesting territories is essential for successful survival and reproduction. Occupancy models (MacKenzie et al. 2003, 2006) are well suited for investigating territory occupancy by spotted owls because the structure of existing spotted owl surveys (Franklin et al. 1996) fits the model framework well. Furthermore, occupancy models allow the inclusion of site-specific covariates, which allows the investigation of fire severity and habitat influences on site occupancy dynamics (i.e., extinction and colonization rates). The Biscuit, Quartz, and Timbered Rock burns in southwest Oregon provided an opportunity to investigate the impacts of wildfire and subsequent salvage logging on site occupancy by spotted owls. Our first objective was to determine if occupancy rates changed substantially following wildfire and subsequent salvage logging when compared to pre-burn occupancy rates and to occupancy rates in a landscape that had not been recently affected by wildfire. We met this objective by comparing occupancy rates of spotted owls before (1992–2002) and after (2003–2006) the Timbered Rock burn to an adjacent unburned landscape in the southern Oregon Cascades. We predicted that occupancy rates of spotted owls would be similar between study areas prior to the Timbered Rock burn but occupancy rates would decline substantially following the Timbered Rock burn in response to modification and loss of owl habitat from wildfire and subsequent salvage logging. Our second objective was to model the impacts of fire severity, salvage logging, and habitat characteristics on site occupancy of spotted owls at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006. We predicted that extinction probabilities would increase as the amounts of past timber harvest, high severity burn, and salvage logging within a territory increased. We also predicted that initial occupancy and colonization probabilities within the 3 burned areas would be greater at territories with decreased levels of disturbance. In particular, we predicted that initial occupancy and colonization probabilities within the 3 burned areas would be greater at territories that had more intermediate-aged and older forest that burned with low or moderate severities.

STUDY AREA

We studied site occupancy by spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon. Each burn was located within a distinct geographic region: the mid-Coastal Siskiyou Mountains (Biscuit burn), the Siskiyou Mountains (Quartz burn), and the southern Oregon Cascades (Timbered Rock burn). We also analyzed site occupancy of spotted owls at the South Cascades Demographic Study Area, which was adjacent to the

Timbered Rock burn and was not affected by a large scale wildfire within the last 100 years. Consequently, site occupancy by spotted owls in this area served as a reference for comparison to the Timbered Rock study area.

Common tree species within our study areas included ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), California red fir (*A. magnifica*), mountain hemlock (*Tsuga mertensiana*), Oregon white oak (*Quercus garryana*), California black oak (*Q. kelloggii*), tanoak (*Lithocarpus densiflorus*), and Pacific madrone (*Arbutus menziesii*). Prior to the implementation of active fire suppression policies by state and federal agencies, most of southwest Oregon was characterized by frequent low-intensity fires and occasional stand-replacing fires at higher elevations (Agee 1993, Taylor and Skinner 1997, Heyerdahl et al. 2001). After active fire suppression policies were implemented, fire frequencies declined and high-intensity wildfires became more common (Agee 1993, Agee and Skinner 2005). The climate regime in southwest Oregon is characteristically temperate with hot, dry summers and cool, moist winters. During our study, the warmest and coldest average daily temperatures occurred in July (21° C) and December (4° C), respectively. Average annual rainfall was lowest at the Quartz burn (66 cm) and highest at the Biscuit burn (113 cm; Oregon Climate Service, Oregon State University, unpublished data).

The Biscuit burn originated from several lightning strikes in July 2002. The small fires eventually merged into a complex fire that covered 201,436 ha. Land ownership within the burn was predominantly public (U.S. Forest Service [USFS], Bureau of Land Management [BLM], Oregon Department of Forestry [ODF], and Josephine County). Fifty documented spotted owl territories were within the burn. We non-randomly selected a sample of 9 territories on the eastern side of the burn to include in our study that were similar to forest types at the Timbered Rock and Quartz burns and provided reasonable access. The 9 territories included in this study were located within the Briggs Creek, Silver Creek, Deer Creek, and Illinois River watersheds, ranging in elevation from 300 to 1,400 m. The remaining 41 territories were not included in our study because of logistical concerns or because they were located in mesic forest types on the western side of the burn. The 9 study territories were surveyed annually from 2003 to 2006. The area within 2.2 km of the 9 study territories burned with a mixed severity and

received the least amount of salvage logging of the 3 burns (Table 1).

The Quartz burn was ignited by lightning in August 2001 and burned 2,484 ha of public (USFS, BLM, and ODF) and private (primarily industrial forest) lands. The fire burned portions of the Glade Creek, Little Applegate, and Yale Creek watersheds at elevations ranging from 600 to 1,850 m. The fire completely or partially burned (i.e., burned the majority of a 2.2-km buffer around the territory center) 9 spotted owl territories. All 9 territories were surveyed annually from 2003 to 2006. The study area burned with a mosaic of fire severities and was subjected to substantial amounts of salvage logging, primarily on private lands (Table 1).

The Timbered Rock burn was ignited by lightning in July 2002 and burned 11,028 ha of land within the Elk Creek watershed at elevations ranging from 450 to 1,350 m. Land ownership was dominated by a checkerboard pattern of public (BLM) and private industrial forest lands in the southern two-thirds of the burn and contiguous USFS managed lands in the northern third. Twenty-two spotted owl territories were within the burn perimeter and were surveyed annually from 2003 to 2006. These 22 territories were also surveyed prior to the burn from 1992 to 2002. The study area burned with a mixed severity and much of the private land was salvage logged (Table 1).

The South Cascades Demographic Study Area (South Cascades) is 1 of 8 study areas included in the range-wide monitoring program for spotted owls (Lint et al. 1999, Anthony et al. 2006), and it served as a reference area for our analyses. From 1992 to 2006, surveys to locate spotted owls were consistently conducted on an annual basis at 103 spotted owl territories by the Oregon Cooperative Fish and Wildlife Research Unit (OCFWRU). The South Cascades area encompasses approximately 223,000 ha of lands managed by the USFS at the southern terminus of the Oregon Cascades and at elevations ranging from 900 to 2,000 m. No large-scale wildfires occurred within the study area from 1992 to 2006. Forest conditions have been influenced historically by mixed-severity wildfire and more recently by forest management, livestock grazing, and fire suppression. Forest management has included individual tree selection, stand thinning, and even-aged management (U.S. Department of Agriculture [USDA] 1997, 1998). Current management activities are guided by the objectives set forth by the Land-use Allocations of the Northwest Forest Plan.

Table 1. The percentage (\pm SE) early seral, intermediate-aged or older forest that burned with a low, moderate, or high severity or was salvage logged within 2,230 m of 40 northern spotted owl territories at the Biscuit, Quartz, and Timbered Rock burns in southwest, Oregon, USA from 2003 to 2006.

Study area	Non-forest or early seral	Intermediate-aged or older forests			
		Low severity ^a	Moderate severity ^b	High severity ^c	Salvage logged ^d
Biscuit	27.2 \pm 6.1	40.5 \pm 6.7	13.6 \pm 1.8	17.1 \pm 3.6	1.6 \pm 0.7
Timbered Rock	27.8 \pm 1.6	35.9 \pm 4.1	10.1 \pm 0.7	9.3 \pm 1.4	16.9 \pm 3.2
Quartz	21.7 \pm 1.5	48.5 \pm 4.4	6.6 \pm 1.5	10.0 \pm 2.3	13.2 \pm 2.7

^a \leq 20% of the forest canopy removed by wildfire.

^b 21–70% of the forest canopy removed by wildfire.

^c $>$ 70% of the forest canopy removed by wildfire.

^d Areas that were intermediate-aged or older forest prior to the burn that were salvage logged.

The main purpose of matrix lands is timber production, whereas the late-successional reserves are for conservation of older forests and silvicultural treatments are intended to promote forest stand structures similar to historical conditions or old forest characteristics (USDA and U.S. Department of the Interior [USDI] 1994).

METHODS

Data Acquisition and Preparation

To assess the effects of wildfire on occupancy of spotted owl territories, we created post-fire habitat maps in ArcGIS 9.1 (ESRI, Redlands, CA) by merging 3 data layers: 1) a pre-fire habitat map (Davis and Lint 2005), 2) a fire severity map, and 3) the boundaries of salvage logged areas (see Clark 2007 for additional details). The final map output had 8 distinct habitat classes (Table 2) and a minimum mapping unit of 2 ha. We used ground plot data to calculate map accuracies, which we estimated to be 68% for the Timbered Rock burn, 69% for the Biscuit burn, and 75% for the Quartz burn. Seventeen of 20 (85%) classification errors at the Biscuit burn, 10 of 15 (67%) at the Quartz burn, and 11 of 22 (50%) at the Timbered Rock burn were within 1 habitat or fire severity class of the correct classification. Based on these estimates, overall map accuracy within 1 habitat or fire severity class was 95% at the Biscuit burn, 92% at the Quartz burn, and 84% at the Timbered Rock burn (Clark 2007).

We conducted annual surveys between 1 March and 31 August to determine the occupancy of spotted owls on nesting territories according to established survey protocols (Franklin et al. 1996) and Oregon State University, Institutional Animal Care and Use Committee guidelines (IACUC Number 3040). Post-fire surveys were conducted as a collaborative effort between the OCFWRU, the BLM, the USFS, and private timber companies. From 1992 to 2006, we surveyed 22 and 103 territories at the Timbered Rock and South Cascades study areas, respectively. We also surveyed 9 territories at both the Biscuit and Quartz burns from 2003 to 2006. The average number of visits conducted varied by study area and year (range: 1.9 [Timbered Rock 2002]–5.8 [Timbered Rock 1994]). The maximum number of surveys at individual spotted owl territories ranged from 7 to 9

depending on the year. The variability in survey effort was a function of occupancy and nesting status (i.e., territories that were occupied by a pair of non-nesting owls were visited less). Occasionally, some territories were not surveyed every year, which was most often because of limited access during years of high snowfall. Fortunately, differences in survey effort and missing observations can easily be accounted for in open population models if you assume that occupancy dynamics are the same at territories that are and are not surveyed (MacKenzie et al. 2006), which is a reasonable assumption as long as survey effort is unbiased.

We used results from demographic surveys to create site-specific detection histories for owl pairs. Owl pairs represent the appropriate ecological unit of interest when modeling site occupancy. Protocols for adapting survey data from spotted owls using methods outlined in Franklin et al. (1996) to fit an occupancy modeling framework were established by Olson et al. (2005). These protocols were used in subsequent occupancy analyses for spotted owls (Kroll et al. 2010, Dugger et al. 2011) and this analysis. If a pair of owls was detected, we coded the visit as a 1 and if 1 or no owls were detected, we coded the visit as a 0. However, if 1 owl was detected and the owl exhibited nesting behavior (e.g., the owl was observed on a nest) or if young were observed with an adult owl, we coded the visit as a 1. If a survey was not conducted, we coded the visit as a missing observation (·). A hypothetical detection history of 10.1 would indicate that a pair of owls was detected on the first and fourth surveys, no owls or a single owl was detected on the second survey, and the territory was not visited during the third survey.

Data Analyses

Basic modeling procedures.—We estimated site occupancy in Program MARK (White and Burnham 1999) using single-species, multiple-season models (MacKenzie et al. 2003, 2006). This analysis generated estimates of 4 parameters: Ψ , the probability that a site is occupied in the first year of the study (initial occupancy); ϵ , the probability an occupied site became unoccupied the subsequent year (extinction); γ , the probability an unoccupied site was occupied the subsequent year (colonization); and P , the probability of detection (detection). In our analyses, primary sampling occasions were years and secondary sampling occasions were visits to

Table 2. Definitions of habitats used in the assessment of the impacts of wildfire and salvage logging on northern spotted owl site occupancy at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA, from 2003 to 2006.

Habitat class	Description
Early seral	Non-forested areas, early seral, and pole sized conifer stands
Intermediate forest ^a —low severity burn	Intermediate-aged conifer stands with $\leq 20\%$ of the canopy removed by fire
Intermediate forest—moderate severity burn	Intermediate-aged conifer stands with 21–70% of the canopy removed by fire
Older forest ^b —low severity burn	Older conifer forest with $\leq 20\%$ of the canopy removed by fire
Older forest—moderate severity burn	Older conifer forest with 21–70% of the canopy removed by fire
High severity	Intermediate-aged and older conifer forests with $> 70\%$ of the canopy removed by fire
Salvage	Intermediate-aged and older conifer forests that were salvage logged
Edge	The interface between the combined area of intermediate-aged and older forest that burned with a low or moderate severity and all other habitat types

^a Forest stands that provide suitable roosting and foraging habitat for spotted owls.

^b Forest stands that provide nesting habitat for spotted owls.

territories within years. This modeling framework was flexible and allowed for time-specific parameter estimates, inclusion of site-specific covariates, the ability to include missing observations, the direct estimation of colonization and extinction, and it assumed detection probabilities were <1 (MacKenzie et al. 2003, 2006).

We modeled the 4 occupancy parameters using a step-wise approach (Olson et al. 2005, MacKenzie et al. 2006, Dugger et al. 2011). We first determined the most parsimonious model for within year detection probabilities followed by among year detection probabilities, retained that model, and then proceeded to model initial occupancy. We then retained the most parsimonious model for initial occupancy and proceeded to model colonization and extinction parameters. We followed the conventions of Lebreton et al. (1992) and White and Burnham (1999) when developing and naming models. We considered several possible temporal effects on detection probabilities both within and among years that included constant detection (\cdot), linear (T), log-linear ($\ln T$), and quadratic (TT) trends. We did not evaluate time-specific models (t) within years because they required estimation of too many parameters to obtain reasonable estimates (Olson et al. 2005); however, we considered models that included time-specific effects among years (year). We also considered models that included differences in detection probabilities between study areas, because experience and effort of survey personnel may have differed. We considered 2 initial occupancy models that contrasted differences between study areas (area) and constant initial occupancy (\cdot). When modeling extinction and colonization parameters, we considered models that compared differences between study areas (area) and no differences between areas (\cdot), and we considered several biologically plausible temporal effects including constant rates among years (\cdot), variable rates among years (t), and linear (T), log-linear ($\ln T$), and quadratic (TT) trends over time. Models that included ≥ 2 study areas included additive and interactive effects between study area and temporal effects, where appropriate.

We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) and the difference between the AIC_c value of the best model and the i th model (ΔAIC_c) to rank and compare candidate models at each step of the analysis. We used Akaike weights to evaluate the strength of evidence for 1 model versus another model (Burnham and Anderson 2002). We considered models that were ≤ 2.0 AIC_c of the best model as competitive. We used estimates of regression coefficients ($\hat{\beta}$) and their 95% confidence intervals to evaluate the relative effect and measure of precision of various covariates in our models. Following the approach outlined by Anthony et al. (2006), we used 95% confidence intervals for the coefficients as a relative measure of support for observed relationships rather than a strict test of the hypothesis that $\beta = 0$. Covariates whose 95% confidence intervals did not overlap 0 had strong evidence for an effect, those that narrowly overlapped 0 had some evidence for an effect, and those that broadly overlapped 0 had little or no evidence for an effect on the parameter of interest. We used this approach because significance testing is not valid under

an information theoretical approach (Burnham and Anderson 2002), and it is best to present estimates of effect size and precision under this analysis paradigm (Anderson et al. 2000).

Comparison of South Cascades and Timbered Rock.—We compared occupancy at Timbered Rock and South Cascades from 1992 to 2006. Our objective was to determine if extinction and colonization probabilities following the Timbered Rock burn were different from unburned landscapes in the South Cascades (i.e., the control) during the same time period. In this analysis, we considered all study area and temporal effects on site occupancy parameters that are outlined above in the basic modeling procedures. In addition, we considered 10 models for colonization and extinction that were modifications of common study area and time effect models (Fig. 1). We considered these models because they may identify distinct changes in extinction and colonization rates following a disturbance such as wildfire and subsequent salvage logging. We predicted that under model [Pre-burn(\cdot)Post-burn(area)] the South Cascades and Timbered Rock would have similar, constant extinction probabilities prior to the Timbered Rock burn, but extinction probabilities would be greater at Timbered Rock following the burn. In contrast, we predicted the opposite for colonization probabilities (e.g., under model [Pre-burn(\cdot)Post-burn(area)], colonization rates would be equal at Timbered Rock and South Cascades prior to the Timbered Rock burn, but colonization rates would be less at the Timbered Rock study area following the burn). We retained the best ranked initial occupancy, extinction, colonization, and detection probability models and combined them to determine our best overall model. We used the best overall model to calculate estimates of year-specific probabilities of site occupancy in Program MARK using the equation from MacKenzie et al. (2003):

$$\hat{\Psi}_t = \hat{\Psi}_{t-1}(1 - \hat{\varepsilon}_{t-1}) + (1 - \hat{\Psi}_{t-1})\hat{\gamma}_{t-1}$$

Relationship between wildfire, salvage logging, and spotted owl site occupancy.—We modeled occupancy of nesting territories after fires from 2003 to 2006 at the Biscuit, Quartz, and Timbered Rock burns. Our objective was to model the potential influence of fire severity, salvage logging, and habitat covariates on site occupancy of spotted owls. In this analysis, we used a multiple step approach outlined in previous occupancy analyses for the species (Olson et al. 2005, Dugger et al. 2011). This approach included 3 steps: 1) determine the occupancy model that best described temporal and study area effects, 2) retain the best model from step 1 and model individual covariates to determine the best spatial scale and relationship of the covariate, and 3) retain the best model from step 1 and the best spatial scale and relationship of covariates from step 2 to test specific hypotheses regarding the effects of covariates on site occupancy.

Our first step was to determine the best model that only included study area and temporal effects by following the methods outlined in the basic modeling procedures. Our objective in this step was to develop a base model upon

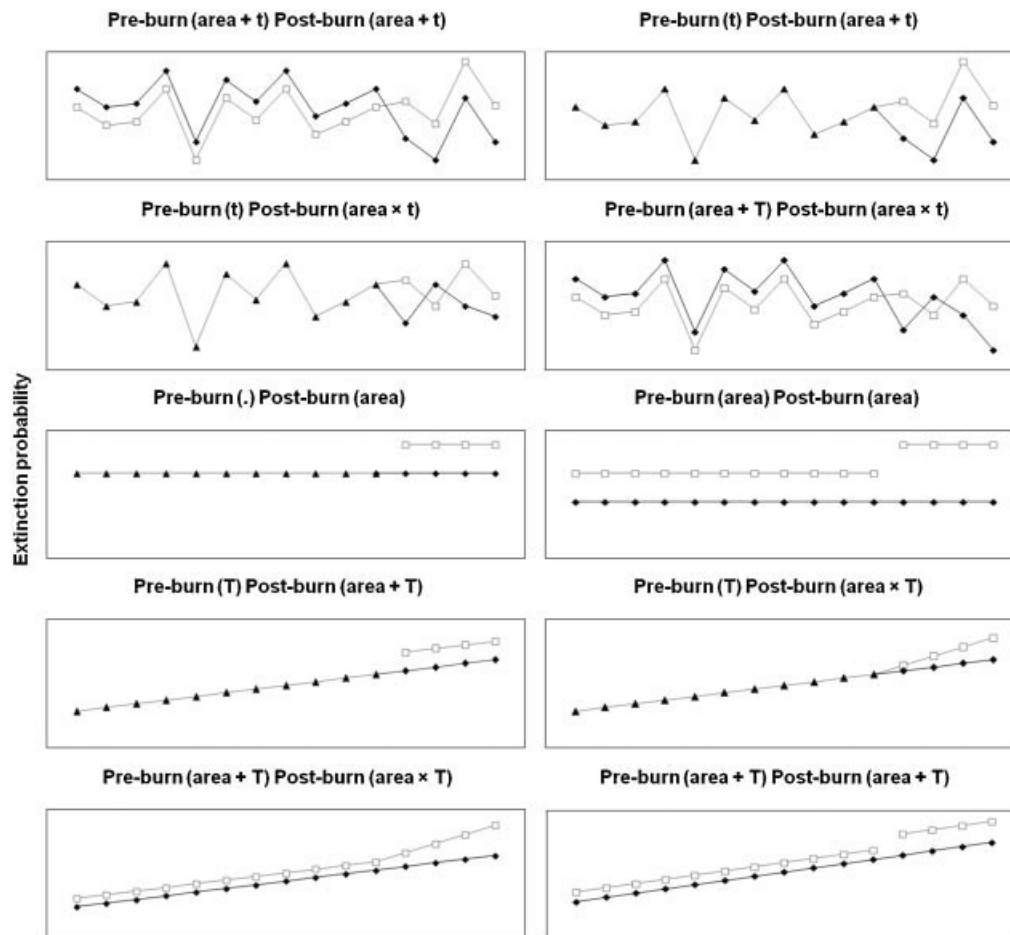


Figure 1. Visual representation of 10 hypothetical models comparing extinction rates of northern spotted owl territories at the Timbered Rock burn and South Cascades Demographic Study Area. We considered models that compared differences between study areas (area) and no differences between areas (\cdot), and we considered several biologically plausible temporal effects including constant rates among years (\cdot), variable rates among years (t), and linear (T) trends over time. The last 4 intervals represent the predicted changes in extinction probabilities following the Timbered Rock burn. The opposite relationship was predicted for colonization rates. Grey lines with open boxes represent the Timbered Rock study area, black lines with black diamonds represent the South Cascades Demographic Study Area, and gray lines with black triangles represent no differences between study areas.

which we modeled the effects of covariates. We considered all models outlined in the basic modeling procedures and 3 additional study area covariates for initial occupancy, extinction, and colonization models that incorporated various study area combinations including, 1) the Quartz and Timbered Rock burns would have similar occupancy dynamics because they include large amounts of private land ($BIS \neq TR = Q$), 2) the Timbered Rock and Biscuit burns would have similar occupancy dynamics because they occurred 1 year after the Quartz burn ($BIS = TR \neq Q$), and 3) the Quartz and Biscuit burns would have similar occupancy dynamics because they are both located in the Siskiyou Mountains ($BIS = Q \neq TR$). Our primary objective during this portion of the analysis was to develop a parsimonious model on which to model covariates; consequently, we did not consider competing models in this step of the analysis. After determining the best study area and temporal effects model, we retained this model and proceeded to the second step of the analysis.

In the second step of this analysis, our objective was to determine the spatial scale and relationship that best

explained the effect of various covariates on initial occupancy, extinction, and colonization probabilities. We calculated site-specific covariates at 2 spatial scales (territory and core area) and with 2 relationships (linear and log-linear), which represented 4 possible models for each covariate. We calculated covariate values in ArcGIS 9.1 from post-fire habitat maps as the percent of each cover type within a 2,230-m radius (1,560 ha; territory scale) and a 730-m radius (167 ha; core area scale) of the territory center. We selected these spatial scales because they were used to model spotted owl survival and reproduction in the same geographic region (Dugger et al. 2005).

For initial occupancy and colonization probabilities, we modeled 9 covariates (Table 3) to determine the best spatial scale and relationship of the covariate. All of the covariates we modeled on initial occupancy and colonization parameters were thought to represent the quality of habitat remaining at the territory and were based on biologically meaningful relationships. Forested areas that burned with a low or moderate severity likely had minimal changes in the amount of canopy cover, snags, and downed woody debris, which are

Table 3. Candidate model sets for initial occupancy, extinction, and colonization parameters in the analysis of covariate effects on site occupancy of northern spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA, from 2003 to 2006.

Initial occupancy (Ψ) and colonization (γ) ^a	Extinction (ϵ) ^b
INTL + INTM + OLDL + OLDM	EARLY + HIGH + SALVAGE
INTL + OLDL	HIGH + SALVAGE
INT + OLD	HARVEST + HIGH
OLDL + OLDM	EARLY + HISALV
OLDL	HISALV
OLD	HARVEST
LOW + MOD	SALVAGE
LOW	HIGH
EDGE	EARHISALV
	EDGE

^a INTL, intermediate-aged forest that burned with a low severity; INTM, intermediate-aged forest that burned with a moderate severity; OLDL, older forest that burned with a low severity; OLDM, older forest that burned with a moderate severity; INT, intermediate-aged forest that burned with a low or moderate severity (combined area of INTL and INTM); OLD, older forest that burned with a low or moderate severity (combined area of OLDL and OLDM); LOW, intermediate-aged and older forest that burned with a low severity (combined area of INTL and OLDL); MOD, intermediate-aged and older forest that burned with a moderate severity (combined area of INTM and OLDM); EDGE, the interface between forested areas that burned with low or moderate severity and areas that were early seral stands, burned with high severity, or were salvage logged; EDGE was modeled as an additive effect with the best ranked covariate model to determine if it improved model fit.

^b EARLY, non-forested areas early seral stands that burned with any severity; HIGH, the combined area of intermediate-aged and older forest that burned with a high severity; SALVAGE, any intermediate-aged or older forest that was salvage logged; HARVEST, any forested area, that was harvested before or after the burn (combined area of EARLY and SALVAGE); HISALV, any forested area, excluding early stands, that burned with a high severity or was salvage logged (combined area of HIGH and SALVAGE); EARHISALV, any early seral stand or forested area that burned with high severity or that was salvage logged (combined area of EARLY, HIGH, and SALVAGE).

all critical components of spotted owl habitat (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). Intermediate-aged forests contribute to landscape heterogeneity, which influenced spotted owl survival in other studies (Franklin et al. 2000, Olson et al. 2004), so we hypothesized that it would also influence site occupancy by the subspecies. Spotted owl territories usually have high proportions of mature and older forests (Ripple et al. 1991, 1997; Meyer et al. 1998; Swindle et al. 1999), so we expected that initial occupancy and colonization probabilities would be influenced by the amount of older forest within the territory.

We elected to use a different set of covariates on extinction probabilities because of the highly correlated nature of extinction and colonization probabilities (MacKenzie et al. 2006). Modeling the same set of covariates on extinction and colonization parameters can result in counter-intuitive results. This is because sites that went extinct are the sites available for colonization. As a result, factors that contribute to increased extinction probabilities could also contribute to increased colonization probabilities. For extinction models, we modeled 7 covariates (Table 3) to determine the best spatial scale and relationship of the covariate. All of the

covariates considered for extinction were thought to be related to the impacts of habitat loss and modification attributable to past timber harvest, high severity fire, and salvage logging. We hypothesized that all 3 of these factors would negatively affect site occupancy. Spotted owl territories that had increased amounts of clear-cut timber harvest had decreased occupancy (Thraill et al. 1998). Timber harvest and post-fire salvage commonly results in large-scale clear-cuts; as a result, site occupancy by owls should be negatively affected by these factors. High severity fire removes downed woody debris and reduces canopy cover and structural diversity. All of these factors influence spotted owl habitat selection (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000), so we hypothesized that increased amounts of high severity fire may increase extinction probabilities.

We considered the effects of the amount of edge habitat on initial occupancy, extinction, and colonization probabilities because we suspected edge could have positive or negative impacts on site occupancy. Greater amounts of edge habitat may increase site occupancy by increasing prey availability, particularly woodrats (*Neotoma* spp.), which are common in edge habitats (Zabel et al. 1995, Ward et al. 1998) and are a primary prey item in this portion of the spotted owl's range (Forsman et al. 2004). In contrast, increased amounts of edge habitat may decrease the amount of interior forest available to owls, which has been associated with decreased spotted owl survival (Franklin et al. 2000). To avoid the potential correlation between extinction and colonization parameters (MacKenzie et al. 2006), we only used edge in 1 of the parameters, not both, in the same model. We used edge as an additive effect with the best ranked covariate model for initial occupancy and extinction or colonization to determine if it improved model fit (i.e., decreased the AIC_c value).

We modeled each of the 4 possible models of each covariate individually, as an additive effect, with the best model from the first step of our analysis. We took this approach to reduce redundancy in the potential list of covariates due to spatial scales and relationships of covariates being correlated and to reduce the number of candidate models that would be considered in the final step of the analysis. We ranked each model using AIC_c values to determine the best spatial scale and relationship of each covariate.

The third step of our analysis combined the best individual covariates from the second step of our analysis into more complex models to test a specific set of biologically plausible hypotheses (Table 3). We did not use covariates on detection probabilities because they are nuisance parameters for which we had minimal interest. Our most complex initial occupancy and colonization models included 4 covariates (combinations of intermediate-aged and older forests and low and moderate burn severity; Table 3). Other models were variations of the most complex model that included a subset of these covariates or combined 2 covariates into a single covariate. Our most complex extinction model included 3 covariates (early seral stands, forests with high burn severity, and salvage logged forests; Table 3). The remaining candidate models were variations of the most complex model that had fewer covariates or combined 2 or more covariates into a

single covariate. Prior to fitting our candidate model set (Table 3), we looked for correlations between variables that may be included in the same model. We did not include candidate models with highly correlated variables ($r^2 > 0.70$). After determining the best covariate model for initial occupancy, extinction, and colonization probabilities, we retained these models and combined them to determine our best overall model.

RESULTS

Comparison of the South Cascades to Timbered Rock

The best model for detection probabilities was P (year + area + $\ln T$), and the second ranked model [P (year + $\ln T$)] was not competitive ($\Delta AIC_c = 13.18$; Table 4). The best model indicated that detection probabilities varied among years, differed between areas, and followed a log-linear time trend within years. Detection probabilities were greater at South Cascades than at Timbered Rock in 10 out of 15 years. In most years (8 out of 15), detection probabilities declined over the survey season, but in the remaining 7 years, detection probabilities increased over the survey season. Detection probabilities during 1 survey over the 15 years of the study varied considerably and ranged from 0.24 to 0.82 at the South Cascades and 0.11–0.79 at Timbered Rock. The range of detection probabilities within years was less variable. The best model for initial occupancy was Ψ (area), and the second ranked model [$\Psi(\cdot)$] was not competitive ($\Delta AIC_c = 7.21$). The best model indicated that the South Cascades had greater initial occupancy ($\hat{\beta} = 2.21$, 95% CI = 0.65–3.76) than Timbered Rock. We estimated initial occupancy probabilities in 1992 to be 0.94 (95%

CI = 0.88–1.00) at South Cascades compared to 0.65 at Timbered Rock (95% CI = 0.44–0.86).

The best model for extinction probabilities was ε [Pre-burn (area + t)Post-burn(area + t)], and 2 models were highly competitive (i.e., $\Delta AIC_c < 2.0$) with the best extinction model (Table 4). However, model ε [Pre-burn(area + t)Post-burn(area + t)] had a weight of 0.42, indicating strong support for the best model. Interpretation of the best model was that extinction rates varied by year and study area, but the study areas followed the same pattern over time (Fig. 2). We found some evidence that the South Cascades had greater extinction probabilities than Timbered Rock prior to the burn because the 95% confidence interval barely overlapped 0 ($\hat{\beta} = 0.69$, 95% CI = -0.06 to 1.43). Following wildfire and subsequent salvage logging at the Timbered Rock study area, extinction probabilities were greater than at the South Cascades ($\hat{\beta} = 1.46$, 95% CI = 0.29–2.62; Fig. 2). Model ε [Pre-burn(t)Post-burn(area + t)] was the second ranked extinction probability model ($\Delta AIC_c = 1.53$; Table 4). This model suggested that extinction probabilities varied by year and the Timbered Rock and the South Cascades study areas had similar extinction probabilities prior to the Timbered Rock burn, but extinction probabilities were greater at Timbered Rock following wildfire and subsequent salvage logging. Model ε (t) was the third ranked extinction model ($\Delta AIC_c = 1.84$; Table 4). This model suggested that extinction probabilities varied by year, and the Timbered Rock and South Cascades study areas had similar extinction probabilities before and after the Timbered Rock burn. We did not consider this model further, because the 2 best ranked models had similar interpretations with a combined model weight of

Table 4. Model selection results for extinction (ε), colonization (γ), and detection (P) probability models in the analysis of site occupancy of northern spotted owls at the South Cascades Demographic Study Area and the Timbered Rock study Area in southwest Oregon, USA, from 1992 to 2006. We presented only models with an Akaike weight ≥ 0.01 . We considered models that compared differences between study areas (area) and no differences between areas (\cdot), and we considered several biologically plausible temporal effects including constant rates among years (\cdot), variable rates among years (t), and linear (T), log-linear ($\ln T$), and quadratic (TT) trends over time. For all extinction, colonization, and detection probability models, the best initial occupancy (Ψ) model was Ψ (area).

Model	AIC _c ^a	ΔAIC_c ^b	w_i ^c	K^d	Deviance
Extinction— ε					
ε (Pre-burn(area + t)Post-burn(area + t)) γ (area + T) P (year, area + $\ln T$)	8689.47	0.00	0.42	66	8552.27
ε (Pre-burn(t)Post-burn(area + t)) γ (area + T) P (year, area + $\ln T$)	8691.00	1.53	0.19	65	8555.96
ε (t) γ (area + T) P (year, area + $\ln T$)	8691.31	1.84	0.17	64	8558.42
ε (area + t) γ (area + T) P (year, area + $\ln T$)	8692.58	3.12	0.09	65	8557.54
ε (Pre-burn(area + t)Post-burn(area \times t)) γ (area + T) P (year, area + $\ln T$)	8692.77	3.30	0.08	69	8549.08
ε (Pre-burn(t)Post-burn(area \times t)) γ (area + T) P (year, area + $\ln T$)	8694.30	4.83	0.04	68	8552.78
Colonization— γ					
ε (area \times t) γ (area + T) P (year, area + $\ln T$)	8700.13	0.00	0.43	78	8536.83
ε (area \times t) γ (area + TT) P (year, area + $\ln T$)	8702.15	2.03	0.16	79	8536.66
ε (area \times t) γ (Pre-burn (area + T)Post-burn(area + T)) P (year, area + $\ln T$)	8702.29	2.16	0.15	79	8536.80
ε (area \times t) γ (Pre-burn(area + T)Post-burn(area \times T)) P (year, area + $\ln T$)	8702.32	2.19	0.15	79	8536.83
ε (area \times t) γ (Pre-burn(area)Post-burn(area)) P (year, area + $\ln T$)	8703.02	2.89	0.10	78	8539.72
ε (area \times t) γ (Pre-burn(T)Post-burn(area \times T)) P (year, area + $\ln T$)	8708.47	8.35	0.01	79	8542.98
Detection probability— P^e					
ε (area \times t) γ (area \times t) P (year, area + $\ln T$)	8729.48	0.00	1.00	103	8510.61
ε (area \times t) γ (area \times t) P (year, $\ln T$)	8742.66	13.18	0.00	88	8557.33

^a Akaike's Information Criterion corrected for small sample sizes.

^b The difference between the model listed and the best AIC_c model.

^c Akaike weight.

^d No. parameters in model.

^e Detection probability modeling notation is P (among year detection, within year detection).

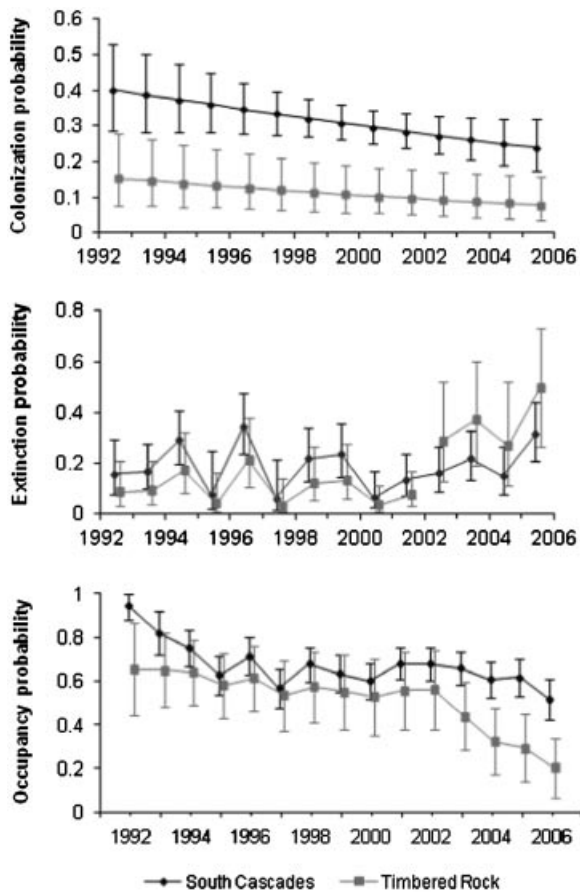


Figure 2. Estimated extinction, colonization, and site occupancy probabilities (95% CI) of northern spotted owls at the Timbered Rock and South Cascades study areas in southwest Oregon, USA from 1992 to 2006.

0.62 and indicated that post-burn, extinction probabilities were greater at Timbered Rock.

The best model for colonization was γ (area + T), and no models were within 2.0 AIC_c units of the best model (Table 4). Model γ (area + T) had a weight of 0.43 indicating strong support for this model. Interpretation of the best model was that colonization probabilities differed between study areas and declined linearly over time. Colonization probabilities were greater at the South Cascades ($\hat{\beta} = 1.31$, 95% CI = 0.60–2.03) than at Timbered Rock and declined over time ($\hat{\beta} = -0.06$, 95% CI = -0.12 to 0.00) at both areas (Fig. 2). Wildfire and salvage logging did not appear to influence post-burn colonization probabilities at Timbered Rock because models that included changes in colonization probabilities following wildfire were not competitive (i.e., $\Delta AIC_c > 2.0$) with the best model (Table 4).

We combined the best ranked models for initial occupancy, extinction, colonization, and detection probabilities to obtain our best overall model (Table 4), which we used to contrast trends in occupancy probabilities over time at the Timbered Rock and South Cascades study areas. We used the best overall model [$\Psi(\text{area})\epsilon[\text{Pre-burn}(\text{area} + t)\text{Post-burn}(\text{area} + t)]\gamma(\text{area} + T)P(\text{year} + \text{area} + \ln T)$] to calculate year-specific occupancy estimates for each study area.

Site occupancy by spotted owls at the South Cascades declined from 1992 to 1994, remained relatively stable from 1995 to 2005, and declined again in 2006 (Fig. 2). In contrast, site occupancy by spotted owls at Timbered Rock declined slightly from 1992 to 2002 and declined in an almost linear fashion from 2003 to 2006, which corresponded to the years following the Timbered Rock burn (Fig. 2). Between 2002 and 2006, the estimated proportion of spotted owl territories occupied by a pair at South Cascades declined from 0.68 to 0.51, a 25% reduction in site occupancy. In contrast, the estimated proportion of spotted owl territories occupied by a pair at Timbered Rock declined from 0.56 to 0.20, a 64% reduction in site occupancy during the same time period. This indicated that occupancy of territories by spotted owls in a recently burned landscape that was subjected to salvage logging declined at a greater rate than in a recently unburned landscape.

Relationship Between Wildfire, Salvage Logging, and Spotted Owl Site Occupancy

Our objective in this portion of the analysis was to determine the best model prior to modeling habitat covariates; consequently, we did not consider any competing models. The best model that described study area and temporal effects on spotted owl site occupancy at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006 was $\Psi(\cdot)\epsilon[\text{BIS} \neq \text{TR} = Q + T]\gamma(\cdot)P(\cdot)$ (Table 5). Detection probabilities were constant within and among years, and equal between study areas. The probability of detecting a spotted owl pair on any 1 visit was 0.46 (95% CI = 0.39–0.53). The probability of initial occupancy was similar between study areas and was 0.46 (95% CI = 0.30–0.62) in 2003 at all 3 study areas. Colonization probabilities were also similar among study areas and constant over time. The probability that an unoccupied territory would be colonized the subsequent year was 0.15 (95% CI = 0.07–0.26). Extinction probabilities were greater at the Biscuit burn ($\hat{\beta} = 5.58$, 95% CI = 1.25–9.91) than the Quartz and Timbered Rock burns and increased from 2004 to 2006 ($\hat{\beta} = 2.96$, 95% CI = 0.97–4.94) at all 3 study areas. Extinction probabilities at the Quartz and Timbered Rock burns increased from 2004 to 2006 (0.11, 95% CI = 0.03–0.36; 0.72, 95% CI = 0.41–0.90, respectively). In contrast, extinction probabilities increased from 0.37 (95% CI = 0.11–0.73) in 2004 to 0.92 (95% CI = 0.58–0.99) in 2006 at the Biscuit burn. Based on the point estimates, extinction probabilities have increased dramatically for all areas (11–92%).

We modeled individual covariates as an additive effect with the best study area and temporal effects model (Table 5) to determine the spatial scale (core or territory) and relationship (linear or log-linear) that best described the effect of the covariate on initial occupancy, extinction, and colonization parameters (Table 6). In most cases, the models for alternative spatial scales and relationships were competitive (i.e., $\Delta AIC_c < 2.0$) with the best model for each covariate; however, our objective was to reduce redundancy between models and reduce the number of models in the final step of our

Table 5. Model selection results for initial occupancy (Ψ), extinction (ϵ), colonization (γ), and detection (P) probability models in the analysis of site occupancy of northern spotted owls without site-specific covariates at the Biscuit (BIS), Quartz (Q), and Timbered Rock (TR) burns in southwest Oregon, USA, from 2003 to 2006. We presented only models with an Akaike weight ≥ 0.05 . We considered models that compared differences between study areas (area) and no differences between areas (\cdot), and we considered several biologically plausible temporal effects including constant rates among years (\cdot), variable rates among years (t), and linear (T), log-linear ($\ln T$), and quadratic (TT) trends over time.

Model	AIC _c ^a	Δ AIC _c ^b	w_i ^c	K ^d	Deviance
Extinction— ϵ					
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$	476.93	0.00	0.28	6	464.38
$\Psi(\cdot)\epsilon(T)\gamma(\cdot)P(\cdot, \cdot)$	477.79	0.86	0.18	5	467.39
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \ln T)\gamma(\cdot)P(\cdot, \cdot)$	477.94	1.01	0.17	6	465.39
$\Psi(\cdot)\epsilon(\ln T)\gamma(\cdot)P(\cdot, \cdot)$	478.65	1.72	0.12	5	468.26
$\Psi(\cdot)\epsilon(t)\gamma(\cdot)P(\cdot, \cdot)$	479.35	2.42	0.08	6	466.80
$\Psi(\cdot)\epsilon(TT)\gamma(\cdot)P(\cdot, \cdot)$	479.35	2.42	0.08	6	466.80
$\Psi(\cdot)\epsilon(\text{area} + t)\gamma(\cdot)P(\cdot, \cdot)$	480.17	3.24	0.05	8	463.21
Colonization— γ					
$\Psi(\cdot)\epsilon(\text{area} \times t)\gamma(\cdot)P(\cdot, \cdot)$	482.39	0.00	0.70	10	460.91
$\Psi(\cdot)\epsilon(\text{area} \times t)\gamma(\text{BIS} \neq \text{TR} = \text{Q})P(\cdot, \cdot)$	487.41	5.02	0.06	13	458.90
Initial occupancy— Ψ					
$\Psi(\cdot)\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	499.61	0.00	0.44	20	453.52
$\Psi(\text{BIS} \neq \text{TR} = \text{Q})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	501.12	1.51	0.21	21	452.37
$\Psi(\text{BIS} = \text{Q} \neq \text{TR})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	501.50	1.89	0.17	21	452.75
$\Psi(\text{BIS} = \text{TR} \neq \text{Q})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	502.27	2.66	0.12	21	453.52
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	503.70	4.09	0.06	22	452.26
Detection probability— P^e					
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	503.70	0.00	0.52	22	452.26
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\ln T, \cdot)$	506.28	2.58	0.14	23	452.11
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(T, \cdot)$	506.44	2.74	0.13	23	452.26
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(TT, \cdot)$	506.51	2.81	0.13	23	452.33
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\text{year}, \cdot)$	507.56	3.86	0.08	25	447.79

^a Akaike's Information Criterion corrected for small sample sizes.

^b The difference between the model listed and the best AIC_c model.

^c Akaike weight.

^d No. parameters in model.

^e Detection probability modeling notation is P (among year detection, within year detection).

analysis. As a result, we did not consider competing models and assumed the highest ranked model best described the relationship of the covariate on each occupancy parameter. After determining the best spatial scale and relationship of each covariate, we looked for correlations between variables that were included in the same model. None of the variables that were included in the same model were highly correlated ($r^2 < 0.31$ in all contrasts). Consequently, we did not exclude any variables from our candidate model set because of collinearity (Table 3).

Fire severity and habitat effects.—The best model that described the relationship between site occupancy and fire severity, salvage logging, and habitat covariates at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006 indicated that initial occupancy was best predicted by intermediate-aged and older forest that burned with a moderate severity at the core scale and amount of edge at the core scale. Extinction was best predicted by early seral stands that burned with high severity or were salvage logged at the core scale and amount of edge at the territory scale with extinction rates differing across time and at Biscuit sites. Colonization was best predicted by intermediate-aged older forests with low and moderate burn severity at the core scale and detection was constant across variables (Table 6). One model was within 2.0 AIC_c units of the best model for extinction probability (Table 6). However, this model was a slight variation of the best model and did not include the covariate

representing edge at the territory scale, so it was not considered further because the amount of edge at the territory scale improved model fit. No models competed with the best initial occupancy and colonization probability models (Table 6). The best overall covariate model ranked substantially higher (Δ AIC_c = 27.12) than the model that only included study area and temporal effects (Table 6). This indicated that the covariates used in this model explained some of the variability observed in post-fire site occupancy by spotted owls at the Biscuit, Quartz, and Timbered Rock burns.

Our best initial occupancy model included variables for the amount of low severity burn and edge (km) within the core use area (Table 6). The confidence intervals of the beta coefficients for the amount of low severity burn within the core area ($\hat{\beta} = 0.52$, 95% CI = -0.22 to 1.26) and the amount of edge (km) in the core area ($\hat{\beta} = -0.42$, 95% CI = -0.92 to 0.10) broadly overlapped zero, which indicated that neither of these variables influenced initial occupancy probabilities. Extinction probabilities increased as the combined area that was previously harvested, burned with a high severity, or salvage logged increased ($\hat{\beta} = 1.88$, 95% CI = 0.10 – 3.66 ; Fig. 3a). We found some evidence that the amount of edge (km) within a territory had a positive effect on extinction probabilities as the 95% confidence intervals overlapped 0 slightly ($\hat{\beta} = 0.18$, 95% CI = -0.01 to 0.37 ; Fig. 3b). We found weak support that colonization proba-

Table 6. Initial occupancy (Ψ), extinction (ϵ), and colonization (γ) models in the analysis of covariate effects on site occupancy of northern spotted owls at the Biscuit (BIS), Quartz (Q), and Timbered Rock (TR) burns in southwest Oregon, USA, from 2003 to 2006. We presented only models with an Akaike weight ≥ 0.05 . For all initial occupancy, extinction, and colonization models the best detection probability model was constant detection among and within years ($P(\cdot, \cdot)$).

Model ^a	AIC _c ^b	Δ AIC _c ^c	w_i ^d	K ^e	Deviance
Best overall model					
$\Psi(\ln \text{ LOWc} + \text{EDGEc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T} + \ln \text{ EARTHISALVc} + \text{EDGEt})\gamma(\text{INTLc} + \text{INTMc} + \text{OLDLc} + \text{OLDMt})P(\cdot, \cdot)$	449.81	0.00	1.00	14	418.89
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\cdot)P(\cdot, \cdot)$ —Base model	476.93	27.12	0.00	6	464.38
Initial occupancy— Ψ					
$\Psi(\ln \text{ LOWc} + \text{EDGEc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\cdot)P(\cdot, \cdot)$	473.78	0.00	0.36	8	456.82
$\Psi(\ln \text{ LOWc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\cdot)P(\cdot, \cdot)$	476.01	2.22	0.12	7	461.27
$\Psi(\text{INTLc} + \text{OLDLc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\cdot)P(\cdot, \cdot)$	476.09	2.30	0.12	8	459.13
$\Psi(\text{RFc} + \ln \text{ NRFc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\cdot)P(\cdot, \cdot)$	476.43	2.65	0.10	8	459.47
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\cdot)P(\cdot, \cdot)$ —Base model	476.93	3.15	0.08	6	464.38
$\Psi(\text{INTLc} + \text{INTMt} + \text{OLDLc} + \text{OLDMt})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\cdot)P(\cdot, \cdot)$	477.43	3.65	0.06	10	455.94
$\Psi(\text{OLDLc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\cdot)P(\cdot, \cdot)$	477.64	3.85	0.05	7	462.89
$\Psi(\ln \text{ NRFc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\cdot)P(\cdot, \cdot)$	477.88	4.09	0.05	7	463.14
Extinction— ϵ					
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T} + \ln \text{ EARTHISALVc} + \text{EDGEt})\gamma(\cdot)P(\cdot, \cdot)$	464.61	0.00	0.60	8	447.65
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T} + \ln \text{ EARTHISALVc})\gamma(\cdot)P(\cdot, \cdot)$	466.50	1.89	0.23	7	451.76
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T} + \ln \text{ HARVESTc} + \text{HIGHc})\gamma(\cdot)P(\cdot, \cdot)$	469.49	4.88	0.05	8	452.53
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T} + \ln \text{ EARLYc} + \text{HISALVc})\gamma(\cdot)P(\cdot, \cdot)$	469.73	5.12	0.05	8	452.77
Colonization— γ					
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\text{INTLc} + \text{INTMc} + \text{OLDLc} + \text{OLDMt})P(\cdot, \cdot)$	462.72	0.00	0.65	10	441.24
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\text{INTLc} + \text{INTMc} + \text{OLDLc} + \text{OLDMt} + \ln \text{ EDGEc})P(\cdot, \cdot)$	464.93	2.21	0.22	11	441.14
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \text{T})\gamma(\text{OLDLc} + \text{OLDMt})P(\cdot, \cdot)$	467.27	4.54	0.07	8	450.31

^a Variables preceded by \ln were modeled using a log-linear relationship, variables followed by a c were modeled at the core area scale, and variables followed by t were modeled at the territory scale. INTL, intermediate-aged forest that burned with a low severity; INTM, intermediate-aged forest that burned with a moderate severity; OLDL, older forest that burned with a low severity; OLDM, older forest that burned with a moderate severity; LOW, intermediate-aged and older forest that burned with a low severity (combined area of INTL and OLDL); MOD, intermediate-aged and older forest that burned with a moderate severity (combined area of INTM and OLDM); EDGE, the interface between forested areas that burned with low or moderate severity and areas that were early seral stands, burned with high severity, or were salvage logged; EDGE was modeled as an additive effect with the best-ranked covariate model to determine if it improved model fit; EARLY, non-forested areas early seral stands that burned with any severity; HIGH, the combined area of intermediate-aged and older forest that burned with a high severity; SALVAGE, any intermediate-aged or older forest that was salvage logged; HARVEST, any forested area that was harvested before or after the burn (combined area of EARLY and SALVAGE); HISALV, any forested area, excluding early stands, that burned with a high severity or was salvage logged (combined area of HIGH and SALVAGE); EARTHISALV, any early seral stand or forested area that burned with high severity or that was salvage logged (combined area of EARLY, HIGH, and SALVAGE); RF, intermediate-aged forest that burned with a low or moderate severity (combined area of INTL and INTM); NRF, older forest that burned with a low or moderate severity (combined area of OLDL and OLDM); T , linear time.

^b Akaike's Information Criterion corrected for small sample sizes.

^c The difference between the model listed and the best AIC_c model.

^d Akaike weight.

^e No. parameters in model.

bilities increased as the amount of intermediate-aged forest that burned with a low severity within the core area increased ($\hat{\beta} = 0.10$, 95% CI = -0.01 to 0.38 ; Fig. 4a) as the amount of older forest that burned with a low severity within the core area increased ($\hat{\beta} = 0.10$, 95% CI = -0.01 to 0.22 ; Fig. 4b), and as the amount of older forest that burned with a moderate severity within the territory increased ($\hat{\beta} = 0.82$, 95% CI = -0.05 – 1.69 ; Fig. 4c). We found no evidence that colonization probabilities were associated with the amount of intermediate-aged forest that burned with a moderate severity within the core area ($\hat{\beta} = -1.20$, 95% CI = -3.21 to 0.80).

DISCUSSION

Comparison of the South Cascades to Timbered Rock

As predicted, the Timbered Rock and South Cascades study areas had relatively similar trends in site occupancy prior to the Timbered Rock burn. However, extinction probabilities

increased at Timbered Rock following wildfire and subsequent salvage logging, which combined with the lesser colonization rates at Timbered Rock contributed to greater declines in site occupancy than were observed in recently unburned landscapes at the South Cascades (Fig. 2). The Timbered Rock study area had an approximately 64% reduction in site occupancy following wildfire, whereas the South Cascades study area had a roughly 25% reduction in site occupancy during the same time period. This supported our prediction that occupancy rates in burned and salvage logged landscapes would decline at a greater rate than unburned landscapes. Our results contrast with those of previous studies that compared occupancy rates of spotted owls in burned and unburned landscapes. Jenness et al. (2004) found that territory occupancy of Mexican spotted owls in burned areas was similar to unburned areas. Roberts et al. (2011) found that site occupancy of California spotted owls in randomly selected burned and unburned areas were similar. Neither of these studies was affected by the high degree of salvage logging we observed following the Timbered Rock

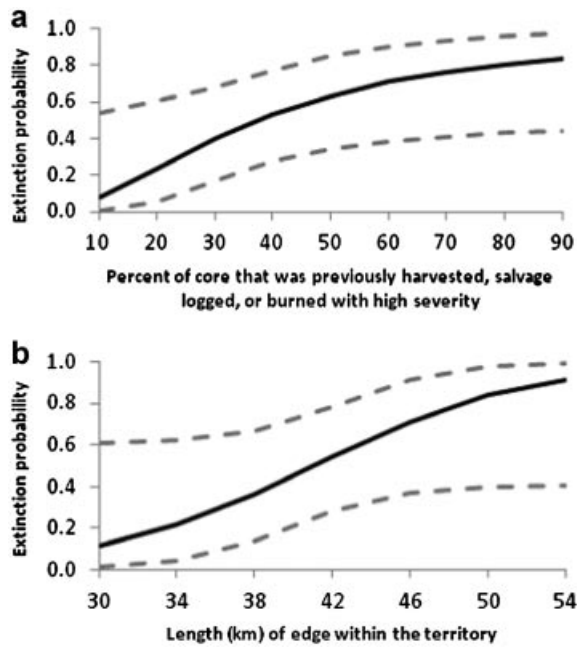


Figure 3. The estimated effects of the percent of (a) forested area that burned with a high severity or was previously harvested or salvage logged and (b) forest edge on extinction probabilities of northern spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA from 2003 to 2006. The 95% confidence intervals for the estimated effects are represented by gray, dashed lines. The median values of the additional covariates in the model were held constant while varying the covariate of interest over the observed range of values.

burn, which may explain the difference between our results and those of previous studies.

The approximately 25% reduction in site occupancy at the South Cascades from 2002 to 2006 was somewhat surprising given that the study area did not have any large scale disturbances during this time. However, several spotted owl populations have been declining throughout the subspecies' range (Anthony et al. 2006, Forsman et al. 2011), and declines in site occupancy at the South Cascades could be related to ongoing population declines that are unrelated to natural disturbances. Dugger et al. (2011) found that barred owls (*Strix varia*) had negative impacts on site occupancy by spotted owls by decreasing colonization rates and increasing extinction rates. This likely explains much of the nearly 25% decline in site occupancy we observed from 2002 to 2006 at the South Cascades. The 64% reduction in site occupancy at Timbered Rock from 2002 to 2006 was substantially greater than the roughly 25% decline observed at South Cascades, which suggests that wildfire, subsequent salvage logging, and past timber harvest contributed to the greater declines in site occupancy at Timbered Rock. We estimated that following the Timbered Rock burn only 46% of the area within 2,230 m of spotted owl territories were intermediate-aged or older forests that burned with a low or moderate severity (Table 1). This amount of habitat is marginal for successful reproduction (Bart and Forsman 1992) and may cause decreases in survival rates of the subspecies (Franklin et al. 2000, Dugger et al. 2005).

The large declines in site occupancy following the Timbered Rock burn are most likely explained by dispersal

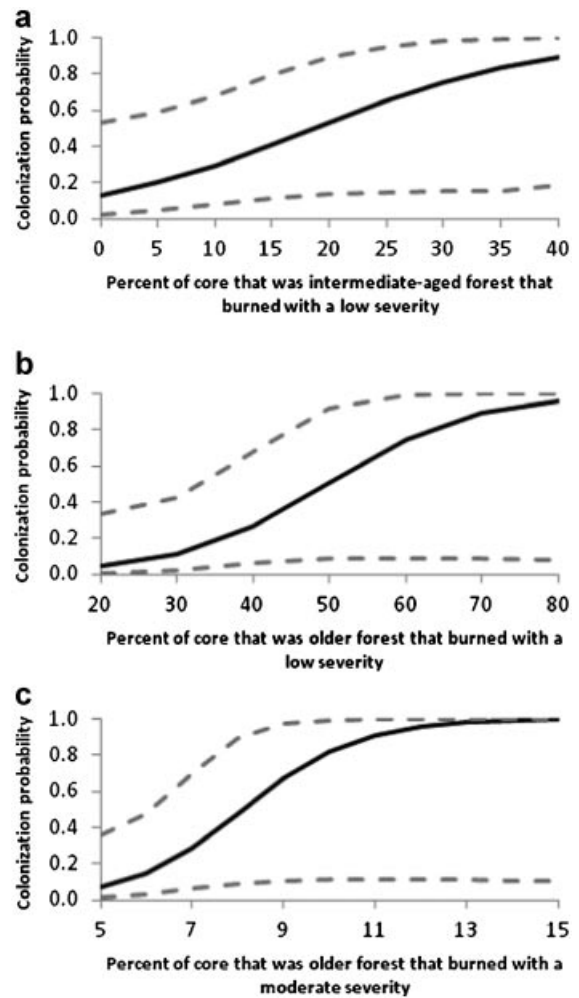


Figure 4. The estimated effects of the percent of (a) intermediate-aged forest that burned with a low severity, (b) older forest that burned with a low severity, and (c) older forests that burned with a moderate severity on colonization probabilities of northern spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA from 2003 to 2006. The 95% confidence intervals for the estimated effects are represented by gray, dashed lines. The median values of the additional covariates in the model were held constant while varying the covariate of interest over the observed range of values.

out of the burn (i.e., emigration) and decreased survival of spotted owls. Several color-banded, adult spotted owls at the Timbered Rock burn (2 pairs and 1 individual, 25% of the known pre-fire population) dispersed to an unburned territory adjacent to the burn, 1–2 years post-fire (OCFWRU, unpublished data). Adult dispersal is a relatively rare occurrence in spotted owls throughout their range (Forsman et al. 2002: 5%, Zimmerman et al. 2007: 2%); however, owl territories may be abandoned when large amounts of mature and older forest are lost (Bart and Forsman 1992, Bart 1995). We believe that the relatively high rate of adult dispersal following the Timbered Rock burn suggests that insufficient habitat remained at abandoned territories to support a spotted owl pair. In addition, radio-marked spotted owls that maintained a territory within the Timbered Rock burn had lower survival rates ($S' = 0.69 \pm 0.12$; Clark et al. 2011) than reported throughout the subspecies' range ($\Phi = 0.75$ to

0.91 \pm 0.01 to 0.05; Anthony et al. 2006). Annual survival of spotted owls was positively associated with greater amounts of older forest within their home ranges or core use areas in other studies (Franklin et al. 2000, Olson et al. 2004, Blakesley et al. 2005, Dugger et al. 2005). High severity wildfire and salvage logging removed and modified 26% of the intermediate-aged and older forests within 2,230 m of spotted owl territories at the Timbered Rock burn, and 28% of the remaining area was previously harvested (i.e., early seral forest; Table 1). Consequently, the large degree of habitat loss and modification from past timber harvest, high severity fire, and salvage logging following the Timbered Rock burn likely contributed to the high levels of dispersal out of the burn, decreased survival rates and subsequent declines in site occupancy that we observed. These declines in site occupancy appear to have continued past the conclusion of our study because no spotted owls were detected during surveys conducted during the 2011 breeding season at the Timbered Rock study site (OCFWRU, unpublished data).

Increased extinction rates following the Timbered Rock burn may have been exacerbated by the checkerboard land ownership pattern of private and BLM lands (Richardson 1980). Private lands within the area of the Timbered Rock burn are managed as industrial forests and are frequently subjected to large-scale timber harvest, which creates large tracts of early seral forest. Following the Timbered Rock burn, much of the private land was salvage logged (17% of the study area), which created large clear-cuts throughout the landscape. Territory occupancy by spotted owls was negatively associated with increased areas of clear-cuts within the territory in another study (Thraillkill et al. 1998). Consequently, the large areas of clear-cuts created by salvage logging and past timber harvest (approx. 45% of the area within 2,230 m of spotted owl territories; Table 1) potentially exacerbated declines in site occupancy following the Timbered Rock burn or confounded the effects of wildfire. Declines in site occupancy may not be as large in burned areas that were not subjected to previous timber harvest or substantial amounts of post-fire salvage logging.

Relationship Between Wildfire, Salvage Logging, and Spotted Owl Site Occupancy

Extinction.—We predicted that occupancy of nesting territories by spotted owls after fires would decline because of increased extinction probabilities attributable to habitat loss and modification from past timber harvest, high severity fire and salvage logging. Our results supported this prediction because extinction probabilities increased as the combined area of high severity burns, salvage logging, and early seral forest increased (Fig. 3a; $\beta = 1.88$, 95% CI = 0.10–3.66). This was the strongest relationship we observed in this analysis because it was the only habitat covariate where the 95% confidence interval for the regression coefficient did not overlap 0. Unfortunately, we were unable to separate the impacts of these 3 variables on extinction probabilities. When these 3 variables were included separately, the models

were not competitive with the model that combined these variables into a single covariate (Table 6). This may indicate that we lacked the precision to separate the impacts of these 3 variables or they were confounded. However, our results suggest that these 3 variables work in concert and generate synergistic effects. Any 1 disturbance event may not generate negative effects on occupancy of territories, but the combined loss and modification of habitat from these 3 factors negatively affected spotted owls in our study. The combined influence of these 3 factors may reduce spotted owl habitat to such an extent that a threshold is passed and spotted owls are no longer able to occupy the territory.

Spotted owls are associated with late-successional forests (Forsman et al. 1984, Thomas et al. 1990), and their territories have greater amounts of older forests than surrounding landscapes (Ripple et al. 1991, 1997; Meyer et al. 1998; Swindle et al. 1999). Forest stands used by spotted owls have large proportions of downed woody debris and snags, high canopy cover, and high structural diversity (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). Timber harvest, salvage logging, and high severity fire remove or alter many of these structural characteristics associated with spotted owl habitat. As a result, we were not surprised that these factors were associated with increased extinction probabilities and declines in site occupancy. Spotted owls have high site fidelity (Forsman et al. 1984, 2002; Zimmerman et al. 2007), and survival rates are positively correlated with increased amounts of older forest in their territories (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005); consequently, owls that occupied territories with a large degree of past timber harvest, salvage logging, and high severity fire were likely forced to emigrate out of the burned area or risk decreased survival.

Radio-marked spotted owls at the Timbered Rock burn were located closer to edge habitats than at random (Clark 2007), which suggests edge habitat may provide a benefit to the subspecies. Spotted owls may prefer to forage in habitat edges because of greater densities of some prey in early seral forests (Carey and Peeler 1995, Franklin and Gutiérrez 2002), particularly woodrats in southwest Oregon and northwest California (Zabel et al. 1995, Ward et al. 1998). Our results provided some evidence that extinction probabilities increased as the amount (km) of edge increased within nesting territories increased (Fig. 3b; $\beta = 0.18$, 95% CI = -0.01 – 0.37), suggesting a negative impact of edge habitat on spotted owl territory occupancy. In our analysis, edge represented a metric of habitat fragmentation. Dugger et al. (2011) observed greater colonization probabilities at spotted owl territories when older forest was less fragmented, and our results were similar. Franklin et al. (2000) indicated that spotted owls are likely to have decreased survival at territories with reduced amounts of interior forest, suggesting that habitat fragmentation negatively affects spotted owls. The patchy nature of high severity fire and salvage logging created large amounts of edge habitat, which likely reduced the amount of interior forest available to owls and contributed to declines in site occupancy in our study. Furthermore, increases in edge may be correlated with in-

creased amounts of nonhabitat (i.e., nonforested and early seral stands) and increases in nonhabitat have contributed to declines in territory occupancy of California spotted owls (Blakesley et al. 2005) and increases in extinction probabilities in this study. Despite indications that spotted owls are negatively affected by habitat fragmentation, the mechanism of these effects is not well understood (Franklin and Gutiérrez 2002). We calculated the amount of edge as the interface between intermediate-aged and older forests that burned with a low or moderate severity and all other habitat types (Table 2). This classification of edge habitat delineated distinct boundaries between stands of larger living trees and high severity burns or early seral stands. Additional types of edge habitats exist at the interface between intermediate-aged and older forests or the interface between low and moderate severity burns, and these types of edges may provide foraging habitat for spotted owls. Additional research between the association of various edge habitats on spotted owl demography and site occupancy is needed to clarify this relationship.

Colonization.—Overall, our estimated effects of habitat covariates on colonization probabilities were relatively imprecise. We attributed this lack of precision to the fact that we observed only 6 colonization events at our 3 study areas from 2003 to 2006. Despite the fact that we observed relatively few colonization events, we were still able to document several biologically meaningful associations between post-fire habitat and colonization probabilities. We suspect that if additional colonization events had occurred during the course of our research, our estimated effects of habitat on colonization probabilities would be more precise.

We found some evidence that colonization probabilities in our study were positively associated with increased amounts of older forest that burned with a low severity within the core area (Fig. 4b; $\hat{\beta} = 0.10$, 95% CI = -0.01 to 0.22). Although this estimated effect had weak support, this finding was expected and follows the well documented association between spotted owls and older forest (Forsman et al. 1984, Thomas et al. 1990). Furthermore, previous research indicated that territory occupancy of California spotted owls was positively associated with older forest (Blakesley et al. 2005), extinction probabilities at northern spotted owl territories were greater at territories with lesser amounts older forest (Dugger et al. 2011) and site occupancy by California spotted owls in areas that primarily burned with a low and moderate severity was similar to unburned areas (Roberts et al. 2011). Older forests that burned with a low severity are likely the highest quality spotted owl habitat in post-fire landscapes. These areas likely retained much of the canopy cover, downed woody debris, snags, and structural diversity that is selected by spotted owls (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). As a result, unoccupied territories that have high quality habitat (i.e., older forest that burned with a low severity) will have the greatest probability of being colonized by spotted owls. Within the Timbered Rock burn, radio-marked spotted owls strongly selected for older forest that burned with a low severity (Clark 2007), further

demonstrating the influence of this habitat on spotted owls in post-fire landscapes.

Moderate severity burns likely remove and modify more of the forest stand features selected by spotted owls than low severity burns, yet many critical habitat features are likely retained and allow moderately burned areas to provide habitat for spotted owls following wildfire. Our analysis provided weak support that colonization probabilities were positively associated with increased amounts of older forest that burned with a moderate severity (Fig. 4c; $\hat{\beta} = 0.82$, 95% CI = -0.05 to 1.69). In addition to potentially providing many of the critical habitat features of forest stands that burned with a low severity, moderately burned stands likely have decreased risk of stand-replacement in the future because of removal of ladder fuels (Agee 1993), which likely increases the resilience of the forest stand to future disturbance. Spotted owls have been shown to disproportionately forage in habitats that have high levels of prey abundance (Carey et al. 1992, Carey and Peeler 1995, Zabel et al. 1995). Moderate severity burns may increase habitat heterogeneity and prey abundance, similar to the effects of heterogeneous thinning of young forest stands (Carey 2001). However, we did not test this hypothesis, and the potential benefits of moderate severity burns in older forests for spotted owls are unclear.

Previous studies have suggested a quadratic relationship between survival and reproduction of spotted owls and the amount of older forest surrounding nesting territories (Franklin et al. 2000, Olson et al. 2004). These studies suggest that territories that are not entirely comprised of older forests are beneficial to spotted owls and that spotted owls may be adapted to natural disturbances such as wildfire that create a mosaic of forest conditions. Our results provided weak support for this hypothesis because owl territories in our study that had increased amounts of intermediate-aged forest that burned with a low severity have a greater probability of being colonized by a pair of owls (Fig. 4a; $\hat{\beta} = 0.10$, 95% CI = -0.01 to 0.38). However, we expect a threshold exists in this relationship because spotted owls are associated with older forest (Forsman et al. 1984, Thomas et al. 1990) and spotted owls that occupy territories with insufficient amounts of older forest will have decreased survival and reproductive rates (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). The amount of intermediate-aged forest that burned with a low severity at any 1 owl territory in our study ranged from 0 to 38%. Territories that have insufficient amounts of older forest will likely not be occupied by spotted owls, but our results provided some evidence of a benefit of habitat heterogeneity for spotted owls.

Initial occupancy.—We were unable to identify any relationships between initial occupancy probabilities and the habitat covariates that we considered in our analysis. Our best model for initial occupancy probabilities (Table 6) included variables for the amount of the core area that burned with a low severity ($\hat{\beta} = 0.52$, 95% CI = -0.22 to 1.26) and the amount of edge habitat ($\hat{\beta} = -0.42$, 95% CI = -0.92 to 0.10); however, both of these estimates were imprecise and the 95% confidence intervals broadly overlapped zero, which

suggested these relationships were not meaningful. Since these relationships were not supported by the data, additional research is needed to investigate the influence of low severity fire and edge habitat on spotted owl site occupancy.

Our analysis of site occupancy at the Biscuit, Quartz, and Timbered Rock burns identified several meaningful relationships between site occupancy and amount of post-fire habitat. All of these relationships were based on biologically plausible hypotheses and have implications for spotted owl management. However, the relationships we observed were based on small sample sizes, non-random samples at the Biscuit burn, and our estimated relationships were often imprecise. Furthermore, our study was opportunistic and observational, which prevents us from assigning cause and effect relationships. Consequently, we suggest a cautionary approach when applying our findings to future land management decisions. In particular, the relationships we observed in our analysis may not be applicable to spotted owls in post-fire landscapes that are not affected by post-fire salvage logging.

Both wildfire and barred owls have been identified as threats to the persistence of spotted owls (USFWS 2011). Barred owls have expanded throughout the entire range of the northern spotted owl (Dark et al. 1998, Pearson and Livezey 2003) and are negatively affecting spotted owls (Kelly et al. 2003, Olson et al. 2005, Dugger et al. 2011). Furthermore, barred owls have a more generalized diet (Hamer et al. 2001, Wiens 2012) and use a wider range of habitats (Hamer et al. 2007) than spotted owls, which suggests that barred owls may be better adapted to persist in burned landscapes. We only detected 2 barred owls at the Biscuit, Quartz, and Timbered Rock burns during demographic surveys conducted between 2003 and 2006, so we believe that barred owls had little to no effect on our results.

Jointly, our analyses suggest that site occupancy by spotted owls in burned landscapes is likely to decline, at least in the short-term. These declines in site occupancy are driven by large increases in extinction probabilities in post-fire landscapes and are attributable to past timber harvest, high severity fire, and salvage logging. Although territories that had increased amounts of older forest that burned with a low severity had the greatest colonization probabilities, we only observed 6 colonization events at our 3 study areas from 2003 to 2006, and this level of colonization was insufficient to offset the high extinction probabilities we observed. This suggests that insufficient habitat remained at many of the spotted owls territories included in our analyses to support a pair of spotted owls following wildfire. Site occupancy by Mexican and California spotted owls in landscapes that burned primarily with low or moderate severities was similar to unburned landscapes (Jenness et al. 2004, Roberts et al. 2011), which suggests that spotted owls may be able to persist in burned landscapes. These findings contrast our results, which suggested that spotted owl site occupancy will decline in burned landscapes; however, our results were confounded by the effects of past timber harvest and salvage logging. Additional research in post-fire landscapes that have not been impact-

ed by past timber harvest and salvage logging are needed to help clarify these relationships.

MANAGEMENT IMPLICATIONS

We identified several factors that influenced occupancy of nesting territories by spotted owls in post-fire landscapes; however, the strongest association we observed was that site occupancy declined because of increased extinction probabilities. Increased amounts of past timber harvest, salvage logging, and high severity burns jointly contributed to increased extinction probabilities and subsequent declines in spotted owl site occupancy. Past timber harvest negatively influenced site occupancy in our analysis, so we recommend increased protection of older forest in dry forest ecosystems to prevent future habitat loss to timber harvest and mitigate potential losses of older forest to stand-replacing fire and subsequent salvage logging. High severity fire was 1 of 3 factors that combined to increase local-extinction probabilities of spotted owls in our study; however, we were unable to separate the impacts of wildfire from land management activities. As a result, we recommend future research to clarify the relationship between high severity fire and spotted owl site occupancy in the absence of past timber harvest and salvage logging. We believe that widespread, stand-replacing wildfires will negatively affect site occupancy by spotted owls, so we suggest efforts should be made to reduce the risk of widespread, stand-replacing wildfire in spotted owl habitat. However, a precautionary approach should be taken when implementing fuel reduction techniques that will reduce that risk of stand-replacing wildfire. Research is needed to ensure that fuel reduction techniques, particularly commercial or non-commercial thinning, are not detrimental to spotted owls, their habitat, or prey before fuel reduction techniques are implemented on a large scale. Our results also indicated a negative impact of salvage logging on site occupancy by spotted owls. We recommend restricting salvage logging after fires on public lands within 2.2 km of spotted owl territories (the median home range size in this portion of the spotted owl's range) to limit the negative impacts of salvage logging. Our results indicated a negative response of spotted owls to wildfire in the short-term, but the response is likely to vary over time; however, little is known about the long-term response of spotted owls to wildfire. As a result, long-term monitoring studies should be implemented in post-fire landscapes to determine the response of spotted owls to wildfire over time.

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Alternative Views of a Restoration Framework for Federal Forests in the Pacific Northwest

Dominick A. DellaSala, Robert G. Anthony, Monica L. Bond, Erik S. Fernandez, Chris A. Frissell, Chad T. Hanson, and Randi Spivak

Franklin and Johnson (2012) outlined elements of what they term an “ecological forestry” strategy for federal forests in the Pacific Northwest. They posit that their strategy will produce ecological and economic benefits from federal forests in Oregon and Washington and that economic returns are necessary for their widespread implementation. Thus, the strategy relies heavily on commercial thinning and an unknown amount of regeneration harvests to create economic returns. Many of their recommendations were recently incorporated into the final recovery plan and critical habitat ruling for the northern spotted owl (US Department of Interior [USDI] Fish & Wildlife Service 2012) over repeated objections raised by The Wildlife Society, American Ornithologists’ Union, and Society for Conservation Biology concerning untested and risky active management proposals in owl habitat (USDI Fish & Wildlife Service Oregon Fish & Wildlife Office 2013).

Franklin and Johnson’s (2012) framework is based on managing forests under the premise that they will be “restored,” while producing timber from sustained yield, yet their recommendations do not adequately recognize fish and wildlife habitat needs, and they rest on inappropriate ecological baselines for judging efficacy of restoration activities. They do, however, acknowledge that their core strategies may face social opposition, insufficient funding for implementation, restrictions due to impacts to northern spotted owls (*Strix occidentalis caurina*), and policy conflicts with the sustained yield provisions of the National Forest Management Act.

Here, we identify shortcomings of ecological forestry and how it is being implemented by managers based on our knowledge of the region’s ecology, habitat needs of the northern spotted owl and other wildlife, and pertinent published literature related to conservation biology, restoration ecology, and management of wildlife and aquatic resources. Although we believe that some aspects of ecological forestry may improve with current management, the framework places economic and political interests above ecological concerns in ways likely to generate new controversies and unintended harmful ecological consequences for natural resources.

Importance of Pacific Northwest Forests

The Pacific Northwest forests constitute some of the most important temperate forests on earth. They contain remaining concentrations of older forests that are currently well below historical levels due to logging (Strittholt et al. 2006). Federal forests in this region are known for exceptional biodiversity (DellaSala et al. 2011), carbon storage (Smithwick et al. 2002), late-successional habitat for >1,000 associated species (Forest Ecosystem Management Assessment Team [FEMAT] 1993), including spotted owls and marbled murrelets (*Brachyramphus marmoratus*), and relatively intact watersheds for numerous stocks of salmon (*Oncorhynchus* spp.). Because of the heated debate over what should be valued most in these “multiple use” public forests, management has been controversial and mistrust among stakeholders pervasive.

The Northwest Forest Plan (NWFP) is the foundation for management of federal land across nearly 25 million acres (FEMAT 1993) and is considered a global model of ecosystem management and biodiversity conservation (DellaSala and Williams 2006). The NWFP eased controversy over logging of older forests on federal lands to some degree. However, the decline in timber receipts to local counties has resulted in considerable pressure from county commissioners, Oregon Governor John Kitzhaber, former Interior Secretary Ken Salazar, and most of the Oregon congressional delegation to increase logging. This political pressure is most apparent for the approximate 2.1 million acres of Oregon and California Revested Lands (O&C) managed by the Bureau of Land Management (BLM) in western Oregon, which has a contentious history (Blumm and Wigington 2013). In response to recent pressures, former Interior Secretary Salazar initiated a series of “pilot projects” to implement ecological forestry in 2009, which could become the foundation for resource management plans across all 2.5 million acres of BLM lands in western Oregon and legislative proposals to address the O&C counties’ fiscal issues through increased timber harvests (Wyden 2012).

Positive Attributes of Ecological Forestry

Franklin and Johnson’s (2012) framework recognizes the conservation importance of late-successional forests on federal lands under the NWFP, which was reaffirmed in the recovery plan and critical habitat rule for the spotted owl (e.g., USDI Fish & Wildlife Service 2012). The importance of older, fire-resistant tree species in dry forests and the need to protect older trees throughout the landscape is also recognized by them. They reaffirm the NWFP’s emphasis on thinning dense, younger (<80 years) plantations to accelerate the acquisition of late-successional characteristics and increase the amount of forests under long rotations. Early seral forests are ac-

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Affiliations: Dominick A. DellaSala (dominick@geosinstitute.org), Geos Institute, Ashland, OR. Robert G. Anthony (robert.anthony@oregonstate.edu), Oregon State University. Monica L. Bond (monibond@gmail.com), Wild Nature Institute. Erik S. Fernandez (ef@oregonwild.org), Oregon Wild. Chris A. Frissell (leakimnywaders@yahoo.com). Chad T. Hanson (cthanson1@gmail.com), Earth Island Institute. Randi Spivak (randispivak@geosinstitute.org), Geos Institute.

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knowledge by them as an important ecological stage, and a distinction is made between forests created by industrial-scale logging that are deficient in biological legacies and biodiversity versus those generated by natural disturbances that are structurally complex and rich in biodiversity (Swanson et al. 2011, DellaSala et al. 2013). Franklin and Johnson's (2012) also recommend a credible adaptive management strategy whereby integrated monitoring and research activities, regional analysis and planning, and systematic assessments of ecological and social outcomes by independent parties are key elements. We generally agree with these aspects of their framework but acknowledge that the details of some of this management are yet to be described.

Ecological Shortcomings of Ecological Forestry

We identify seven major areas in which the framework of ecological forestry or its implementation by BLM may create adverse consequences to natural resources and conflicts over forest management.

1. Oversimplified Forest Classifications

Franklin and Johnson (2012) stratify the landscape into moist forests (MFs) and dry forests (DFs). In MFs, older stands are reserved and previously logged plantations are logged again using variable retention regeneration harvests (VRHs). In DFs, silvicultural treatments retain and release older trees (>150 years old), reduce stand densities, shift composition toward fire- and drought-tolerant species, and incorporate multiscaled heterogeneity. Unfortunately, the moist/dry classification and associated fire regimes are much too coarse and will create on-the-ground uncertainties where forest communities are highly complex (i.e., fine-grained heterogeneity). For example, inclusion of mixed-conifer forests in the DF type within the Klamath Province of southern Oregon and northern California will subject these forests to inappropriate commercial thinning based on false notions that these forests were historically more open (see below). Plant communities and fire regimes in this region vary widely across moisture gradients, soil types, microclimates, slope exposure, elevation, and bedrock geology with different forest patches grading into one another over short distances (i.e., high beta diversity) (Odion et al. 2004). Mixed-severity fires historically created landscape mosaics in this province that included a por-

tion of high-severity burn patches (DellaSala 2006, Donato et al. 2009, Halofsky et al. 2011) as well as those in the DF of the eastern Cascades (Hessburg et al. 2007, Baker 2012). These forests do not lend themselves to simplistic binary classifications. We disagree with the generalization of Franklin and Johnson (2012) that climate change is increasingly likely to shift plant associations toward the dry end of the moisture spectrum where plant associations straddle gradients because this assumption is not well supported and discounts considerable regional climatic variation. For example, Mote (2003) projected increased precipitation in some regions, including summer precipitation, and uncertainties in climate change modeling.

2. Lack of Clarity on Where to Draw the Line on Old Tree and Old Forest Retentions

Franklin and Johnson (2012) recognize the importance of both mature (>80–159 years) and old-growth (≥ 160 years) MFs but state that the age at which forests are “deemed older is a social decision influenced but not defined by scientific input.” The goal of the NWFP is to restore a functional, interconnected late-successional (both mature and old-growth) forest ecosystem and to produce timber. This means building on the NWFP through additional protections for old forests as recommended in critical habitat designations for the spotted owl and marbled murrelet. It also requires clear tree protection standards for older forests with greater recognition of mature forests (>80 years), given their rarity and ecological importance (FEMAT 1993, Stritholt et al. 2006). Instead, Johnson and Franklin (2009) analyzed various tradeoffs of setting tree protection thresholds at 80 to 160 years in MFs and >150 years in DFs, creating uncertainties in what to protect that have resulted in implementation controversies and poor policy choices.

Such lack of clear tree protection standards has generated considerable mistrust among stakeholders who monitor the management practices of BLM pilots in southwest Oregon (Reilly 2013, Wheeler 2013) (Figure 1A–D). For instance, of seven recent timber sales monitored on BLM pilot sites (MFs) by conservation groups, there were portions of mature forests and owl critical habitat included in logging proposals, and one logging site was adjacent to a 450-year-old forest occupied by nesting murrelets that will probably create edge effects

(Table 1). The net result of these sales was the incidental “take” of four spotted owls, triggering project-level appeals. These are examples of how immediate economic and political pressures have trumped older forest protections because mature forest protections were not clearly defined by the guidelines of ecological forestry. Without clear and ecologically appropriate age class restrictions, unintended ecological consequences will occur in project implementation.

Another example is the O&C legislative principles proposed by Oregon Senator Ron Wyden (2012), which cite Franklin and Johnson's (2012) and prescribe tree protection cutoffs at 120 years, thereby missing an important part of the mature forest cohort (80–120 years). The ecological consequences of this cutoff are not evaluated, and the guideline appears to be economically and politically motivated, not ecological. For instance, mature forests (80–120 years), which are well below historical levels, play a critical role as foraging and roosting habitat for spotted owls (Thomas et al. 1990). Without adequate protection of these forests, a successional debt will accrue on federal lands over time that will reduce ecosystem resilience and habitat for hundreds of associated species.

The latest data from the BLM Forest Cover Operations Inventory for all western Oregon BLM lands (including public domain, acquired, Coos Bay Wagon Road, and O&C lands) is a good example of how successional debt can accrue from not protecting older forests in such policy formulation. For instance, these data indicate that the highest proportion (43%) of forests on the BLM lands are <80 years old, whereas mature forests (80–120 years) account for only 15%, forests of 120–150 years account for 11%, and old-growth forests (>150 years) account for 24% of BLM lands (Figure 2A). Legislating ecological forestry provisions as proposed (Wyden 2012) would fail to protect the severely underrepresented mature forest (80–120 years) cohort. Thus, many of the 395,000 acres in this age bracket (MFs and DFs) would potentially be vulnerable to increased logging. Further, if the age limit for logging DFs was set at 150 years, as proposed by Franklin and Johnson (2012), up to 215,200 acres of DFs (80–150 years) would be potentially at risk (Figure 2B). Importantly, both the critical habitat rule and recovery plan for the spotted owl recommended protecting structurally complex older forests; thus, many mature forests with



Figure 1. Ecoforestry applications on BLM pilots in southwest Oregon as documented by independent project monitoring.² Many large (24- to 36-in. dbh) fire-resistant Douglas-firs are being removed under the guise of restoration. Clusters of large trees are marked for removal to “accelerate development of old-growth characteristics,” and new permanent roads are built for site access (BLM pilot Environmental Assessments). A. A 32-in. dbh Douglas-fir marked for removal in BLM ecoforestry Pilot Thompson unit 19-4. (Photo credit: Luke Ruediger.) B. In Pilot Thompson unit 20-1, a large 27-in. dbh Douglas-fir marked for removal and a 14-in. dbh ponderosa pine marked for retention. (Photo credit: Luke Ruediger.) C. BLM Pilot Joe mark before implementation. Numbers correspond to tree dbh. The blue mark is cut; the yellow mark (Ponderosa pine) is retain. (Photo credit: Aaron Krikava.) D. BLM Pilot Thompson unit 28-2, grouping of Douglas-firs >24-in. dbh marked for removal. (Photo credit: Luke Ruediger.)

important habitat attributes could be eliminated by logging under both proposals. Notably, the total amount of mature forest acres open to logging ultimately depends on how spotted owl Recovery Action 32 and other NWFP regulations and environmental laws are interpreted and maintained. Nonetheless, targeting mature forests for logging would mean that federal lands would never attain adequate habitat levels for numerous species associated with late-successional forests.

3. Lack of Appropriate Baseline Compromises Restoration in Mixed-Severity Fire Regions

Franklin and Johnson's (2012) approach to restoration focuses on commercial thinning to achieve desired conditions; however, for restoration to be ecologically based, foresters need an appropriate baseline from which to gauge the efficacy of restorative actions. For instance, under ecological forestry what does a restored site look like if not compared with an appropriate reference condi-

tion (e.g., comparable area of high ecological integrity) (DellaSala et al. 2003) or historical baseline? How will managers know when a site is restored, given the long time periods necessary to restore degraded sites?

In particular, baseline studies in the Klamath-Siskiyou ecoregion have questioned dry fuel models that are being incorrectly applied to justify VRHs and thinning in BLM pilots. For example, fire regimes in this region are of mixed severity (DellaSala 2006, Halofsky et al. 2011) and are within

Table 1. BLM ecological forestry pilots in MFs of western Oregon using VRHs, commercial thin, and density management.

District	Location	Treatment	Ecological shortcomings	Status
Roseburg	Myrtle Creek	3,145 acres total pilot; 500 acres VRH, remaining areas CT and DM	Oldest units ~75–124 yr; mostly spotted owl critical habitat	Scoping; no environmental assessment yet
	Camas Valley 2011 Harvest Plan	1,574 acres of CT and 239 acres of VRH	Some spotted owl critical habitat, mostly <70 yr	No environmental assessment yet
	White Castle	187 acres of VRH	Mature forest ~110 yr old; critical spotted owl habitat; suitable spotted owl habitat and core owl areas	Sold and under appeal; part of Roseburg District demonstration pilot
	Buck Rising	60 acres of VRH and 19 acres of DM	Mostly young forests but includes spotted owl critical habitat	Protest denied; logging in progress; part of Roseburg District demonstration pilot
Coos Bay	Soup Creek	300 acres of VRH	Mostly owl critical habitat; ~72 yr old; previously commercially thinned	Scoping
	Wagon Road	121 acres of VRH	Formerly considered spotted owl critical habitat in the 1992 determination; includes a 9-acre alder conversion next to old growth Port Orford cedar (<i>Chamaecyparis lawsoniana</i>) and 450-yr-old occupied marbled murrelet (<i>Brachyramphus marmoratus</i>) habitat; incidental “take” of 4 spotted owls	Appealed and sold
Eugene	Upper Willamette	2,000 acres of regeneration harvest and CT	Variable retention on 350 acres of a forest 80–90 yr old; regeneration harvest on stands infected with laminated root rot that would otherwise create high-quality early-seral habitat	Scoping

Monitoring data were provided by F. Eatherington, Cascadia Wildlands. CT, commercial thin; DM, density management.

historical bounds (Colombaroli and Gavin 2010), and open plant communities were of minor importance historically (Leiberg 1900, Duren et al. 2012). Hessburg et al. (2007) and Baker (2012) also demonstrated that small (<16 dbh) trees were abundant historically and actually numerically dominant in forests east of the Cascades in Oregon and Washington and that open stands were less common than assumed. Thus, this lack of an appropriate baseline may result in approaches that appear restorative because they are based on presumed historical conditions but that incorrectly calibrate a forest stand against a baseline that instead represents significant departures from an earlier state not considered (Papworth et al. 2009) and that could lead to novel ecosystems (Figure 3). Novel ecosystems, systems that have been sufficiently altered in structure and function most often by human action, can favor nonnative species and flip ecosystem dynamics to altered states (Lindenmayer et al. 2011). The altered state may not be resilient to climate change because of accumulating land-use stressors, particularly from multiple stand entries that can compound the effects of ecological perturbations (Paine et al. 1998).

Franklin and Johnson (2012) and many managers assume that the absence of fire at the stand or landscape level constitutes an a

priori risk due to a buildup of hazardous fuels in DFs. However, empirical studies have not shown this to be the case in the Klamath-Siskiyou ecoregion (Odion et al. 2004, Halofsky et al. 2011) where fire severity declined as the time between fire return intervals increased (Odion et al. 2010). Thus, the more complex systematics and processes at play in regions of mixed-severity fires require precautionary principles that first define and then test assumptions about baselines before deciding on what desired future conditions should be, let alone the interventions necessary to attain them.

4. Impacts to Aquatic Ecosystems Will Probably Increase

Franklin and Johnson (2012) acknowledged that they did not adequately address aquatic and riparian impacts, and this omission error can be costly to aquatic ecosystems in implementation. Freshwater and forest ecosystems share the same landscape. Because water quality and habitat conditions for fish and wildlife are determined in part by the condition of roads, vegetation, and erosion processes across the landscape, any forest management plan or conceptual framework should account for these factors a priori. For instance, Colombaroli and Gavin (2010) offered a critical environmental context across a 2,000-year sediment core record in which logging events over the past

century have pushed sedimentation rates far outside the range attributable to fires and climate variability.

Implementation of the timber prescriptions of Franklin and Johnson (2012) would create a need to maintain or expand the already extensive road system. However, roads and associated landings are the primary cause of landslides and chronic elevation of sediment delivery to streams, lakes, and wetlands (Gucinski et al. 2001). Roads permanently distort surface and subsurface drainage patterns that may trigger slope failure and channel erosion. Forest roads deliver sediment- and nutrient-laden runoff directly to surface drainage networks. Road densities are currently very high on previously logged lands in western Oregon (Firman et al. 2011), and agency resources are already insufficient to maintain the existing road network to prevent ongoing harm to watersheds. Stream conditions have improved markedly only where large reductions in roads have occurred under the NWFP (Reeves et al. 2006). Climate change forecasts indicate increasing hydrologic stress on road systems that will place additional strain on watershed resilience in the future (Furniss et al. 2010). Whatever the silvicultural objective, any restoration-focused management must reduce the forest road network and its impact on streams. More-

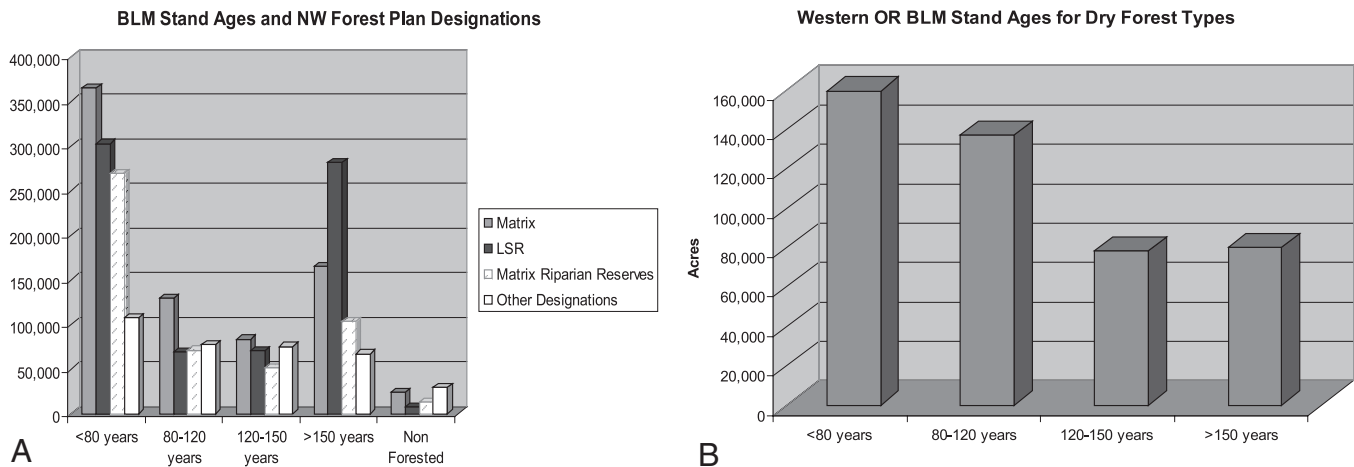


Figure 2. A. Stand ages and Northwest Forest Plan land-use allocations (units in acres) for BLM lands in western Oregon based on BLM Oregon Forest Cover Operations Inventory¹ compiled for 2013. The following notes apply. (1) BLM geographic information systems (GIS) data are most accurate in identifying forests <80 years followed by >150 years with lower levels of accuracy for intermediate age classes. Age classifications in southwest Oregon are not as accurate as those in other regions due to the complexity and diversity of the stands. (2) BLM data also include 153,000 acres of null value acres. These are predominately nonforested areas such as lakes and meadows. A small percentage of these stands should have been assigned stand age data because they are forested. (3) BLM stand age data extend farther east than our study area and into the Klamath Falls region. No distinction is made between DF versus MF forest types because Senator Wyden's principles do not differentiate these forest types. B. Stand ages for DF types on western Oregon BLM lands. The following notes apply. (1) The 159,400 acres of forests <80 years includes 67,200 acres of stands classified by the BLM as having a dominant age <80 years but with a minority component of trees >80 years old. (2) Oregon Gap Analysis 1998 Land Cover for Oregon GIS data was used as the source data to differentiate MF versus DF types and to mimic the moist/dry breakdowns in Franklin and Johnson (2012). The source data should not be considered an exact match, given that the data are a general overview of plant association groups that we then grouped as moist or dry. This was not an ideal data set for our study area given the classification errors. One example is that the source data incorrectly classified a number of forestlands as agricultural lands in the Roseburg area.

over, depletion of near- and medium-term large-wood recruitment can result from thinning in and near riparian areas (Spies et al. 2013), and more extensive ground disturbance from logging in and near headwater riparian areas will probably increase chronic sediment delivery to streams (Rashin et al. 2006).

5. Impacts to Northern Spotted Owls Are Grossly Underestimated

Extensive commercial thinning and/or regeneration harvest in stands >80 years will degrade spotted owl habitat with possible negative consequences on their movements and habitat use (Forsman et al. 1984, Thomas et al. 1990, Meiman et al. 2003). Spotted owls nest and roost in forests with high canopy closure, large trees, large woody debris, and vertical and horizontal diversity in stand structure (Thomas et al. 1990), all characteristics that thinning and logging will affect negatively. Franklin and Johnson (2012) assume that skips and gaps in thinning and retention of dense patches in places will provide for spotted owls, but there is no empirical evidence to support this claim. They also assume that retaining one-third to one-half of DFs on public lands in dense forest conditions is sufficient for spotted

owls; however, only about half the forest landscape is publicly owned in the BLM checkerboard lands of western Oregon. Because many private forestlands are managed under short rotations, maintenance of this amount of public lands as dense forests represents only one-fourth to one-sixth of the entire forest landscape. To compound this problem, survival rates of owls decline dramatically when home ranges include <50–60% late-successional forest (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). Unfortunately, the DF provisions call for extensive thinning in the Klamath Province where spotted owl populations are most numerous and currently most stable (Forsman et al. 2011). Pilot projects on BLM lands also have proposed controversial VRHs and thinning in critical habitat in mature MFs (>80 years), leading to incidental take of owls (Table 1; Figure 1).

Thinning in mature forests (>80 years) also has been shown to have negative effects on the abundance of the owls' primary prey species, including northern flying squirrels (*Glaucomys sabrinus*) (Waters and Zabel 1995, Carey 2000, 2001, Gomez et al. 2005, Wilson 2010, Manning et al. 2012, Wilson and Forsman 2013), red-backed

voles (*Myodes rutilus*) (Suzuki and Hayes 2003), and red tree voles (*Arborimus longicaudus*) (Swingle and Forsman 2009, Wilson and Forsman 2013). Further, thinning affects the composition and biomass of hypogeous fungi (Gomez et al. 2003), an important food item for flying squirrels and other small mammals. The food web of mycorrhizal fungi/small mammals/spotted owls is an important ecosystem function (Maser et al. 1978), and it should receive more attention if forest restoration is truly the goal. Franklin and Johnson (2012) note only one of the above references, but acknowledge probable restrictions, given the potential effects of thinning on small mammals as spotted owl prey.

Vegetative changes created by commercial thinning of mature MFs and extensive thinning (one-half to two-thirds as proposed by ecological forestry) in DFs will have a negative effect on primary prey (e.g., northern flying squirrel) for both spotted owls and barred owls (*Strix varia*) who exploit this common food source (Wiens 2012). This, in turn, will likely increase the competitive pressures on spotted owls that appear to be competitively inferior to barred owls (Dugger et al. 2011, Wiens 2012). It is not known

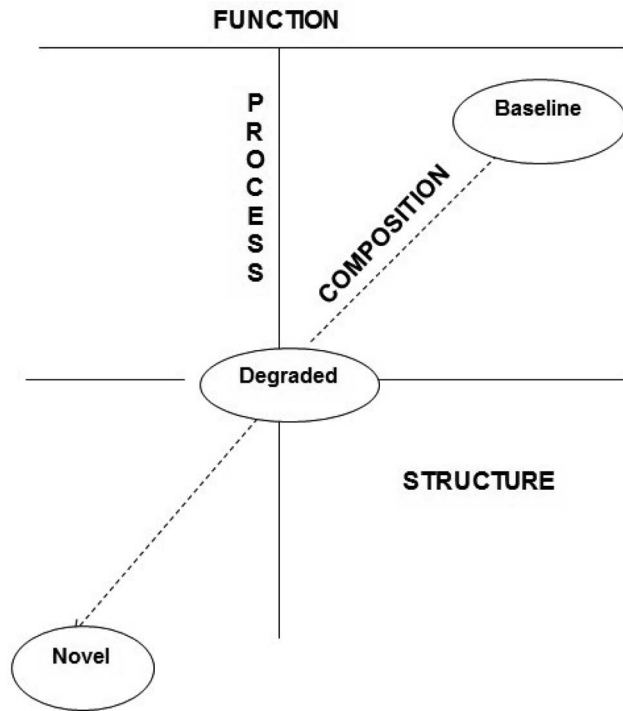


Figure 3. Restoration schematic diagram for forest ecosystems based on comparisons of degraded versus baseline sites with respect to forest structures, functions, and species composition. Ecological restoration would move a site from low (degraded) to high ecological integrity (upper right) based on comparisons to a historic baseline or a reference area of high ecological integrity (DellaSala et al. 2003).

whether there are thinning approaches that will not have these negative effects on prey of either or both species, or whether there will be ample research funds to address this question. This concern needs to be studied in more detail before commercial thinning is implemented beyond the pilot projects on BLM lands.

Notably, at least for California spotted owls, they select high-severity fire areas (unsalvaged) for foraging (Bond et al. 2009) and have higher reproduction successes in mixed-severity fire areas than in unburned forests (Roberts et al. 2011); in addition, mixed-severity fire without postfire logging does not reduce occupancy (Lee et al. 2012) nor does it change home-range size (Bond et al. 2013). Thus, whether active management is needed in owl habitat for fire concerns remains questionable. Moreover, estimates of forest disturbance by fire versus natural regrowth in DF provinces within the region show an increasing amount of older, closed canopy forests at the landscape scale even with fire (Hanson et al. 2009, Odion et al. in review). Only when the ratio of stand replacing fire to forest regrowth is >1 do closed canopy forests decrease over time. Thus, fire would have to increase about 5

times the current rates in dry provinces before this ratio would switch to a decreasing state (Odion and Hanson 2013, Odion et al. in review). Consequently, the assumptions of high fire risk to closed canopy forests and fire as a risk to spotted owls that are continually used to justify ecological forestry appear to be considerably overstated and lack empirical evidence.

6. Lack of Recognition for Natural Pathways to Complex Early Seral Forests

An important tenet of ecological forestry is that VRHs are needed to produce timber volume while creating early seral habitat for wildlife. VRHs can be an improvement over clearcutting practices, depending on structural retentions, but they remain untested hypotheses regarding benefits to early seral communities. Franklin and Johnson (2012) omit natural pathways to complex early seral forests, and this alternative approach to generate early seral forests is missing from the BLM pilots. Instead, the contemporary pattern of early seral forests generated by commercial logging has resulted in widespread distribution of more simplistic forests across large landscapes (e.g., “checkerboard” BLM ownerships in southern Oregon) and presumably a lack of

complex early seral forests generated by natural disturbance processes (Swanson et al. 2011, DellaSala et al. 2013). Notably, some rare wildlife species such as the black-backed woodpecker (*Picoides arcticus*) respond positively to complex early seral habitat created by natural disturbance but negatively to early seral habitat created by even-aged logging (Hutto 2008). The same appears to be true for spotted owls (Lee et al. 2012). Complex early seral forests created by high-severity fire also support species richness comparable to that of old-growth forests, but this stage is ephemeral (lasting <20 years) as conifer crowns close off understory development (Fontaine et al. 2009, Swanson et al. 2011, Donato et al. 2012, DellaSala et al. 2013).

Generally, the only known pathway to complex early seral forests is to allow them to go through succession unimpeded after natural disturbance (Swanson et al. 2011, DellaSala et al. 2013). Postfire logging can adversely affect conifer regeneration (Donato et al. 2006), wildlife habitat (Noss and Lindenmayer 2006, Hutto 2008), soils (DellaSala et al. 2006), survival and territory occupancy of spotted owls (Clark et al. 2011, 2013, Lee et al. 2012), and aquatic ecosystems (Karr et al. 2004), retarding development of complex early seral forests. Interestingly, postfire logging represents significant timber volume on BLM lands with some BLM districts reporting 27.5% of annual sale quantity (1995–2006) from “mortality salvage” (e.g., Lakeview BLM District; US-DOI Bureau of Land Management 2013). Much of this volume came from forests likely to have complex early seral features such as those in key watersheds, late successional reserves, and riparian reserves; areas with large, old trees killed by fire or insects are the best places to naturally regenerate complex early seral forests (Swanson et al. 2011). Cessation of postfire logging would certainly help compensate for the likely underrepresentation of complex early seral forests across the landscape and alleviate the perceived need to create them silviculturally.

7. Landscape Context Is Often Neglected During Implementation

When it comes to context, managers need to see the forest not just for the trees but for the landscape (Figure 4) before deciding on stand-level prescriptions. For instance, BLM pilots are nested in a landscape highly fragmented by roads and clearcuts and thus creating early seral forests through VRH at the stand level is not necessary,

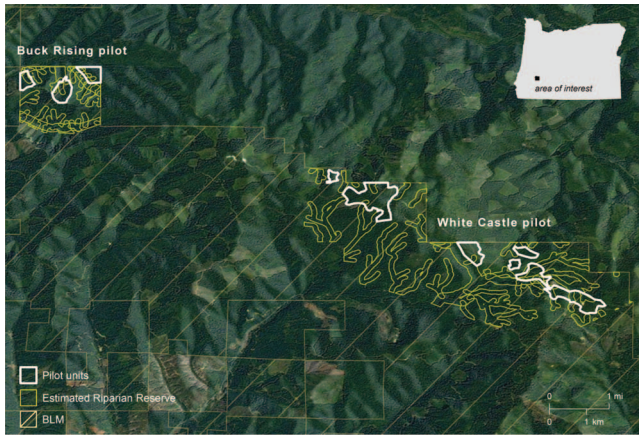


Figure 4. Landsat view of BLM pilots in southwest Oregon showing a highly fragmented landscape with BLM cut units (white polygons) in variable retention harvests and adjoining Riparian Reserve (linear polygons) in “density management” within a surrounding landscape of mostly early seral forest created by logging. Northwest units (3) are the Buck Rising pilot; other units are in the White Castle pilot. Data sources: Esri, Bureau of Land Management, US Department of Agriculture, i-cubed.

given that it is not in short supply nor is VRH a substitute for natural disturbance processes. Additional harvests in remaining older forests to create early seral forests would also result in cumulative impacts to late-successional species and further contribute to the successional debt of older forests. A more fragmented landscape, where the remaining mature forest blocks are broken up into smaller and structurally simplistic patches (Figure 4) lacking interior conditions, may exacerbate predation of marbled murrelet nest sites by corvids (Malt and Lank 2009).

Conclusions and Recommendations

Whereas Franklin and Johnson (2012) offer ecological forestry as a new paradigm for federal lands in the Pacific Northwest, key elements of their proposal and the way it is being implemented by managers conflict with conservation biology, ecological restoration, and prudent management of aquatic and wildlife resources. The most significant shortcomings of their approach are that it is driven largely by economic returns and political pressures, uses an inappropriate baseline for evaluating restoration, will degrade habitat for spotted owls and many other late seral species, will increase aquatic impacts from extensive thinning and road networks, and may create novel ecosystems that flip ecosystem dynamics to altered states with undesirable consequences to biological diversity. Implementation problems with the pilot projects further demonstrate how approaches lacking in well-defined tree age

cutoffs create mistrust, a greater need for multidisciplinary monitoring, and scientific input from forest and wildlife ecologists.

We offer 14 recommendations to improve the framework and its implementation:

1. Adhere to the NWFP standards and guidelines, especially the reserve network and riparian and watershed conservation measures in the Aquatic Conservation Strategy because there have been measurable improvements to watersheds under this strategy (Reeves et al. 2006).
2. In MFs and areas with mixed-severity fires, prohibit thinning in forests >80 years and prohibit VRHs in spotted owl and marbled murrelet critical habitat. There is scientific precedent for this age threshold (FEMAT 1993); mature forests are in short supply regionally (Strittholt et al. 2006), are the only precursors to old-growth forests, and are habitat for these and other imperiled late seral species such as red-tree voles. Lacking specific prohibition on harvesting of mature forests, we anticipate continued conflict over ecological forestry as evidenced by the BLM pilots.
3. If experiments with VRHs are done, they should be confined to previously managed stands <80 years outside critical habitat for any listed species or species of concern. The effects on early seral species should be addressed.
4. In DFs, if thinning is conducted in a particular location due to land manag-

ers' concern about hazardous fuels, use an upper cut limit (trees ≤ 80 years or trees <21 in dbh; “eastside screens”) (US Department of Agriculture 1995) to protect large trees that are scarce (Henjum et al. 1994, Van Pelt 2008) and to remove small trees for fire concerns (Martinson and Omi 2003). Do not alter the composition of multistrata stands with large trees or single-stratum stands with large fire-intolerant white firs (*Abies concolor*) below their natural range of variability (e.g., as in the existing eastside ecosystem strategy guidelines in place, US Department of Agriculture 1995). Include snag creation (Hanson et al. 2010) of larger white firs to shift species composition in fire-suppressed forests.

5. Prioritize managed wildland fire and prescribed fire for ecological restoration.
6. Retain at least 60% canopy closure in DFs (USDI Fish & Wildlife Service 2012) and >50% late-successional forests at the territory scale (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005) for spotted owls and other species associated with closed canopy, older forests. Include high densities of large snags and small/medium-sized trees for late seral wildlife such as Pacific fishers (*Martes pennanti*) (Zielinski et al. 2006) and spotted owls (Pidgeon 1995, North et al. 1999) and high snag basal area for black-backed woodpeckers (Hutto 2008).
7. Avoid creation of novel ecosystems by using both back casting (e.g., stand age reconstructions) and forecasting (e.g., downscaled climate change models) techniques to set restoration targets. We are not suggesting that ecosystems return to some specific past condition; however, clearly defined baselines with historical context or comparable reference areas of high ecological integrity should be a restoration prerequisite to avoid creation of novel ecosystems.
8. Fully assess the impacts of “ecological forestry” and ensure that forest restoration addresses the complete range of ecological concerns, including reductions in carbon stores caused by VRHs and thinning (Campbell et al. 2011), soil compaction, and reduced recruitment of dead wood, invasive species, roads, and forest fragmentation.
9. Restore hydrologic functions to areas

damaged by roads through road obliteration and recontouring of the road prism and prohibit postfire logging in riparian reserves and key watersheds.

10. Support well-designed and fully funded experiments to resolve conflicts over thinning to spotted owls, prey species, and barred owl invasions.
11. Develop a finer classification system than moist/dry to resolve uncertainties and place forests with mixed-severity systems in the MF category to limit inappropriate thinning. Forest classifications need to correlate more specifically with plant association groups, site-specific factors, and historical fire regimes before conclusions can be drawn on appropriate management, particularly in mixed-severity systems (Halofsky et al. 2011, Perry et al. 2011). This issue should be periodically reviewed, given the emerging evidence of climate change.
12. Conduct research to estimate historical amounts and distribution of complex early seral forests versus current spatio-temporal distribution of simple and complex early seral forests to document any current deficiencies and differences in forest quality (Odion and Hanson 2013).
13. Prohibit postfire logging and replanting after disturbance to ensure adequate structure and composition of complex early seral forests.
14. Incorporate landscape context in environmental assessments to determine the cumulative effects of thinning and logging on late seral species and distribution of complex early seral forests.

Franklin and Johnson (2012) state that stakeholders have created polar opposites for federal lands: either managing them for intensive wood production or for spotted owls. However, the NWFP was designed to meet the viability requirements of >1,000 late-successional species, not just owls, and is a compromise between these two competing views. Many scientists and conservation groups have offered ways to restore forests beyond thinning (DellaSala et al. 2003), have proposed thinning measures with less impact (Kerr 2012), and other active management approaches that constitute more comprehensive restoration measures (Hanson et al. 2010). Ecological forestry as currently conceived will create more tension over management of federal forests than it

resolves, initiating questions about its adequacy as an ecologically credible framework. Whereas we have presented ecological concerns, others have identified significant controversy in policies that seek to increase timber volume by overturning environmental protections (Blumm and Wigington 2013). This is especially the case for BLM lands in western Oregon because these lands have a history of overcutting and recent proposals to undermine the NWFP; thus, increased logging would come at a significant expense to important ecological values already in short supply and to the public trust.

Endnotes

1. Data from BLM Oregon Forest Cover Operations Inventory obtained from www.blm.gov/or/gis/data-details.php?data=ds000045.
2. Please visit thesiskiyoucrest.blogspot.com for more information.

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RESPONSE

Ecologically Based Management: A Future for Federal Forestry in the Pacific Northwest

Jerry F. Franklin and K. Norman Johnson

In their opinion piece, DellaSala et al. (2013) (hereafter, called the “Critique”) offer a miscellany of criticisms of the peer-reviewed article in which we proposed some restoration strategies for federal forests in the Pacific Northwest (PNW) (Franklin and Johnson 2012). We respond below to aspects of their critique, primarily what they view as our major “ecological shortcomings.” Their assertions re-

garding potential negative impacts of our proposals on the northern spotted owl (NSO) are addressed by Henson et al. (2013).

Ecological Forestry

Ecological forestry (EF) is conceptually based on utilizing processes and conditions characteristic of natural forest ecosystems as models for forest management and is not defined by a specific silvicultural practice or management proposal, which the Critique apparently does not recognize. EF differs fundamentally from production forestry (PF), which is conceptually grounded on agro-economic models constrained by economic considerations (Table 1).

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Affiliations: Jerry F. Franklin (jff@u.washington.edu), School of Environmental and Forest Science, University of Washington, Seattle, WA. K. Norman Johnson (norm.johnson@oregonstate.edu), Oregon State University.

Table 1. Conceptual basis and some exemplary elements of ecological forestry in contrast with those of production forestry.

Ecological forestry	Production forestry
<i>Conceptual basis</i>	
Utilizes ecological models from natural forest systems as basis for managing forests	Utilizes agronomic models combined with economic models as basis for managing forests
<i>Exemplary philosophical contrasts</i>	
Maintains full array of ecosystem structures, functions, and biota at larger spatial scales	Maintains limited set of ecosystem structures, functions, and biota consistent with economic goals except where legally required to do more
Tends to increase management and societal options	Purposely limits management and societal options in pursuit of high economic returns
Values complexity and heterogeneity	Values simplicity and homogeneity
<i>Exemplary definitional elements of ecological forestry</i>	
Provides for continuity in structure, function, and biota between forest generations	Creates discontinuity in structure, function, and biota between forest generations
Utilizes natural stand development models, including effects of disturbances, in developing silvicultural prescriptions	Utilizes agronomic models in developing silvicultural prescriptions
Spatial heterogeneity at stand and landscape levels is typically a goal	Spatial uniformity at stand and landscape levels is goal
Considers and incorporates impacts of natural disturbances	Attempts to eliminate or evade potential for natural disturbances
<i>Exemplary attributes of silvicultural systems and prescriptions</i>	
Multi- or uneven-aged management regimes	Even-aged management regimes or economic selection on low-production sites
Incorporates biological legacies into all regeneration harvest treatments	Does not incorporate concept of biological legacies except as legally required
Variable-density thinning practices	Uniform density thinning practices
Retains woody debris and defective trees and structures	Eliminates coarse wood and defective trees and structures, except as legally required

The hierarchical structure of EF in which specific silvicultural activities are grounded in the general ecological attributes of forest ecosystems is illustrated in Table 1 and contrasted with practices and attributes of PF. In general, management approaches using EF principles do not attempt to optimize singular outcomes but, rather, integrate multiple ecological, economic, and cultural objectives. As such, EF provides a philosophical basis for management; management proposals can be judged as to whether or not they are philosophically consistent with EF.

Northwest Forest Plan

The Northwest Forest Plan (NWFP) is described as a “global model of ecosystem management and biodiversity [protection]” in the Critique and represented as an undeviating guide to federal forest management since its adoption in 1994. In fact the NWFP was never implemented as written and almost immediately began undergoing alterations in interpretation and agency practices (Thomas et al. 2006). Regeneration harvests of mature and old-growth forest in the Matrix, which were a foundational element of the NWFP, were litigated, eventually leading agencies to quietly adopt a “thinning only” strategy of timber harvest.

New provisions in the NSO recovery plan and critical habitat designation (USDI Fish & Wildlife Service 2011, 2012) effectively represent major revisions in the NWFP.

Hence, we view the Critique’s claim that “pressures for change in the NWFP are recent and solely in response to economic concerns” as nonsense! Essentially all of the significant changes in the NWFP have involved increasing ecological protections and restricting timber harvests, such as by greatly reducing the area actually available for sustained timber harvests. We do not judge the merits of these changes but their reality must be acknowledged in any discussions about the NWFP.

Recognizing Forest Diversity in Policy

The distinction between dry forests and moist forests of the PNW is identified as first among our ecological shortcomings in the Critique. We viewed this distinction as the critical starting point for any national policy regarding retention of old-growth forests because: (1) active management is imperative to restore and sustain old forests on many sites with natural disturbance regimes of frequent low- to mixed-severity wildfire (our

dry forests, or DFs); in contrast, (2) active management is generally unnecessary and even potentially destabilizing in existing old-growth forests growing on sites characterized by infrequent high-severity wildfires (our moist forests, or MFs). Further, our proposed policy for active management of DFs is permissive, meaning that managers would be allowed (but not required) to actively restore DFs, depending on such variables as their condition and landscape context.

Of course, a “simplistic binary classification” of forests without further elaboration would be inadequate so we identified and assigned each of the several hundred, geographically relevant and scientifically documented plant associations and habitat types to MF or DF categories. This approach explicitly recognizes the diversity of forest types and conditions and the intricate landscape-level mosaics of forest, habitats, and disturbance regimes in a way that is appropriate in federal legislation and it provides managers with needed flexibility in applying the management strategy so that they can tailor it to site-specific considerations. In addition we strongly urge managers to do on-the-ground surveys to identify plant associations that are present and their distribu-

tion rather than depending on generalized maps.

Defining Old Forests

Policy decisions about federal forests *are* ultimately social decisions, including decisions about which forests should be reserved from timber harvest. Goals in a policy analysis are to analyze an array of possible alternatives without prejudice. Hence, we used three different ages at which MFs might be declared “old” and reserved from harvest. All three ages—80, 120, and 160 years—have been part of the social dialogue (Johnson et al. 1991, Johnson and Franklin 2009, Johnson and Franklin 2012) and their disposition on NWFP land allocations available for harvest (Matrix and Adaptive Management Areas) intensely debated. We were members of a congressionally chartered committee (Johnson et al. 1991) that first identified 80 years as the age when forests began to exhibit some “late successional attributes” and documented that mature forests (80–200 years old) are relatively common on federal lands in the PNW. Large areas of such forests are incorporated into the Late Successional Reserves of the NWFP. Further, Recovery Actions 10 and 32 in the recovery plan for the NSO (USDI Fish & Wildlife Service 2011) are likely to result in retention of many forests in the 80–160 year age range. Given all of these circumstances, we suggested that MF variable-retention regeneration harvests focus primarily on younger forests, with retention of any trees 150 years when they occur in younger stands subject to harvest. In any case, we reiterate that the disposition of these mature forests *is* a social decision.

We certainly do propose restoration treatments of DF stands that have individual trees >150 years and, indeed, often argue that stands containing these older trees should be high priorities for restoration since the old trees in these stands are often at high risk of accelerated mortality (Franklin et al. 2013). Our DF strategy is a landscape-level approach in which approximately one-third of the landscape is retained in denser patches and all older trees in the remaining two-thirds are not only retained but nurtured (by reductions of fuels and competition) to increase their longevity. Our proposals are largely consistent with the DF strategy adopted in the NSO recovery plan (USDI Fish & Wildlife Service 2011).

Impacts to Aquatic Ecosystems

The Critique charges that our proposed timber harvesting program will “. . . create a need to maintain or expand the already extensive road system,” which would presumably have undesirable impacts on aquatic ecosystems. In fact, resumption of regeneration harvests would almost certainly result in less road-related impacts than the extensive thinning programs apparently favored by authors of the Critique (e.g., proposals of Kerr 2012). Thinning programs not only require a much greater mileage of road per unit of wood harvest but also produce much lower stumpage returns, resulting in fewer dollars being available for maintenance or closure of roads.

Baselines for Dry Forests

The Critique appears to lump all DFs into the category of “mixed severity fire regions.” Our restoration strategy for the DF landscapes in eastern Oregon is detailed in Franklin et al. (2013). Included in the DF category are ponderosa pine, dry mixed-conifer, and moist mixed-conifer forest types with more detailed specification by specific plant associations. We again note that active management of such forests is optional and not mandatory under our proposals, providing managers the flexibility to respond as appropriate to individual plant associations, stand conditions, landscape contexts, and management goals.

Our baseline includes analyses of historical timber cruises of the Klamath and Warm Springs Reservations (Hagmann et al. 2013, Hagmann 2013). It is clear from this revealed historical baseline that pine and dry and most moist mixed-conifer forests were low-density stands dominated by large diameter ponderosa pine. It is also clear from the historical cruises that Baker's (2012) attempted reconstructions in these two locations grossly overestimate historical stand densities.

We agree with the Critique that there is high forest diversity in southwestern (SW) Oregon, including Oregon's portion of the Klamath–Siskiyou (KS) region but in subsequent discussions the Critique largely treats SW Oregon as a singularity (i.e., a region of mixed-severity wildfire). In fact, conditions vary from coastal areas, which are clearly MF with infrequent severe wildfire regimes, to dry interior river valleys, where natural frequent wildfire regimes dominated (DF).

Great care is, therefore, required in characterizing conditions in SW Oregon on both local and larger scales. The Critique cites several studies from the Klamath National Forest, which is in moister portions of the KS region, and not applicable to interior valleys in SW Oregon. A cited study of lake sedimentation (Colombaroli and Gavin 2010), which is used to infer widespread occurrence of mixed-severity wildfires, lies in a watershed that is dominantly MF,¹ where such fires would be expected. After visiting more than 50 locations, we have found that many DF sites in the interior valleys of SW Oregon are occupied by maturing (<150 year old) Douglas-fir forests, which appear to be the first generation of closed-canopy conifer forests on these sites. This interpretation is consistent with recent fire history studies in the Applegate River drainage.²

As before, we conclude that research and management in SW Oregon requires close attention to local environmental conditions and a highly adaptive approach so as to create and incorporate additional understanding of this complex region.

High-Quality Early Seral Ecosystems

The Critique charges that we failed to recognize natural pathways to “complex early seral forests.” First, we need to clarify that the issue is about high-quality early seral ecosystems (ESEs), not “complex early seral forests;” the ESEs that characterize the initial period following a disturbance are not forests (ecosystems dominated by trees) but ecosystems dominated by diverse plant life forms—cryptogams, herbs, shrubs, and individual trees. Second, while we agree that ecological forestry can provide conceptual approaches to producing “. . . timber volume while creating early seral habitat,” such a goal is certainly not a “tenet of ecological forestry”!

Cessation of postfire logging could provide high-quality ESEs as noted in the Critique and we have opposed salvage logging on MF sites where primary management goals are ecological, such as on much federal land (e.g., see Lindenmayer et al. 2008).

ESEs are the ecologically critical first stage in the multcentury successional sequences or seres that develop on MF sites in the PNW. The ESEs arguably sustain the highest biodiversity of any stage in the sere

by a variety of measures; this biodiversity includes many ESE habitat specialists as well as ecosystem processes weakly represented elsewhere in the sere (e.g., accretion of nitrogen stocks) (Swanson et al. 2011). Consequently, ESEs need to be predictably and adequately represented in time and space and, just as with old-growth forests, the only landownership on which high-quality examples of such ecosystems can reliably be provided are federal lands. Hence, we argue that provision of ESEs is a goal that needs to be incorporated into federal management plans and suggest achieving this by a program of variable retention regeneration harvests with adjustments periodically made for ESEs created by natural disturbances.

The Critique's assertion that ESEs were "ephemeral" is inaccurate. ESEs typically persisted for several decades. For example, the duration of Douglas-fir establishment in natural stands throughout the Douglas-fir region—a useful index to persistence of ESE conditions—averaged 50–60 years in two independent studies of natural Douglas-fir-dominated stand establishment (Tepley 2010, Freund 2013).

Conclusion

Our proposals are motivated by ecological goals and the desire to see that all management of federal lands is ultimately based on ecological principles. However, we admit to seeking solutions that provide economic as well as ecological benefits in the belief that such approaches represent the only viable future for federal forest lands. We also admit to raising the issue of whether society wishes for forestry to have a continuing and active role in management of the federal forests of the PNW. If so, we have suggested some ways for forestry to play that role that integrate ecological, economic, and social values. If raising these issues increases tensions over management of federal lands, so be it; the time for this discussion is long past!

Endnotes

1. Moist forest plant associations as modeled in Johnson and Franklin (2009 and 2012).
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RESPONSE

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Using Ecological Forestry to Reconcile Spotted Owl Conservation and Forest Management

Paul Henson, Jim Thrailkill, Betsy Glenn,
 Brian Woodbridge, and Brendan White

In their opinion article, DellaSala et al. (2013) identify the potential shortcomings of Franklin and Johnson's (2012) ecological forestry (EF) management principles. DellaSala et al. also criticize the incorporation of some of these principles into the recently completed northern spotted owl (*Strix occidentalis caurina*) (NSO) revised recovery plan (USDI Fish & Wildlife Service 2011) and revised critical habitat (CH) designation (50 CFR 17; 77 FR 71875). Although we agree with several of their points, we think components of their criticisms and recommendations mischaracterize our application of EF principles. DellaSala et al. also understate the risk of climate change and associated disruptions in forest ecosystem disturbance processes, whereas they overstate the potential impacts of certain EF management prescriptions on those same ecosystems. We focus below on their comments concerning NSO conservation and its relationship to climate change, active forest management, and the Northwest Forest Plan (NWFP) (USDA Forest Service/US Department of Interior Bureau of Land Management 1994).

Many of the recommendations made by DellaSala et al. (2013) are sound and were originally included in the NSO recovery plan and CH. The recovery plan takes an ecosystem approach. It encourages managers to (1) conserve older forests and manage them for resilience, (2) restore fire and other natural disturbance processes where they have been suppressed or altered, (3) conserve legacy habitat elements in postfire landscapes, (4) design and implement restoration treatments at the landscape scale, and (5) reconcile any short-term impacts of this management with long-term NSO conservation. Areas of disagreement with DellaSala et al. are mostly a matter of degree and risk tolerance: What are the risks of taking management action versus inaction? And what are the respective tradeoffs between near-term impacts to NSO for longer-term gains for forest health, other wildlife species, and other societal values (Ager et al. 2007, Gaines et al. 2010a)?

DellaSala et al. (2013) seem to question most active management within NSO habitat because they believe that (1) current and projected patterns of wildfire occurrence in much of the NSO range are acceptable and within historical bounds, (2) the related California spotted owl (*Strix occidentalis occidentalis*) evolved with fire and use burned areas (therefore, fire may have a mostly positive impact on the NSO), (3) management is risky or counterproductive and

should not be taken until some (unspecified) level of certainty or risk tolerance is reached, and (4) political and economic interests, rather than science, are driving EF management recommendations. Each of these positions deserves careful consideration.

We believe the preponderance of scientific evidence suggests that climate change and past management practices are intensifying disturbances in western forest ecosystems, including wildfire, disease, and insect outbreaks. Wildfire size and total burn area have been increasing in the dry, fire-prone forests of the western United States (Westerling et al. 2006, Littell et al. 2009, Chmura et al. 2011) and are projected to increase significantly during the next century (Marlon et al. 2012, Vose et al. 2012, Yue et al. 2013). Larger wildfires west of the Cascade Mountains are also more likely (Littell et al. 2010, Rogers et al. 2011), including all major forest types in Oregon (Shafer et al. 2010) and in northwestern California (Miller et al. 2012). Davis et al. (2011) found a marked increase in large wildfires in the NSO range in the last 30 years.

The overriding management issues are the following: how “departed” are these disturbance processes and vegetation patterns from both retrospective baselines and reasonable estimates of likely future conditions, and what, if anything, should land managers do to influence these patterns in the face of climate change? DellaSala et al. (2013) generally downplay the challenges that climate change has brought to forest management decisions, suggesting that ecological departure in northwest forests is low and uncertainty in localized predictions means that managers should defer taking most management action if there are short-term adverse effects of NSO or associated wildlife species. We disagree with both their interpretation of climate science and their advocacy of a passive approach. Rather, we believe it is necessary to weigh the relative risks of action and inaction and make timely management decisions that take into account broader, longer-term goals for wildlife and ecosystem conservation (Agee 2002, Carey 2006, North et al. 2010). The Endangered Species Act of 1973 directs us to “conserve the ecosystems” on which listed species depend (Endangered Species Act, Section 2), and NSO conservation is consistent with and, in fact, relies on these broader ecosystem conservation objectives.

Our perspectives also diverge from those of DellaSala et al. (2013) regarding the relative risks to the NSO from wildfire, and their conclusions discounting the potential impacts of fire on spotted owl populations and habitat rangewide are premature (Kennedy and Wimberly 2009, Halofsky et al. 2013). Wildfire is now the leading cause of NSO habitat loss on federal lands (Davis et al. 2011), and Clark et al. (2013) found that NSO site occupancy of nesting territories declined after wildfire. The NSO recovery plan describes how individual spotted owls use burned areas to varying

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Affiliations: Paul Henson (paul_henson@fw.s.gov), USDI Fish & Wildlife Service, Oregon Fish and Wildlife Office. Jim Thrailkill, USDI Fish & Wildlife Service. Brian Woodbridge, USDI Fish & Wildlife Service. Betsy Glenn, USDI Fish & Wildlife Service. Brendan White, USDI Fish & Wildlife Service.

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degrees, and we agree that pre- and postfire management intervention is not warranted or would be counterproductive in many areas (USDI Fish & Wildlife Service 2011, p. III-30). We also agree that there is tremendous variation in disturbance processes and vegetation patterns due to ecological complexity (Hessburg et al. 2007) and that high-severity fire is an appropriate and desirable component of natural fire regimes in some areas (Stephens et al. 2012). However, valuable and rare (in absolute and historical terms) older forests in the range of the NSO are being removed by fire (Spies et al. 2006, Davis et al. 2011), and these losses will probably increase in the future (Healey et al. 2008). DellaSala et al. acknowledge that “mature forests are in short supply regionally” and should be conserved, and they advocate adherence to the NWFP guidelines, but they disregard the NWFP direction to conserve these forests from catastrophic disturbance (USDA Forest Service/US Department of Interior Bureau of Land Management 1994, p. B-5, C-12). Their general conclusions that large areas of these older forests, including areas in the eastern Cascade Mountains of Washington (Lehmkuhl et al. 2007, Haugo et al. 2010) and Oregon (Kennedy and Wimberly 2009, Spies et al. 2010), in southwest Oregon (Perry et al. 2011, Hagmann et al. 2013), and in northern California (Miller et al. 2012), are at low risk of loss or ecological conversion are at odds with those of many other scientists.

The NSO recovery plan seeks an appropriate balance between action and inaction in view of disturbance risk and past management practices. It recommends little or no management intervention in areas of high-quality NSO habitat or where disturbance risk is relatively low or acceptable (e.g., older moist forest). However, in other areas, especially drier forests, it recommends that land managers consider intervention based on careful planning at the appropriate landscape level (Roloff et al. 2012, Safford et al. 2012, Halofsky et al. 2013). Much of this science is focused on explicitly weighing the tradeoffs between single species conservation and broader ecosystem goals (e.g., White et al. 2013a). DellaSala et al. call for more research before management actions are taken, but there is already much specific guidance on how to minimize risk and impacts to NSO and other wildlife when im-

plementing appropriate management (e.g., Lehmkuhl et al. 2007, Buchanan 2009, Spies et al. 2012). Although there is still much unknown about these ecosystems and no decision is risk-free, there is solid scientific insight that enables informed management decisions to move forward. Applying EF principles is not a “one size fits all” approach, and we support monitoring and incorporating those results into subsequent decisions as part of an adaptive management process. Good examples of landscape strategies that apply EF and adaptive principles within the NSO range include Gaines et al. (2010a), Smith et al. (2011), Davis et al. (2012), North et al. (2013), and Hessburg et al. (2013).

Similar to their generalizations concerning wildfire, DellaSala et al. (2013) oversimplify how various types of vegetation management might negatively affect NSO populations or other wildlife, but they do not provide the same level of speculation on how inaction might negatively affect the NSO or other species. Our approach is based on considerations of both action and inaction. In reality, these management decisions are quite complex and context- and taxa-specific. Wildfire, prescribed fire, and vegetation management affect species in many different ways—positively and negatively—over space and time, and there are ecological tradeoffs for many species and values (e.g., Forsman et al. 2010, Fontaine and Kennedy 2012). Many other scientists recommend active management of various types to help conserve forest wildlife due to threats of uncharacteristic disturbance (e.g., Gaines et al. 2010b, Kalies et al. 2010, Stephens and Alexander 2011). For example, high fuel loading and ladder fuels can reduce foraging or nesting habitat quality for California spotted owls in Sierra Nevada forests (Roberts and North 2012, Keane 2013). A vegetation treatment may accelerate the development of NSO nesting habitat (Wimberly et al. 2004) or reduce the risk of high-severity fire for forest birds (White et al. 2013b), even if it temporarily degrades existing habitat and “takes” owls in the near term (Franklin et al. 2006). Forest management projects may adversely affect and take NSOs, but these projects might still be compatible with NSO recovery and CH if the overall magnitude of the impacts is limited in scope temporally and geographically, especially where the primary intent of the

project is long-term restoration (Gaines et al. 2010a). Scheller et al. (2011) described similar tradeoffs for the fisher (*Martes pennanti*) in the Sierra Nevada. The NSO recovery plan recommends that these tradeoffs be carefully evaluated on a case-by-case basis at the appropriate landscape scale, with a joint goal of restoring or emulating natural disturbance processes and recovering NSOs.

DellaSala et al. (2013) criticize these projects for having an impact on the NSO. They do not acknowledge, however, the possibility that the known adverse effects associated with a well-crafted project may be preferable to potential adverse effects associated with doing nothing in highly departed landscapes (North et al. 2010). We appreciate the many sources of uncertainty that impinge on such a choice, but as we described above, tools and techniques are available to create detailed, site-specific, risk assessments to inform these difficult management decisions. We recommend ongoing research and monitoring to better understand the effects of forest restoration treatments on the NSO and other plant and animal species (USDI Fish & Wildlife Service 2011, p. III-35).

DellaSala et al. (2013) suggest that application of Franklin and Johnson's (2012) EF principles or the NSO recovery plan might result in a decrease in protections provided by the NWFP or other environmental safeguards. We believe the opposite is more likely. Each of the pilot projects they criticize (DellaSala et al. 2013, Table 1) not only are consistent with the requirements of the NWFP but also are more restrictive than what the NWFP otherwise permits. They leave more downed wood and more standing trees than the NWFP requires, they incorporate natural disturbance processes into management decisions, and the prescriptions do a better job addressing broader wildlife goals than traditional silviculture. The approach is a marked improvement over previous types of permitted federal timber harvest, including what is allowed on “matrix” lands under the NWFP.

On a broader level, DellaSala et al. (2013) discourage active forest management because of the risk of unintentionally creating “novel” ecosystems. Yet the majority of researchers (Hagmann et al. 2013, Lydersen et al. 2013, Sensenig et al. 2013, and others) agree that the cumulative effects of fire suppression and past timber harvest have already created novel conditions across large

areas, particularly within the eastern Cascades and diverse Klamath-Siskiyou forest ecosystems. Are these changes to forest structure and function, taken separately from wildfire risk, assumed by DellaSala et al. to be neutral or beneficial to the NSO and other wildlife, now and in the long term? We agree that caution is always warranted when one takes any habitat-altering action. But what of the potential for novel conditions to be created or perpetuated as a consequence of management *inaction*? Many scientists are concerned about climate-driven disturbances speeding up ecological conversions among forest types and recommend research and intervention (e.g., Collins et al. 2011, Perry et al. 2011, Davis et al. 2012). Given the tremendous landscape scale of climate-driven changes, we suggest that this is a much more serious conservation challenge for northwest forests (Millar et al. 2007, Vose et al. 2012). We have structured NSO recovery to fit within science-based landscape strategies that address this challenge and to work closely with our land management partners such as the USDA Forest Service (Tidwell 2012) and other landowners.

In conclusion, the EF principles such as those articulated by Franklin and Johnson (2012) and many others (e.g., Franklin et al. 2002, 2007, Drever et al. 2006, North and Keeton 2008, Long 2009, others) should be applied to forest management where appropriate. They provide an important foundation for restoring natural ecological processes, and if also applied to commercial timber harvest, they are likely to result in a net conservation improvement compared with what is currently permitted on many federal, state, and private lands. DellaSala et al. (2013) acknowledge this potential, saying that "some aspects of ecological forestry may improve on current management," but this endorsement is overshadowed by their suggestion that the EF principles place economic and political interests above ecological concerns. Viewed from a historical perspective and in the face of climate change, the emergence of EF principles during the last decade—and their growing acceptance by both forestland managers and practical conservationists—is a positive incremental step in reconciling forest management goals with wildlife conservation and other socioeconomic values. This reconciliation is essential to building the trust that allows sus-

tainable policy decisions, especially those related to conservation of endangered species and at-risk ecosystems, to be carried out with broader public support.

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Climate Change May Trigger Broad Shifts in North America's Pacific Coastal Rainforests

DA DellaSala, Geos Institute, Ashland, OR, USA; Oregon State University, Corvallis, OR, USA

P Brandt, Karlsruhe Institute of Technology, Karlsruhe, Germany; International Livestock Research Institute (ILRI), Nairobi, Kenya

M Koopman, Geos Institute, Ashland, OR, USA

J Leonard, Geos Institute, Ashland, OR, USA

C Meisch, Leuphana University Lüneburg, Lüneburg, Germany

P Herzog, Martin Luther University Halle-Wittenberg, Halle, Germany

P Alaback, University of Montana, Missoula, MT, USA

MI Goldstein, University of Alaska Southeast, Juneau, AK, USA

S Jovan, Portland Forestry Sciences Lab, Portland, OR, USA

A MacKinnon, BC Forest Service, Victoria, BC, Canada

H von Wehrden, Research Institute of Wildlife Ecology, Vienna, Austria

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Introduction

Climate change threatens biodiversity and ecosystem integrity all over the globe (IPCC, 2014) and is already triggering pronounced shifts of species and ecosystems (Chen et al., 2011; Parmesan et al., 2000). Climate change is also expected to exacerbate effects of forest fragmentation (Bossuyt and Hermy, 2002; Opdam and Wascher, 2004), especially where only small fractions of formerly intact ecosystems remain (Heilman et al., 2002), presumably by magnifying local edge effects (Chen et al., 1995; Harper et al., 2005) and by reducing opportunities for dispersal and range expansion (Thompson et al., 2009; Watson et al., 2013). Thus, mitigating such effects in areas of global conservation importance is critical as biodiversity losses are especially significant.

The conservation importance of the coastal temperate rainforest region of North America is exemplified by the inclusion of six World Wildlife Fund Global 200 ecoregions (Ricketts et al., 1999), some of the most carbon dense ecosystems on earth (Leighy et al., 2006; Smithwick et al., 2002), extraordinarily productive salmon (*Oncorhynchus* spp.) runs and relatively intact forests northward (DellaSala et al., 2011). The highest epiphytic lichen biomass of any forest system also occurs here (McCune and Geiser, 2009). Thus, maintaining extant biodiversity in a changing climate has biodiversity significance on a global scale given the region's importance.

Already confirmed climate change effects in this region include elevated temperatures (Karl et al., 2009), declining mountain snowpack (Mote et al., 2005), shifts in species distributions (Wang et al., 2012), and reduced fog levels (Johnstone and Dawson, 2010). Diminished snowpack combined with late winter freezes has triggered dieback of Alaska yellow-cedar (*Cupressus nootkensis*) in southeast Alaska (Hennon et al., 2012) and northern British Columbia (Wooten and Klinkenberg, 2011).

Vegetation along the northern Pacific coast has been sensitive to climatic changes since the last glaciation, resulting in large shifts in species distributions, and providing strong evidence that future climate change will result in substantial ecological changes (Brubaker, 1988; Heusser et al., 1985). Even small changes in temperature often result in large species displacements, which

explains contemporary pattern of species distributions along the coastal region (Alaback, 1996). A 125 000-year record of vegetation change from the eastern slope of the Cascades, for example, shows that while species movements are individualistic, depending on species characteristics and geography, at the millennial scale global climatic variation is the dominant factor controlling vegetation distribution (Whitlock and Bartlein, 1997). Conifer species' distributions have changed since the glacial maximum reflecting differences in dispersal ability, effects of refugia, and changes in glacial dynamics from central Alaska southward. The physiography of the region, with north-south trending cordillera, has facilitated species movements, helps explain the rarity of species extinctions in the past, and importance of dispersal in the future if species are to adapt to even more abrupt climatic changes. Additionally, dramatic changes in vegetation in the past 20 000 years (Whitlock, 1992) corresponded to warming of 2.5–7.8 °C (median values, including uncertainty) that is similar to what most general circulation models (GCMs) predict for the Western USA by the end of the twenty-first century (IPCC, 2014).

There is no broad adaptation plan that addresses potential range-wide shifts of ecologically and commercially valuable species in this region, although there is a growing body of relevant adaptation work as reflected by the North Pacific Landscape Conservation Cooperative (NPLCC) of the U.S. Fish & Wildlife Service (<http://northpacificlcc.org>, accessed October 14, 2014). Our primary objectives were therefore to: (1) model current potential distributions of focal conifers considered of commercial importance to land managers and to project future potential distributions of focal species and broad rainforest vegetation types in response to anticipated climate change; (2) identify areas that may exhibit higher vegetation stability, including those in currently protected areas where biodiversity conservation is emphasized; and (3) illustrate how uncertainty can be addressed in designing effective adaptation strategies in a changing climate.

Notably, attempts to predict future shifts in species' ranges have employed a variety of approaches. One widespread approach, climate envelope modeling, considers the climate conditions where a species is currently or historically distributed and estimates where those same suitable climate conditions are expected to be found in the future based on GCM outputs. This approach has both benefits and shortcomings, which have been thoroughly reviewed (Wiens et al., 2009). A criticism of climate envelope modeling is the strict focus on climate variables with little to no consideration of non-climate drivers such as competition, predation, soils, elevation, and dispersal. Thus, in our assessment of potential climate change effects, we employed both climate envelope models and a dynamic vegetation model, despite differences in input data and analysis scales, to qualitatively compare gross differences regarding the spatial patterns produced. Using correlative and mechanistic modeling approaches independently might increase the reliability of predictions (see Coops and Waring, 2011; Kearney et al., 2010), reducing uncertainties inherent in relying on any individual modeling effort.

Also, in this paper, our findings are used to illustrate some key concepts in climate adaptation planning for managers wishing to maintain extant biodiversity in a changing climate for a rainforest region that straddles two countries (USA and Canada) and large swaths of public and private lands. Additional analyses not presented, including detailed appendices and datasets, are available online (<http://databasin.org/articles/172d089c062b4fb686cf18565df7dc57>; accessed October 28, 2014).

North America Pacific Coast Temperate Rainforest Region

The Pacific Coast of North America contains the largest proportion of temperate rainforests in the world, representing 35% of the global total (DellaSala et al., 2011). Stretching from the coast redwoods (38° N), California to northern Kodiak Island and Prince William Sound (61° N), Alaska, these rainforests span a wide climatic gradient (Alaback, 1996). Coastal rainforests are associated with cool, moist oceanic air masses, a narrow range of temperature extremes, high frequency of clouds and fog, and high annual precipitation, with most precipitation in the winter (Redmond and Taylor, 1997) and up to 20% in the summer in northern latitudes (DellaSala et al., 2011). The region consists of four distinct rainforest zones that differ climatically and floristically: (1) subpolar – north of southeast Alaska to Prince William Sound and Kodiak Island; (2) perhumid – southeast Alaska to northern Vancouver Island; (3) seasonal – central Vancouver Island to southern Oregon; and (4) warm – southern Oregon coast to San Francisco Bay area (Alaback, 1996; Figure 1).

Climate Data

In order to predict potential shifts in species and rainforest distributions, we used the downscaled WorldClim dataset at 30 arc-s (1-km) resolution (Hijmans et al., 2005). We obtained 19 climatic variables for baseline conditions (1950–2000) and for two future time periods (2050s, 2080s) under the A2A ensemble-high-emissions scenario. This scenario assumes continued global population growth and focus on regional economic growth rather than global collaboration. It is one of the scenarios that most closely tracked the emissions trajectory at the time of our 2012 study. Thus, we used three GCMs: CCCMA-CGCM2 (third assessment, Flato and Boer, 2001), CSIRO-MK2 (third assessment, Gordon et al., 2002), and HADCM3 (third assessment – Johns et al., 2003) that covered a broad range of temperature and precipitation projections spanning dry and wet projections.

For climate envelope modeling, we employed a 1000-km buffer on the coastal rainforest study area to capture the entire current ranges of focal species and potential future shifts. Due to the small distribution of coast redwood, the buffer for the baseline model was set to 100 km around the most outer available localities.

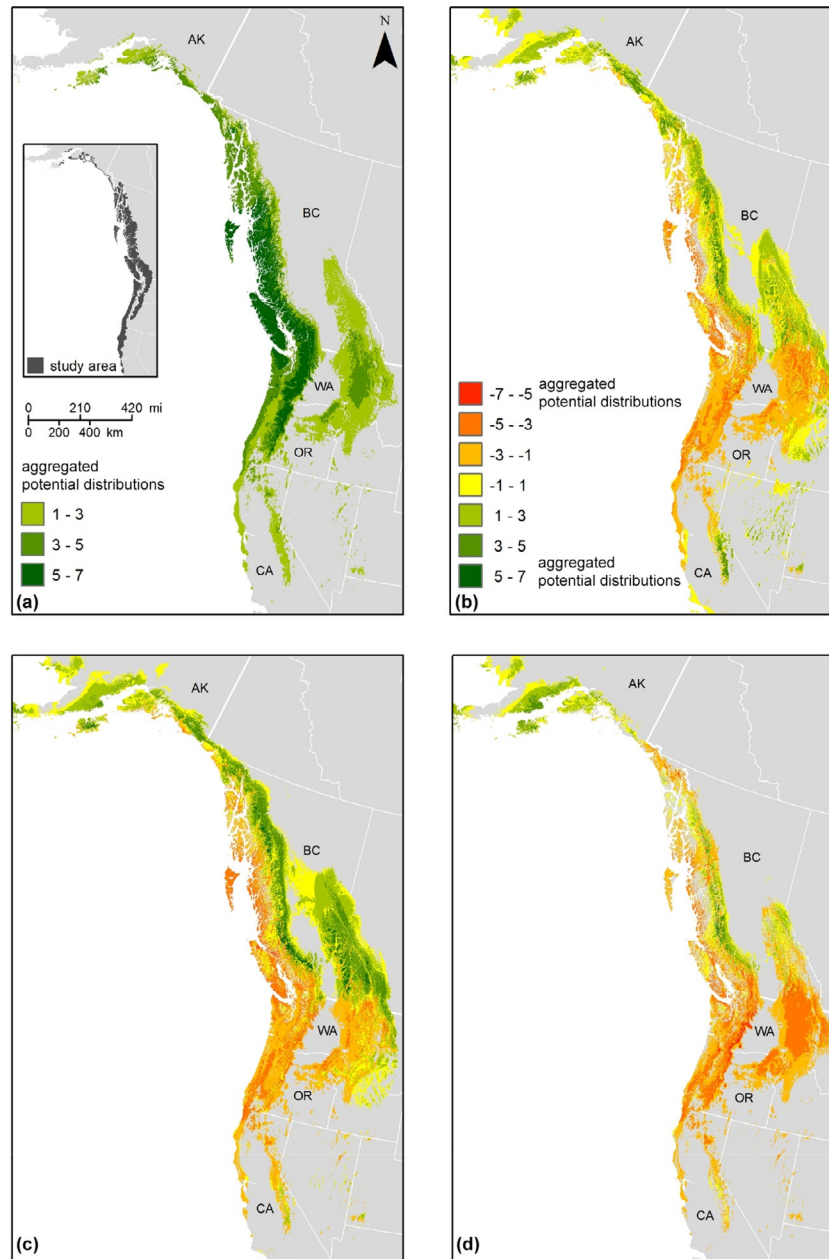


Figure 1 Aggregated potential distribution of eight focal conifer species (Pacific silver and grand fir, Alaska yellow-cedar, Sitka spruce, western red cedar, western and mountain hemlock, coast redwood) for the baseline period (a) and the richness changes for 2080s under scenario A2A ensemble-emissions based on three General Circulation Models (CSIRO (b), CCCMA (c), and HADCM3 (d)).

Selection of Focal Species of Commercial Importance

Based on prior discussions with land managers, we selected eight dominant conifer species of commercial, conservation, and cultural importance to model potential range shifts related to climate change. These species also were chosen because there was readily available location data and their geographic range overlapped primarily with our study area. They included Sitka spruce (*Picea sitchensis*), western and mountain hemlock (*Tsuga heterophylla*, *T. mertensiana*), western red cedar (*Thuja plicata*), Alaska yellow-cedar, Pacific silver and grand fir (*Abies amabilis*, *A. grandis*), and coast redwood (*Sequoia sempervirens*). We did not include other conifers with wide distributions that extended well outside our study area buffer such as Douglas-fir (*Pseudotsuga menziesii*, see [Coops and Waring, 2011](#)) or hardwoods (see [Hamann and Wang, 2006](#)) given their lower importance to land managers in this region.

Presence-only Modeling of Focal Species

To build the baseline species distribution models, we obtained presence-only data (point and polygon locations) for focal species from numerous databases (USDA Forest Inventory Assessment DataMart v5.1 – apps.fs.fed.us/fiadb-downloads/datamart.html; Biogeoclimatic Ecosystem Classification Program – www.for.gov.bc.ca/hre/becweb/resources/codes-standards/standards-becdb.html, active October 14, 2014; herbaria collections; museum records; published atlases) and from regional specialists that provided more than 30 000 species localities ranging from 710 occurrence points for coast redwood to 7999 points for western hemlock.

Presence-only models outline areas that are predicted as suitable space for a given species according to the predictor dataset (Soberón and Peterson, 2005); these models are known to overestimate realized distributions due to missing information of unvisited locations (Kent and Carmel, 2011). To examine the impact of climate change on species distributions, we only took climatic predictors into account, therefore, focusing on a species' climate envelope (Pearson and Dawson, 2003). Potential distribution was thus determined by projecting this climate envelope across the geographic study area (Soberón and Peterson, 2005).

We applied Maxent 3.3.3k (Elith et al., 2011; Phillips et al., 2006) to model current and future potential distribution for each focal species. Maxent frequently outperforms other presence-only modeling algorithms (Wisz et al., 2008). Instead of real absences, Maxent uses random background points to approximate the best fitting probability distribution for estimating habitat suitability (Elith et al., 2011). We used area under curve (AUC) statistics to assess model discrimination performance (Phillips et al., 2006). All models were replicated 25 times using the bootstrap replicate run type. The final average outputs were used for further analyses. The species datasets were split into 70% training and 30% test data sets randomly chosen for each model run.

We used jackknife procedures from initial model runs to exclude predictors that showed low importance in predicting included presence points when modeled in isolation, expressed by low values of model gain. We activated the 'fade by clamping' option in Maxent to mitigate clamping issues arising from projection values extending beyond the range of training data (Phillips et al., 2006) and chose the logistic output format. The automatic feature selection was applied since it has been validated with respect to a broad range of species, environmental conditions, numbers of occurrences, and degrees of sample selection bias (Phillips and Dudík, 2008). Using ARCGIS 10, the continuous grid outputs of the Maxent models were transformed into binary data showing either potential presence or modeled absence of a given species based on species-specific thresholds that minimized falsely excluded presences while retaining the similarity to published ranges (Little, 1978). Thus, for every species we created one baseline (1950–2000) potential distribution layer and six future potential distribution layers based on the two time periods (2050s, 2080s) and three GCMs.

Identifying Areas of Persistence, Gain, and Loss

For each focal species, we analyzed and mapped differences and commonalities between current and all variants of future potential distributions that were categorized as: (1) 'persistent distribution' where baseline and future potential distributions overlap, (2) 'distribution gain' where baseline potential distributions are absent but future potential distributions are present, and (3) - 'distribution loss' where baseline potential distributions are present but future potential distributions are absent. This is important for managers wishing to assess broad patterns in species distributions related to projected climate changes.

GCM outputs may differ widely, leading to variation in output among different climate envelope projections (Beaumont et al., 2008). Using three GCMs that spanned much of the range of possible futures, from wetter to drier and from faster warming to slower warming, allowed us to assess the level of disagreement among model output as an indirect measure of model uncertainty for managers wishing to plan for future distribution shifts. Importantly, we were able to assess climate envelope model outputs regarding model uncertainty inherent in climatic projections: uncertainty being lowest in areas where future potential distributions of all model projections showed a full consensus (spatial agreement) and highest in cases where they completely differed (Araújo and New, 2007). Obviously, model uncertainty is still inherent based on the complexity of climate and ecological systems, the potential for unexpected events related to climate change, and human behavior concerning greenhouse gas emissions abatement. Nonetheless, we propose that projections with relatively high agreement among models are useful in predicting broad trends important in robust reserve design and forest management decisions.

We calculated Cohen's kappa coefficients (K) (R Development Core Team, 2013 v. 2.1.12), indicating the degree of agreement (Fielding and Bell, 1997) between baseline and future potential distribution for all modeled species in order to quantify possible divergences in potential distributions over time as a proxy for expected shifts in species distribution (online appendix).

Outputs of climate envelope models can also be used to compile richness maps based on aggregated potential species distributions (McKenney et al., 2007). We used binary, aggregated potential distributions of focal tree species as an index of broad potential changes in species richness patterns across the entire study area.

Future Vegetation Stability, Intact Late-Seral Forests, and Current Protection Schemes

In addition to potential species shifts, we used the MC1 dynamic vegetation model outputs, biogeography module (Bachelet et al., 2001) to assess potential stability of dominant types of vegetation under a changing climate. The MC1 model was derived from physiologically based biogeographic rules derived from the MAPSS model (Neilson, 1995) adapted to dynamic environmental gradients using site production information (Bachelet et al., 2001). While the Maxent climate envelope analysis (above) focused on individual rainforest species and species richness, the MC1 output provided information on overall functional types of potential vegetation (temperate coastal needleleaf forest, for example) but not individual species. We compiled MC1 outputs produced under current and future climatic conditions using three GCMs (third assessment models): Hadley (HadCM3; Johns et al., 2003), MIROC (Hasumi and Emori, 2004), and CSIRO (Gordon et al., 2002) under the A2 emissions scenario. MC1 explicitly simulates vegetation dynamics, nutrient cycles and dynamic impacts of disturbance due to fire and has been used in analyses of vegetation responses to climate change (Lenihan et al., 2008). However, MC1 does not incorporate anthropogenic disturbances such as timber harvest, agriculture, urbanization, invasive species introductions, and human-wildfire ignition sources.

All applied MC1 model outputs have a $1/12^\circ$, unprojected, grid-cell resolution that is nominally 8-km (Daly et al., 2008). We assessed vegetation stability by comparing the dominant type of vegetation predicted to be supported under modeled baseline conditions (1961–1990) to that predicted to be supported for two future time periods (2035–45 and 2075–85). We identified areas as ‘stable’ or ‘unstable’ based on whether the future climate is expected to continue to support the same dominant vegetation type through late-century based on agreement across the three GCMs.

Notably, Pacific coastal temperate rainforests are highly fragmented in southern locales, which may be more vulnerable to large-scale changes in precipitation and temperature if magnified by local edge effects. Therefore, we accessed the most current intact late-seral rainforest datasets to identify areas that overlap with stable vegetation areas as potential refugia (Keppel et al., 2012; Olson et al., 2012; Watson et al., 2013). For intactness, we downloaded the only seamless forest fragmentation dataset available for the entire Pacific coastal temperate rainforest region and published in 1995 (<http://databasin.org/datasets/7f72a68ac6c343bda3ffff4bef3926de>; accessed October 28, 2014).

We also intersected protected area feature classes with the MC1 stability areas to determine areas that are currently protected and projected to support climatically stable vegetation types overtime. In the USA, we used GAP status codes 1 (‘strict’) and 2 (‘relaxed’) obtained from the Protected Area Database (PAD-US CBI edition v1.1). In most cases, this database does not include administrative protections such as late-successional reserves of the Northwest Forest Plan (USFS and BLM, 1994) unless they overlapped with more stringent protections such as Wilderness and Congressionally Withdrawn Areas. The protected area data in British Columbia were obtained from Global Forest Watch Canada. Thus, we were able to show how areas of future stable vegetation, current late-seral forests and protected areas coincide in order to assess if the current conservation scheme across the entire region is well adapted to climate change or not.

Climate Envelope Model Evaluation and Most Important Climate Parameters

For the focal species, the AUC values based on the test data averaged across Maxent model runs ranged from 0.82 (western hemlock) to 0.93 (coast redwood), indicating that the models satisfactorily discriminated between presence and background information (online appendix).

The two most influential variables from the Worldclim dataset that most frequently show highest prediction power among the predictive Maxent models for focal species were ‘Precipitation of Coldest Quarter’ and ‘Precipitation of Driest Quarter’ (online appendix).

Key Findings for Focal Species and Rainforest Assemblages

Shifts of Potential Species Distributions

Aggregated potential distributions of focal conifer tree species predicted a shift for all applied GCMs by 2080s (Figure 1). More detailed species by species analysis are available in the online appendix. Although the intensity of shifts differed slightly among GCMs, the overall pattern showed a substantial reduction of aggregated potential species distributions for large parts of the seasonal and warm rainforest zones (south) and a broadly stable richness pattern of aggregated potential species distributions along the perhumid zone (north) – except for some northerly, island parts, and rain shadow areas (e.g., Olympic Peninsula). Quantitative comparisons of potential species distributions through time periods indicated that future distributions, in part, differ substantially compared to their baseline counterparts (Table 1). Averaged Cohen’s kappa coefficients across all species and applied GCMs per time period revealed that differences are more pronounced by 2050s ($K=0.71$) compared to 2080s ($K=0.57$) in relation to baseline distributions.

By 2080s, potential distributions of western red cedar, Sitka spruce, and western hemlock show marked persistence (55–82%) mainly in northern portions of their range with minor contractions (2–7%) in the south (Table 1, Figure 1). Pacific silver fir, grand fir, Alaska yellow-cedar, and mountain hemlock had more substantial reductions (15–39%) in potential distributions throughout their range by 2080s. Coast redwood is expected to experience reduction of nearly one-fourth of its modeled climate envelope by 2080 (Figure 2, inset). Small (3%) climate related potential distribution gains were possible to the north; however, these are gone by 2080.

Table 1 Percent of baseline (1950–2000) potential distribution loss, persistence, and gain for focal species in the Pacific Coastal temperate rainforest by two time periods (2050s, 2080s), the A2A ensemble-emissions scenario, and full agreement among three General Circulation Models (CCCMA-CGCM2; CSIRO-MK2; and HADCM3)

<i>Species</i>	<i>Period</i>	<i>Loss (%)</i>	<i>Persistence (%)</i>	<i>Gain (%)</i>
Western red cedar	2050s	4	65	18
	2080s	6	59	28
Sitka spruce	2050s	0	83	9
	2080s	2	82	15
Western hemlock	2050s	4	74	8
	2080s	7	55	12
Pacific silver fir	2050s	24	35	3
	2080s	39	21	5
Grand fir	2050s	20	35	6
	2080s	36	17	10
Alaska yellow-cedar	2050s	8	66	4
	2080s	21	34	4
Mountain hemlock	2050s	7	59	7
	2080s	15	33	4
Coast redwood	2050s	21	16	3
	2080s	23	1	0

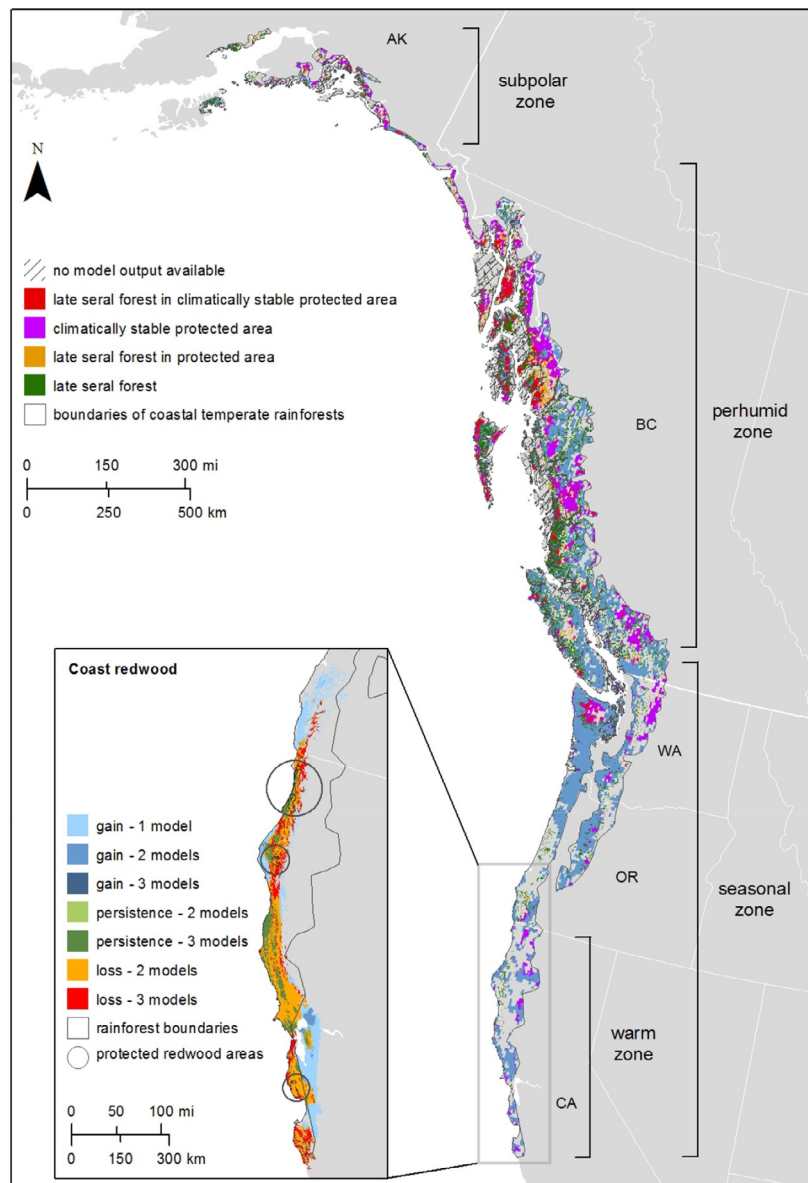


Figure 2 Predicted areas of vegetation stability (scenario A2, 2080s), protected areas, and late-seral forests in the Pacific coastal rainforests. Inset map shows potential distribution gain, persistence, and loss of coast redwood based on three GCMs (CSIRO, CCCMA, and HADCM3). The three circled areas in the redwood insert indicate protected areas where redwoods are currently found. Only the upper circled area has parks that coincide with projected redwood persistence in green.

Future State of the Ecosystem and Conservation Areas

Results from the MC1 dynamic vegetation model largely resembled the pattern obtained from climate envelope models on a broader scale (Figure 3 vs. Figure 1). Areas with potentially stable dominant vegetation communities were most densely spread across the perhumid zone and the coastal regions of the northern seasonal zone while southern areas changed more dramatically as also depicted in the species distribution models. In general, northern regions are expected to retain climate suitable for the baseline dominant vegetation types through 2080s, mostly the maritime evergreen needleleaf (e.g., western hemlock, Sitka spruce) type. Unstable areas also occur in the North, including portions of the Queen Charlotte and Haida Gwaii island and much of the mid and southern British Columbia coastline where temperate deciduous broadleaf woodland (e.g., red alder, *Alnus rubra*) is expected to expand, and the Kenai Peninsula of Alaska where the climate is expected to be more suited to temperate cool mixed forest rather than the baseline needleleaf forest. The climate currently supporting baseline subalpine forest in many areas is expected to shift toward conditions more suitable for patches of maritime evergreen needleleaf forest, temperate evergreen needleleaf forest, and temperate deciduous broadleaf forest.

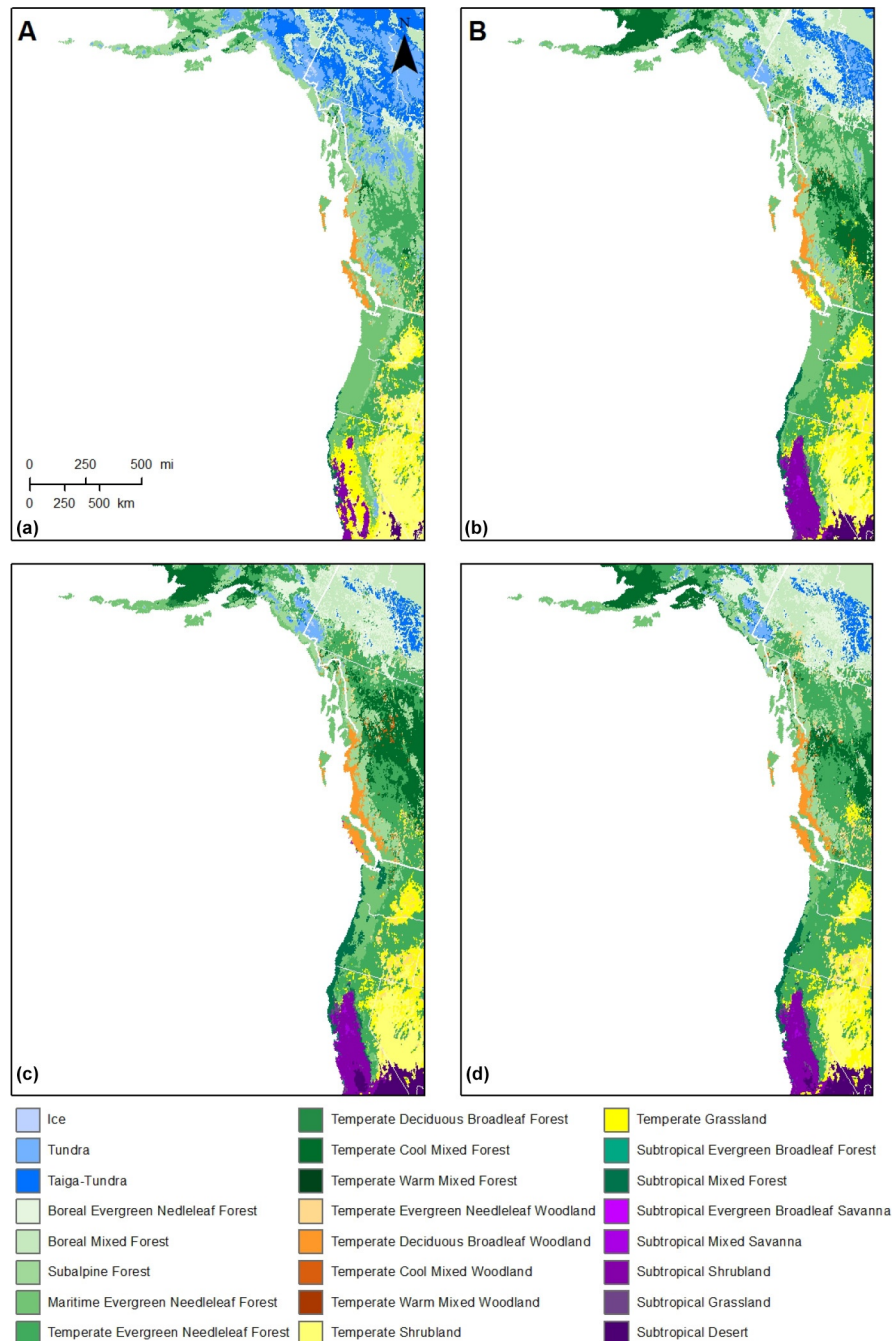


Figure 3 Outputs from MC1 functional vegetation model show baseline (a) and future dominant types of vegetation for 2080s (2075–85) based on three GCMs: CSIRO (b), MIROC (c), and HADCM3 (d).

In southern areas, shifts in dominant vegetation types were well dispersed throughout the warm zone and within the seasonal zone, especially the Cascades and southern coastal areas. For instance, starting just north of the Oregon/California border, the climate niche supporting maritime evergreen needleleaf (redwood, Douglas-fir zone) is expected to contract.

There was often a mismatch between current protected areas of coastal temperate rainforests with areas of future potential stability in dominant vegetation types, or with larger extents of late-seral forests, in particular, within the perhumid zone where older forests are especially concentrated and relatively intact (see [Figure 2](#)). This pattern was also shown when the proportion of vegetation stability for all protected areas that are completely located within the study area is plotted per state or province that intersects the coastal temperate rainforests ([Figure 4](#)). For instance, Washington and Oregon show the lowest vegetation stability, British Columbia the highest.

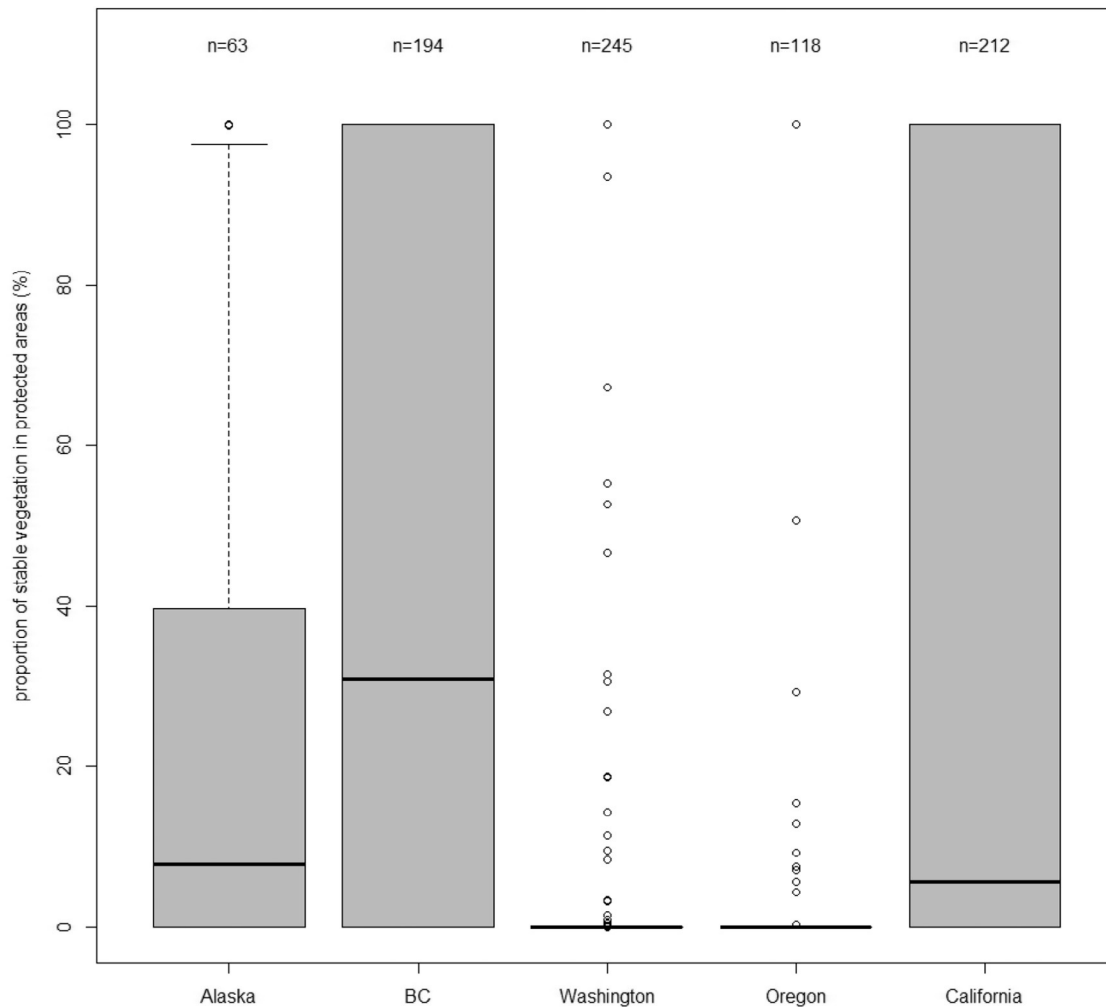


Figure 4 Predicted vegetation stability in protected areas per state or province derived from outputs of the MC1 model based on the agreement of three GCMs under the A2 scenario for 2080s (2075–85) (BC = British Columbia).

Relevance to Climate Adaptation Strategies and Land Management

Shifting Potential Distributions as a Surrogate for Ecosystem Change

Our focal species results correspond well with recent literature on range shifts of tree species caused by climate change ([Chen et al., 2011](#); [Hickling et al., 2006](#); [Parmesan and Yohe, 2003](#); [Shafer et al., 2001](#); [Wang et al., 2012](#)) and, while the magnitude of shifts differed, the trends were similar. For instance, using different GCMs than ours, [Hamann and Wang \(2006\)](#) found the distribution of western hemlock may increase by 50% over baseline area in British Columbia, shifting up in elevation and northward under the A2 emissions scenario by 2085. [Coops and Waring \(2011\)](#) also found a 50% gain for western hemlock and for other coastal

conifers that are likely to remain 'highly adapted' through the 2080s under the A2 emissions scenario. Others also have predicted northward shifts and shrinking baseline ranges of tree species in North America (McKenney et al., 2007; Murphy et al., 2010).

We found a core zone featuring the highest richness of potential focal species distributions in British Columbia between Vancouver Island and southeast Alaska, and areas of higher potential vegetation stability in these same areas. These regions could potentially act as refugia for temperate rainforest conifer species and assemblages and, because they have the lowest levels of forest fragmentation, may also be relatively insulated from edge-related local climate effects (Chen et al., 1995; Harper et al., 2005). Similarly, both approaches indicated greater loss and instability in the southern portion of the study area, particularly within the seasonal zone, supporting the generalized patterns of declining focal species richness southward.

What Is Driving the Projected Shifts?

A downside of our modeling approaches is that they do not provide us with definitive information on what is driving the projected shifts in communities or species. However, increases in frequencies and duration of extreme events have been documented in many regions and are expected to increase (Field et al., 2012). Extreme events are expected to be the primary drivers for many species and ecosystem impacts (Jentsch and Beierkuhnlein, 2008). Droughts have been correlated with elevated rates of forest dieback in North America due to water deficiency (Birdsey and Pan, 2011; Michaelian et al., 2011; van Mantgem et al., 2009), and might thus be crucial drivers of future distribution of temperate rainforest (DellaSala et al., 2011). For instance, water deficit may contribute to reductions of species distributions (both aggregated and species-specific) in the drier, southern parts of coastal temperate rainforests in our study area. However, declining low elevation snow and summer fog (southern rainforest distribution), not modeled in our study, might have a bigger effect on the distribution of yellow-cedar (Hennon et al., 2012) and coast redwood (Johnstone and Dawson, 2010), respectively, than the climate variables that we modeled. Further, projected increases in fires in southern rainforest areas may exacerbate climate-related changes to rainforest assemblages (Littell et al., 2009).

Model Limitations and Uncertainties

Climate envelope models are often criticized for relying on over-simplistic assumptions such as equilibria among species and their environment, omitting other predictors such as biotic interactions that might determine the fundamental niche (Araújo and Pearson, 2005), and lacking predictor quality (Soria-Auza et al., 2010). Biotic interactions and dispersal limitations are known to contribute to mismatches between model outputs and reality (Soberón and Peterson, 2005; Zimmermann et al., 2009). However, climate envelopes are known to perform best at a regional scale because they show general ecological trends and patterns (Boucher-Lalonde et al., 2012; Warren, 2012), as was the case in our study area. Moreover, the Worldclim predictor set is currently the most abundantly used set of climatic parameters, and to date the only one allowing for high resolution predictive modeling on a global scale. The applied model scale is appropriate, especially for species featuring smaller ranges or for modeling of complex terrain (Seo et al., 2009).

The MC1 dynamic vegetation model has been frequently used to investigate potential ecosystem vulnerability to climate change (Gonzalez et al., 2010). Comparing static climate envelope predictions with the dynamic MC1 vegetation model outputs revealed a more robust pattern (Kearney et al., 2010) of the bigger picture of shifting vegetation types across the Pacific coastal temperate rainforest region and also allowed us to apply our results on different data and spatial scales.

None of the models integrate human disturbances. There is no quantitative connection between Maxent and MC1 model outputs because focal tree species do not fully coincide with broad vegetation types. However, information derived from both model types complement each other on a coarse level and thus can more reliably inform management decisions by reducing uncertainty arising from any one model alone (also see Coops and Waring, 2011 for similar cross-model applications). Moreover, we propose that human impact is most likely to increase throughout the region, thus our models most likely under-estimate climate change effects exacerbated by human disturbance.

Rainforest Management Implications

At broad spatial scales, northern coastal regions and their protected areas (BC, Alaska) may be more resilient to climate change than southern areas that are highly fragmented and more vulnerable to edge effects (also see Thompson et al., 2009). That pattern holds true for coastal regions compared to interior drier regions (Wang et al., 2012) perhaps because of climatic buffering of maritime climates. Our results therefore are important for maintaining ecological integrity and climate resilience in high priority conservation areas from north to south such as the Tongass Rainforest of Alaska, Great Bear rainforest of BC, Olympic National Park of Washington, portions of the Western Cascades, and coast redwoods (DellaSala et al., 2011). Notably, ecological integrity and climate resilience are emphasized in the 2012 National Forest Planning Rule and climate resilience is emphasized in President Obama's Climate Action Plan (Executive Office of the President, 2013). Thus, the largely intact nature of the Tongass National Forest should provide important opportunities for meeting both policy objectives and for the northward expansion of rainforest communities in the face of climate change. Managers may also increase resilience potential by maintaining or restoring climatically stable vegetation along elevation and north-south gradients to accommodate shifting distributions. However, the slightly reduced richness of potential distributions and climatic instability in southern parts of the region show that some of the currently protected old forest stands are also vulnerable to climate change (online appendix) and may require additional actions. In particular, declines

in yellow-cedar may warrant consideration of assisted migration if this species is not able to colonize new climate spaces (Loss et al., 2011).

The Great Bear rainforest located in the perhumid zone is among the world's last remaining large extents of old-growth rainforest (DellaSala et al., 2011). Large portions of this rainforest show vegetation stability under a changing climate, including large extents of remaining old forest and high richness of focal tree species' potential distributions. Thus, we suggest that this region might also serve as broad-scale refugia if sufficiently protected from anthropogenic stressors that might exacerbate climate change impacts (Thompson et al., 2009; Watson et al., 2013).

Olympic National Park is situated in the seasonal rainforest zone and features exceptional plant richness, including many unique epiphytes (McCune and Geiser, 2009). Climate envelope richness of focal tree species is high within the core area of the park suggesting upslope shifts assuming melting glaciers. Importantly, the boundary regions of the park, including old-forest stands, show potential stability (online appendix) but are surrounded by highly fragmented private lands where conservation incentives are needed to retain stable dominant vegetation.

The Western Cascades are a secondary rainforest belt located in the northern portion of the seasonal zone that has been subjected to intensive logging. Lower resilience to climate change is indicated by unstable vegetation and decreasing climate envelope richness of focal tree species. Large proportions of remaining old forest remnants will likely be affected. While the larger protected areas, such as North Cascades National Park, Glacier National Park, and Alpine Lakes Wilderness show potential vegetation stability, some smaller areas (generally <1000 km²) may experience climate-related stress to the dominant vegetation (online appendix).

Coast redwoods are situated in the warm zone within the most southern region of coastal temperate rainforests; the last, heavily diminished, redwoods are a conservation priority (Noss, 2000) and the apparent vulnerability of redwood to climate change in a significant portion of its range adds to conservation significance. Restorative actions within higher stability but previously logged areas may help to alleviate climate stressors for redwood. In addition, it is possible that redwood is resilient, at least initially, to shifts in its climate niche as increased growth rates measured in old-growth redwood forests are thought to be related to a lengthening of the growing season (Sillett et al., 2010). Our projections indicate that this apparent positive climate response of redwood might be short lived due to its projected shrinking climate niche.

Conclusions

Future temperate rainforest communities of the Pacific Coast of North America may persist mainly in northern latitudes and upper elevations where land-use disturbances are less likely to exacerbate changes to the focal species' climate envelope. They also may persist in pockets of relatively stable microrefugia (e.g., north-facing older forests) in the south if buffered from human disturbances (Olson et al., 2012). Projected changes in dominant vegetation types and focal species distributions, and identification of relatively stable intact patches, can aid managers in developing strategies for persistence of extant rainforest communities. Our work also provides valuable management insights into where important tree species may require assisted migration (e.g., yellow-cedar and redwood).

Finally, we note that in the time to peer review and publish this manuscript (>2 years) climate change models have been updated (IPCC, 2014). Thus, our projections need to be continuously updated (every five years or when new models come out) based on ongoing refinements to downscaled GCMs. Nevertheless, our broad-scale findings should prove useful in helping managers with comprehensive adaptation planning now for climate shifts in rainforest species and assemblages over a large region in order to avoid ecologically costly lags in conservation and management options given climate shifts are already underway.

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Review

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

Dominick A. DellaSala ^{1,*}, Rowan Baker ², Doug Heiken ³, Chris A. Frissell ⁴, James R. Karr ⁵, S. Kim Nelson ⁶, Barry R. Noon ⁷, David Olson ⁸ and James Strittholt ⁹

¹ Geos Institute, 84-4th Street, Ashland, OR 97520, USA

² Independent Consultant, 2879 Southeast Kelly Street, Portland, OR 97202, USA;

E-Mail: watershedfishbio@yahoo.com

³ Oregon Wild, P.O. Box 11648, Eugene, OR 97440, USA; E-Mail: dh@oregonwild.org

⁴ Flathead Lake Biological Station, 32125 Bio Station Lane, University of Montana, Polson, MT 59860-6815 USA; E-Mail: leakinmywaders@yahoo.com

⁵ 102 Galaxy View Court, Sequim, WA 98382, USA; E-Mail: jrkarr@u.washington.edu

⁶ Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331-3803, USA; E-Mail: kim.nelson@oregonstate.edu

⁷ Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA; E-Mail: Barry.Noon@colostate.edu

⁸ Conservation Earth Consulting; 4234 McFarlane Avenue, Burbank, CA 91505, USA; E-Mail: conservationearth@live.com

⁹ Conservation Biology Institute, 136 SW Washington Ave #202, Corvallis, OR 97333, USA; E-Mail: stritt@conbio.org

* Author to whom correspondence should be addressed; E-Mail: dominick@geosinstitute.org; Tel.: +541-482-4459 (ext. 302); Fax: +1-541-482-4878.

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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

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.

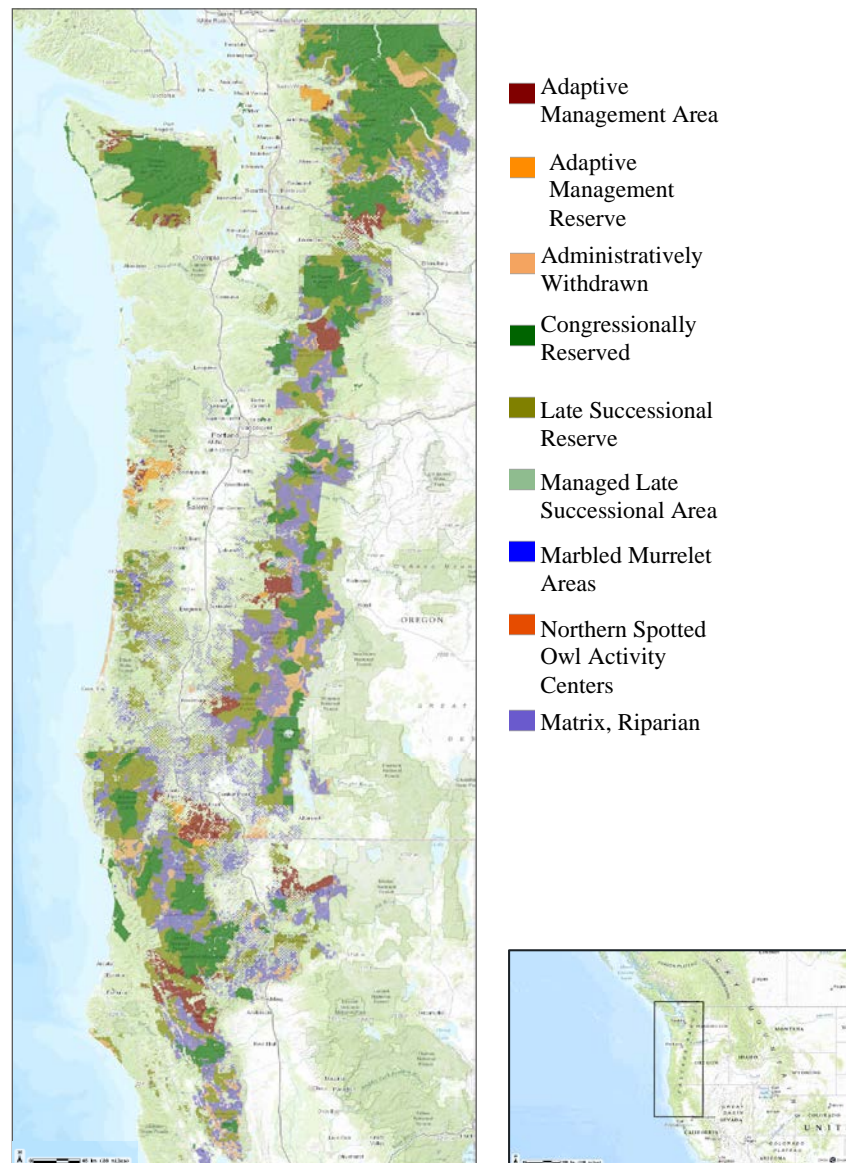


Figure 1. Land-use allocations within the Northwest Forest Plan (NWFP) area: Congressionally reserved—2.93 million ha (30%); Late Successional Reserves (LSRs)—2.96 million ha (30%); Managed Late Successional Reserves—40,880 ha (1%); Adaptive Management Areas—608,720 ha (6%); Administratively Withdrawn 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 amabilis*, *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 m³ 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).

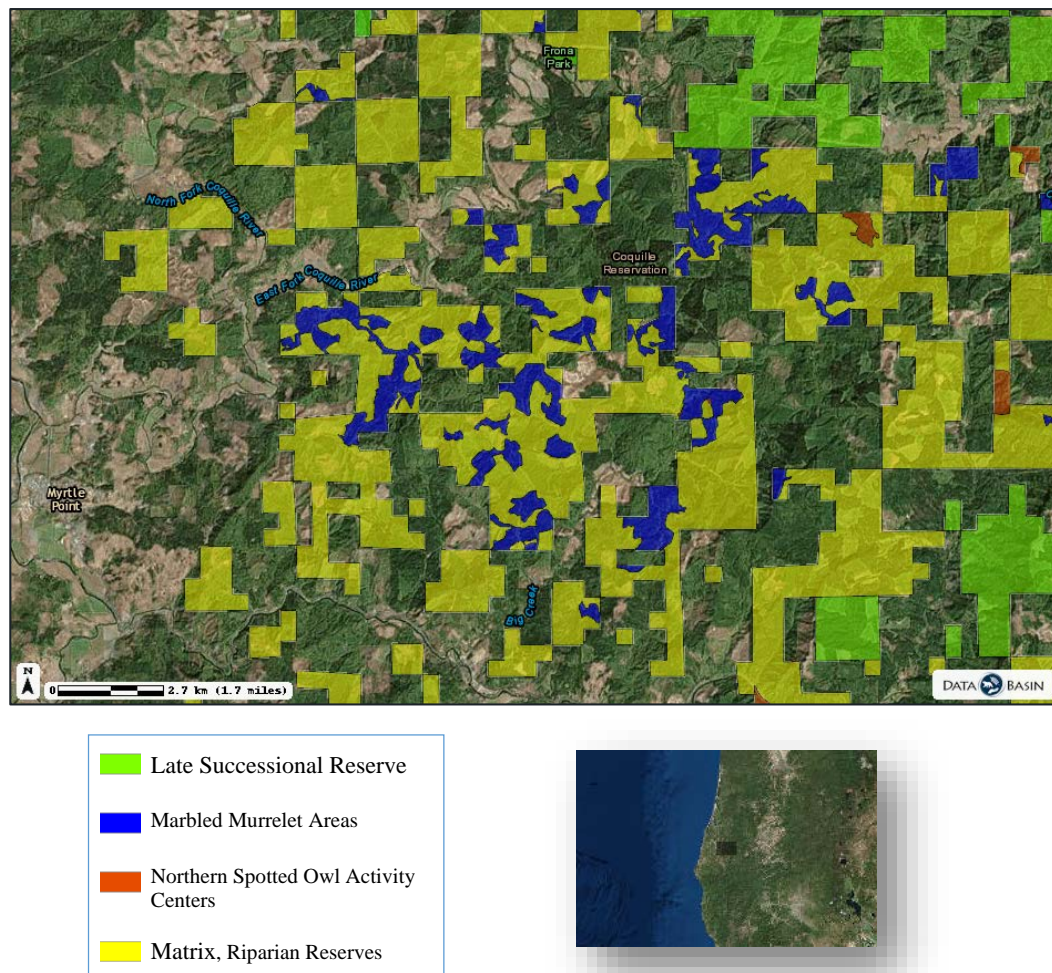


Figure 2. Satellite image of Southwest Oregon showing extensive fragmentation from a “checkerboard” pattern of clearcuts on private and public lands with NWFP land management allocations. Map created using Data Basin (www.databasin.org; accessed on 15 September 2015).

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 *	<i>p</i> -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 CO₂ [82]. Reduced logging levels and increased regrowth under the NWFP has resulted in the regional forests shifting from a net source of CO₂ 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 CO₂ 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 (<i>Oncorhynchus kisutch</i>)	~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 (<i>O. tshawytscha</i>)	~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 (<i>O. mykiss</i>)	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 (<i>Arborimus longicaudus</i> , 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 CO₂ emissions.

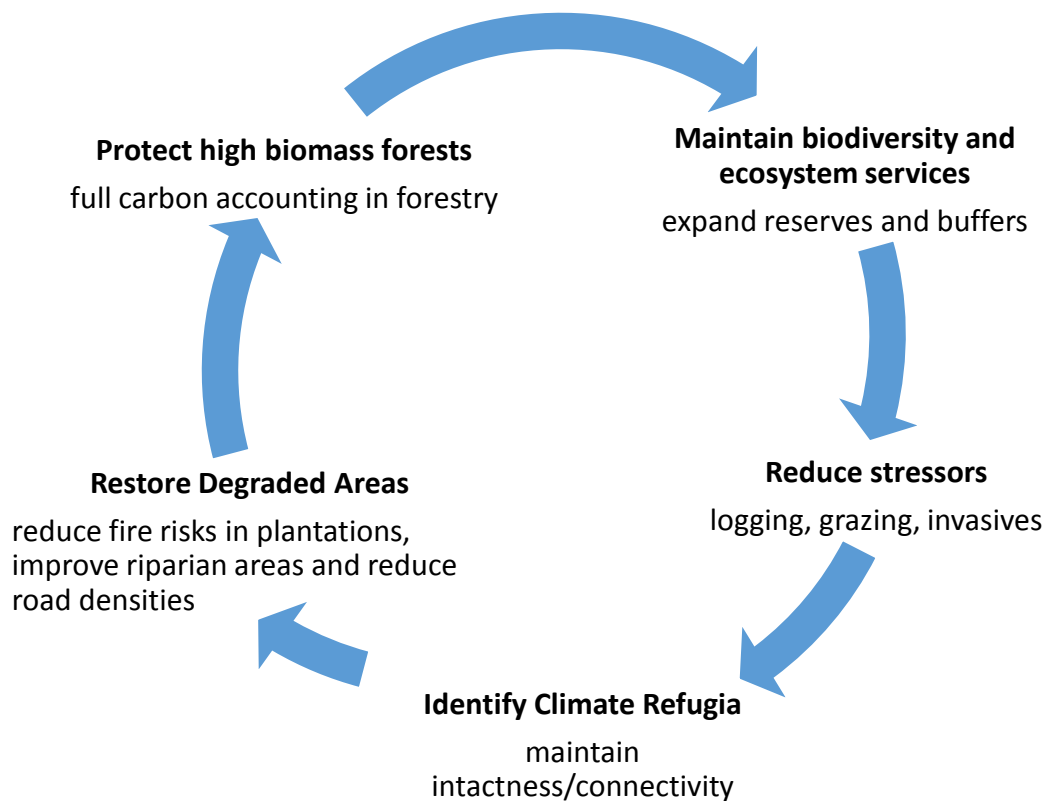


Figure 3. Integrating ecosystem management and conservation biology with recent forest policies related to climate change (e.g., President Barack Obama’s 2013 Climate Change Executive Order), forest carbon, and ecosystem integrity in forest planning [87].

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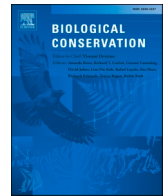
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Have western USA fire suppression and megafire active management approaches become a contemporary Sisyphus?

Dominick A. DellaSala^{a,*}, Bryant C. Baker^{b,c}, Chad T. Hanson^d, Luke Ruediger^{e,f}, William Baker^g

^a Wild Heritage, a Project of Earth Island Institute, 2150 Allston Way, Berkeley, CA 94704-1346, United States of America

^b Los Padres ForestWatch, PO Box 831, Santa Barbara, CA 93102, United States of America

^c California Chaparral Institute, PO Box 545, Escondido, CA 92033, United States of America

^d John Muir Project, a Project of Earth Island Institute, 2150 Allston Way, Berkeley, CA 94704, United States of America

^e Klamath Forest Alliance, 2274 Eastern Avenue, Arcata, CA 95521, United States of America

^f Applegate Neighborhood Network, PO Box 114, Jacksonville, OR 97530, United States of America

^g Program in Ecology, University of Wyoming, Laramie, WY 82071, United States of America

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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/>).

* Corresponding author.

E-mail addresses: dominick@wild-heritage.org (D.A. DellaSala), bryant@lpfw.org (B.C. Baker), cthanson@gmail.com (C.T. Hanson), elliottcreek@yahoo.com (L. Ruediger), bakerwl@uwyo.edu (W. Baker).

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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://goodda ysacramento.cbslocal.com/2021/08/02/doug-lamalfa-forest-servi ce-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 Sisyphian 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).

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 menziesii*). 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

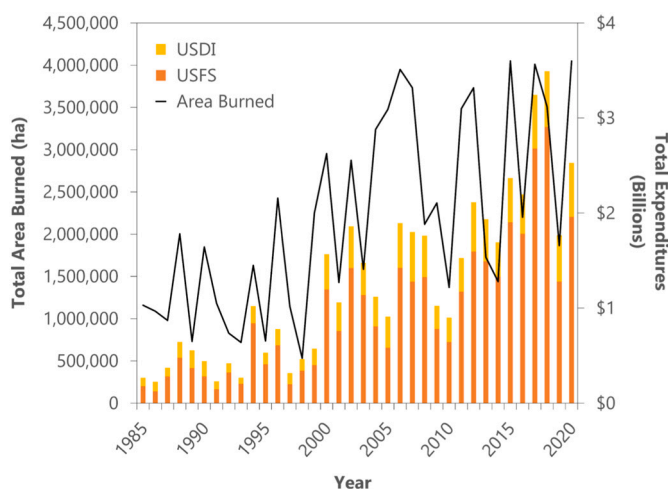


Fig. 1. Total area burned and wildfire suppression expenditures by federal land management agencies from 1985 to 2020. Data compiled from the National Interagency Fire Center suppression reports and from fiscal year agency budgets, with USDI mainly being National Park Service that since 1972 has been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

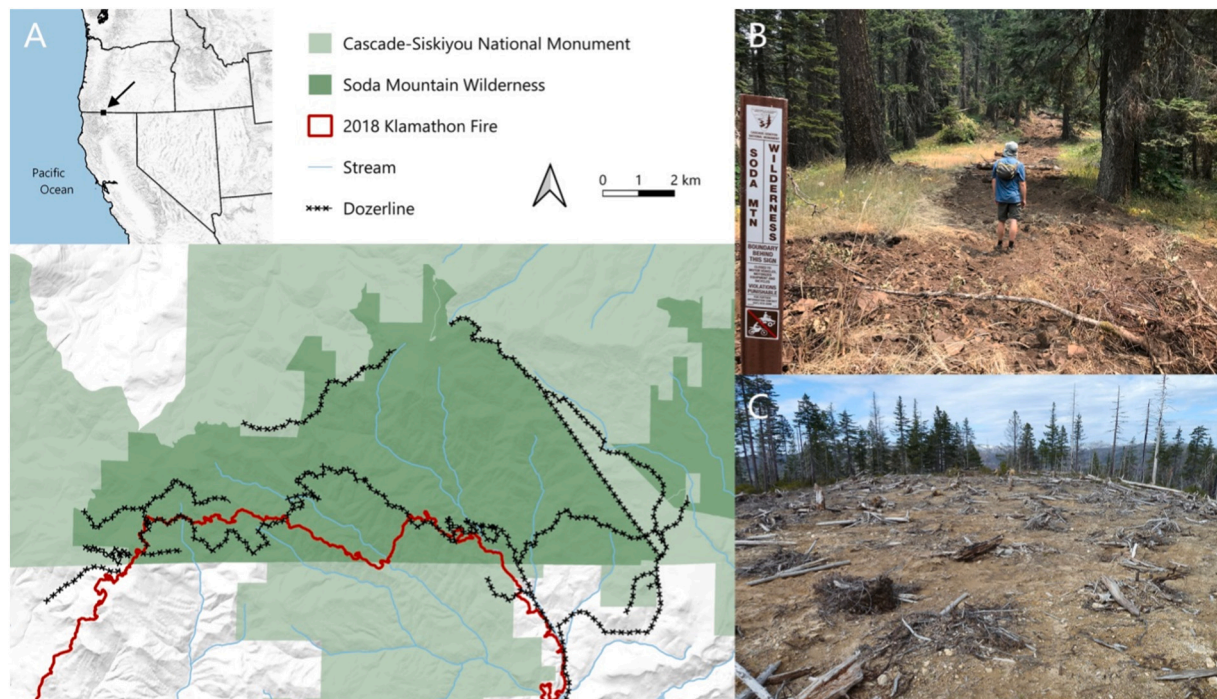


Fig. 2. (A). Extent of dozerlines built during the 2018 Klamathon fire in the Soda Mountain Wilderness within the Cascade-Siskiyou National Monument, southwest Oregon. (B) Close up of dozerline within the Soda Mountain Wilderness. The fire never reached this fireline because handlines built below were 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 over-emphasizes 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 subsidies 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 heterogeneous 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 West-erling, 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 $\leq 1\%$ 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 Sipshean 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

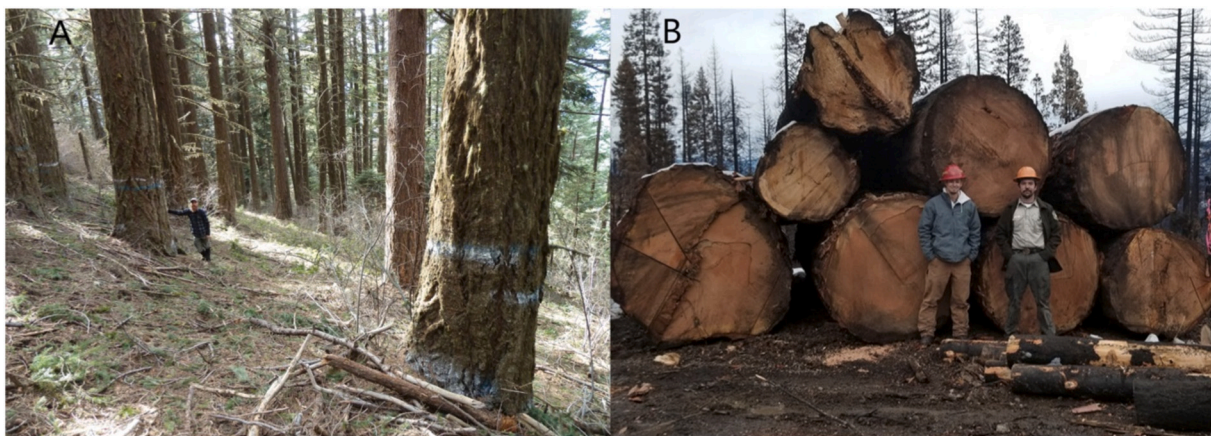


Fig. 3. (A) Nedsbar Timber Sale Medford District BLM Applegate Watershed (for “fuel reduction”) showing “take tree” markings. (B) Postfire logging on Takilma Happy Camp Road in response to the Slater fire, Rogue River-Siskiyou National Forest. These trees were regarded as fire hazards. Photos: L. Ruediger.



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 subsidies 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/energy-environment/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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Appendix A. Supplementary data

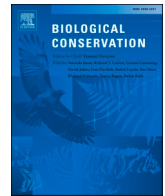
Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109499>.

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Measuring forest degradation via ecological-integrity indicators at multiple spatial scales

Dominick A. DellaSala^{a,*}, Brendan Mackey^b, Cyril F. Kormos^a, Virginia Young^b, Julee J. Boan^c, Jennifer L. Skene^c, David B. Lindenmayer^d, Zoltan Kun^e, Nuria Selva^{f,g,h}, Jay R. Malcolmⁱ, William F. Laurance^j

^a Wild Heritage, a Project of Earth Island Institute, 2150 Allston Way, Berkeley, CA 94704, United States of America

^b Climate Action Beacon, Griffith University, Parklands Drive, Southport, Queensland 4215, Australia

^c Natural Resources Defense Council, 1152 15th Street NW Suite 300, Washington, DC 20005, United States of America

^d Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2601, Australia

^e Wild Europe Foundation, 9011 Győr Posa Lajos Road 11, Hungary

^f Institute of Nature Conservation, Polish Academy of Sciences, Adama Mickiewicza 33, PL-31-120 Kraków, Poland

^g Departamento de Ciencias Integradas, Facultad de Ciencias Experimentales, Centro de Estudios Avanzados en 36 Física, Matemáticas y Computación, Universidad de Huelva, 21071 Huelva, Spain

^h Estación Biológica de Doñana CSIC, Sevilla, Spain

ⁱ Institute of Forestry and Conservation, University of Toronto, Toronto, ON M5S 3B3, Canada

^j Centre for Tropical Environmental and Sustainability Science and College of Science and Engineering, James Cook University, Cairns, Queensland 4878, Australia

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ABSTRACT

Forests harbor some 80 % 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 significant cause of biodiversity decline. Addressing this loss is critically important for fulfilling the Paris Climate Agreement and the Kunming-Montreal Global Biodiversity Framework. Additionally, the United Nations (2021a) Strategic Plan for Forests 2017–2030 calls for a halt to both deforestation and degradation by 2030. However, many countries, particularly in the Global North, fail to fully acknowledge forest degradation as a problem within their own borders, and countries are not presently on track to meet the 2030 deadline. Building from established literature, we propose a principle, criteria, indicator and verifier (PCIV) approach that would enable monitoring of degradation at various scales, ranging from the loss of large, old trees to intact landscapes relative to reference conditions derived from primary, mature, historic, and semi-natural conditions. Degradation drivers include multiple forms of commercial logging and road building that alters native species composition, structure, and functionality. Case studies from three major forested biomes (temperate, boreal, and tropical) illustrate the geographic extent and types of degradation. We highlight an urgent call for countries to better detect and assess the cumulative damages of forest-degradation and to end it as promised.

1. Introduction

UN Secretary General António Guterres issued a planetary “red alert” in 2021 in response to the alarming findings of the IPCC 6th assessment (IPCC, 2021) that time is running out on avoiding calamitous losses to

nature and people from unprecedented global overheating and humanity's expansive ecological footprint (IPBES, 2019). Integrated solutions involving emissions reductions across all sectors, combined with natural climate solutions are essential for addressing this mounting crisis (IPCC, 2021). Forests are the largest terrestrial carbon sinks and

* Corresponding author.

E-mail addresses: dominick@wild-heritage.org (D.A. DellaSala), b.mackey@griffith.edu.au (B. Mackey), jboan@nrdc.org (J.J. Boan), jskene@nrdc.org (J.L. Skene), David.Lindenmayer@anu.edu.au (D.B. Lindenmayer), zoltankun@wildeurope.org (Z. Kun), jay.malcolm@utoronto.ca (J.R. Malcolm), bill.laurance@jcu.edu.au (W.F. Laurance).

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stocks on the planet (Pan et al., 2011; IUCN, 2021) and contain ~80 % of all terrestrial species (United Nations, 2023a). Additionally, forests with the highest ecological integrity are considered to be in the most stable state, even as they are naturally dynamic, because they lack anthropogenic disturbances (Funk et al., 2019).

Primary forests, which have the highest integrity and stability, are undisturbed by industrial uses, have functional processes, including the range of successional stages, and support characteristic native species (Kormos et al., 2017; Rogers et al., 2022). The large, old trees in these forests store disproportionate amounts of aboveground carbon (Stephenson et al., 2014), while the old-growth forest stage generally is among the most carbon dense ecosystems on the planet (Keith et al., 2009). Old-growth forests, in particular, may also function as important wildfire refugia (Lesmeister et al., 2021; DellaSala et al., 2022) and climate refugia (Wolf et al., 2021). However, only ~27 % of the planet's total forest cover remains in primary forest condition (FAO, 2020) and some countries (Europe, contiguous USA) are nearly devoid of the old-growth forest stage.

Given the critical ecosystem services that forests, particularly primary forests, provide, deforestation (permanent loss of forest cover) has been an ongoing focus of international forest policy since at least the United Nations Conference on Environment and Development in 1992. Importantly, from 2002 to 2023, deforestation of tropical rainforests increased at an alarming pace of 76.3 M ha (Global Forest Watch, 2024). However, deforestation is not the only threat to forests. Although estimates of global degradation are lacking, there is ample evidence that degradation is exerting major pressures on forests. For example, the United Nations Food and Agriculture Organization (2009) estimated that there were 800 M ha of degraded forests in the tropics alone. Haddad et al. (2015) reported that some 20 % to 70 % of forests globally were within 100-m and 1-km of a forest edge, respectively. Ibisch et al. (2016) found that while 80 % of the planet was roadless, these areas, which include many forest types, were fragmented into ~600,000 patches, more than half of which were < 1 km², and only 7 % of which were > 100 km². The most extreme impacts to biodiversity occur in heavily degraded areas (>68 % biomass removed) (Ewers et al., 2024). Additionally, the recent State of the World's Forests report (FAO, 2024) found that nearly 75 % of the world's total land area, particularly forests, rangelands and wetlands, had been degraded and transformed, and those losses would likely increase to >90 % within 30 years. Degraded forests are at a much higher risk of emitting carbon and reaching tipping points that increase with climate change effects, such as severe drought and wildfire, compared to forests undisturbed by industrial impacts (Lindenmayer et al., 2011).

Ending forest degradation has been a 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 (United Nations, 2007), and in the Global Forest Goals and Targets of the UN Strategic Plan for Forests 2030 (United Nations, 2015). At the United Nations (2021b) 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 (Convention on Biological Diversity, 2022) proposed 23 action-oriented global targets, including ensuring that at least 30 % 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."

In December 2023, at the COP 28, 193 countries signed a decision

under the United Nations Framework Convention on Climate Change (UNFCCC) on the outcome of the first global stocktake, emphasizing the importance of "enhanced efforts to halt and reverse deforestation and forest degradation by 2030" to meet global climate targets (UNFCCC, 2023), as well as the need for synergistic climate and biodiversity actions. This decision reflects the growing calls for integrated solutions since the Conferences of the Parties (COP) 25 and that escalating biodiversity loss and greenhouse gas emissions are intertwined, existential threats to humanity. Following the UNFCCC's decisions at COP 28, the Declaration of the High-Level Segment of the 19th session of the United Nations Forum on Forests (2024) also reaffirmed the United Nations (2021a) Strategic Plan for Forests, issuing a call for halting and reversing forest degradation.

At the regional level, policymakers in the European Union, for instance, have advanced marketplace standards limiting trade in commodities tied to deforestation and forest degradation (European Union, 2023), and major investors and companies have been integrating degradation avoidance efforts into their wood purchasing policies (e.g., Kimberly-Clark, 2018). Despite all this attention, not a single country is on track to meet the timeline of halting and reversing deforestation and degradation by 2030 (Forest Declaration Assessment, 2024). Degradation also has financial consequences as such losses have an estimated USD 4.3 trillion–20.2 trillion cost, affecting 3.2 billion people (Gibbs and Salmon, 2014; FAO, 2024).

2. Forest degradation tracking limitations

Tracking forest degradation is complicated by differences in definitions (Ghazoul et al., 2015) and methodologies (Betts et al., 2024). The Food and Agriculture Organization (FAO, 2020) introduced national reporting on in its Forest Resource Assessment. However, because only 58 governments representing 38 % of the world's forests responded, and methodologies and indicators varied greatly, results were deemed inconclusive. Notably, most responses came from tropical countries. Those that responded reported on degradation to the FAO (via Global Forest Resources Assessments) were based on a range of indicators, including the presence of forest disturbances (e.g., logging, wildfire); changes in forest structure (e.g., decreases in forest canopy); loss of productivity; loss of biodiversity; soil damage/erosion; reductions in the provision of ecosystem goods and services; negative effects on other land uses (e.g., by causing a loss of downstream water quality); loss of carbon, biomass, and growing stock. The UNFCCC also lacks a definition of forest degradation, and further compounded the issue with its adoption of forest carbon accounting rules that allow nations to utilize accounting methods that represent logging as carbon neutral, ignoring the significant reduction in carbon stock compared to unlogged forests, and failing to report on the loss of ecosystem integrity (Krug, 2018, Funk et al., 2019, Rogers et al., 2022, Mackey et al., 2022). Further, the utility of the United Nations (2023b) Sustainable Development Goal 15 in addressing forest degradation is limited by its focus solely on forest extent and not on indicators of forest ecosystem integrity.

While Betts et al. (2024) offered important insights into tracking degradation, their approach was based on net accounting whereby the loss of forest attributes at any given location could be "offset" by theoretical gains in another area over time. However, we argue that loss of high integrity forests cannot be offset. The ecosystem benefits that these forests, particularly primary forests and the old-growth stage provide, which includes long-term carbon accumulation and biodiversity maintenance, are so great that recovery times far exceed time frames for addressing the climate and biodiversity crises, and at worst they may be altogether irrecoverable (Gatti et al., 2015; Putz and Thompson, 2020). For instance, Bourgoin et al. (2024) concluded that the full recovery of forest structure after deforestation or degradation would require a centennial timescale. Importantly, Gasser et al. (2022) simulated forest degradation for Amazonia based on three scenarios: (1) End Gross Forest Loss; (2) End Net Forest Loss; and (3) End Tree Cover Loss (forest cover

remains constant regardless of age class distributions). They concluded that the End Gross Forest Loss produced the greatest ecosystem benefits and the most meaningful compliance with halting and reversing forest loss and degradation by 2030. We agree that forest degradation should be assessed in terms of gross losses rather than a net accounting system.

Our objective is to provide a comprehensive framework to assess forest degradation based on tracking losses to ecosystem integrity as imposed by anthropogenic disturbances, ranging from the removal of individual large, old trees to stand and landscape alterations. Our approach differs from other studies that focus on large-scale ecological footprint analyses (Thompson et al., 2013; Potapov et al., 2017) and forest landscape integrity based largely on tree cover loss and connectivity (Grantham et al., 2020). Here, we compare anthropogenic impacts across scales to specific attributes in reference areas that have the highest ecosystem integrity for any given forest type.

3. Ecological integrity vs forest degradation

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-organization and regeneration capacity (Mackey et al., 2024). 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 our 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., 2024).

4. Reference conditions

Where they exist, the reference condition against which loss of ecological integrity will be measured is a primary or old-growth forest. However, in places lacking such forests, the reference can be derived from an historical determination of key features of a natural forest, mature forests in advanced post-disturbance successional stages, and naturally regenerating forests that are structurally complex (i.e., complex early seral, Swanson et al., 2010).

The integrity of primary and, where those no longer exist, near-natural forests, is due, in part, to their resistance to natural disturbances as a result of stable microhabitats within forest interiors, presence of large trees that can buffer fires and floods, and functional redundancy of species assemblages. High integrity forests are also resilient to natural disturbances via their ability to return to optimal operating conditions after a state-altering perturbation via natural successional pathways. Resilience in this case allows for succession to proceed in a circular fashion (i.e., “circular succession”) from pioneering stage immediately after stand-replacing disturbance to old growth stage and back again when disturbed again and is a component of ecosystem integrity. Resilient properties of forests may include “seed rain” and germination after stand-replacing natural disturbances, epicormic branching, and biological legacies (e.g., dead trees, surviving shrubs and

seed-dispersing animals) that lifeboat forests through successional stages (Swanson et al., 2010).

Importantly, we disagree with the FAO (2022) and the USDA Forest Service (2024) that natural processes such as insect outbreaks and wildfires are a form of degradation (i.e., a “threat” to ecosystems). Rather, many forest ecosystems are uniquely adapted to natural disturbances operating within historic bounds and require them to maintain integrity (Swanson et al., 2010). However, we acknowledge that this is complicated by the expanding impacts of climate change amplified by land use stressors that are shifting ecosystem dynamics in novel ways (IPCC, 2021).

We also consider forest management for commodity production to be a potential driver of degradation. While some (sensu Puettmann et al., 2015) exclude forest management from degradation considerations, we argue that it is indeed the case because compared to primary, old growth, and near-natural forests, logging, including under notional sustainable forest management regimes, typically results in highly skewed forest age classes toward young stages (stand and landscape), a loss of key components of structural complexity (Thorn et al., 2020), depleted carbon stocks (Malcolm et al., 2020), loss of biodiversity (including contributing to or driving decline of threatened or endangered species; Stewart et al., 2020), and/or reduced resistance and resilience to disturbances (DellaSala et al., 2022). Indeed, many legal, regulated forestry practices have a high risk of driving degradation.

5. Assessing degradation using a conceptualized framework

Anthropogenic impacts can accumulate spatially and temporally across a continuum of tree, stand, and landscape integrity losses that can be generally scored based on a broad suite of relative factors (Fig. 1, Table 1). In developing an evaluation framework, we drew upon a principle, criteria, indicator and verifier (PCIV) approach that is commonly used in the ecological literature (e.g., Gatica-Saavedra et al., 2017; Lemke et al., 2017; Schick et al., 2019; Soubry et al., 2021) and applied it in the context of ecological integrity changes (as in Mackey et al., 2023, 2024) (Table 1).

While degradation is represented as a continuum of ecosystem integrity loss, there are thresholds where ecosystems can flip to a fundamentally altered state that represent a substantially degraded landscape condition approaching deforestation (Fig. 1) (Lindenmayer et al., 2011). In juxtaposed situations, deforestation from one area may also interact with degradation of another via edge penetrance into the remaining fragment (Fig. 2).

Our framework can provide greater consistency and transparency in tracking degradation at multiple scales for government reporting, while helping to guide market-based solutions involving wood product supply chains that seek to avoid degradation (e.g., Kimberly-Clark, 2018). Moreover, ongoing monitoring of forest conditions using our framework can reveal where and when a degraded forest has partially or entirely recovered through natural or assisted ecological restoration. An example

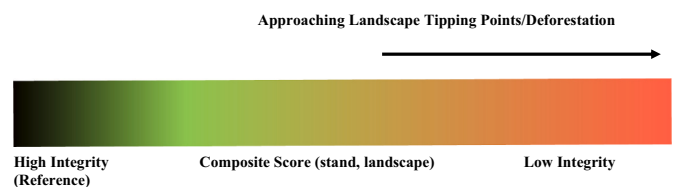


Fig. 1. Ecosystem integrity composite factors based on principles, criteria, indicators, and verifiers, as adapted from Mackey et al., 2024 and displayed in Table 1. Each of the factors in Table 1 can receive a scoring based on comparisons to reference conditions and site or regionally specific literature on those conditions relative to altered areas. For instance, many regions have information on road densities that impact hydrology and aquatic species and carbon stocks.

Table 1

Generalized framework for tracking forest degradation, building on the PCIV (principle, criteria, indicator, and verifier) ecosystem integrity approach (Mackey et al., 2023, 2024). The actual verifiers used in any given integrity assessment will vary depending on the availability of data and costs. For example, the Floristic Quality Assessment (Spyreas, 2019) requires detailed floristic knowledge, and the delineation of “young” from “mature” and “old growth” forest can be based on cutoffs in the reference forest condition. Some verifiers may overlap with others elsewhere in the table.

Principle	Criteria	Indicators	Verifiers
Ecosystem integrity	Structural quality	Vegetation structure	Basal area or tree density by young, mature, old stages (e.g., floristic quality assessment)
			Large snags, coarse woody debris
	Ecosystem processes	Natural disturbances	Carbon stock levels (Mg/ha) all pools and by age classes
			Tree heights, canopy layering, biomass
		Nutrient cycling	Degree of altered fire and other disturbance regimes
			Coarse woody
	Ecological composition	Optimal hydro-ecology	Soil compaction
			Soil productivity
		Ecosystem stability	Mycorrhizae functionality
			Unlogged watersheds
			Road-stream intersections
			Water quality limited streams
	Ecosystem functionality (e.g., see Freudenberger et al., 2012)	Ecosystem complexity	Surface runoff
			Evapotranspiration rates
	Landscape characteristics	Spatial extent	Carbon stock (Mg/ha, all pools) average and range relative to reference
			Exotic vs native species (ratio)
		Climate buffering	Potential genetic adaptations (e.g., natural resistance to pests), site factors (e.g., biological legacies following disturbance)
			Rare, threatened, at-risk species (e.g., IUCN Redlist, USA endangered species), focal species determinations
			Plant and animal richness
			Micro and macrorefugia (e.g., cool temperature, high moisture related to biophysical factors from within sites to landscape position)
			Vegetation density, topographical heterogeneity, carbon storage, species richness of vascular plants, tree height, plant functional richness
			Temperature remote-sensed data of forest patches (e.g., see Mann et al., 2023)

Table 1 (continued)

Principle	Criteria	Indicators	Verifiers
		Spatial configuration	area)
			Gamma diversity
		Temporal extent	Barriers to wildlife movements
			Road density, mean/median roadless areas size (e.g., Ibisch et al., 2016)
			Intra-patch connectivity/fragmentation
			Degree of cumulative impacts from roads, logging, other disturbances

is the northeastern forests of the United States that are reaching maturation (100+ years), recovering from expansive logging over a century ago. Mature (semi-natural) forests are approaching the reference or historical condition in this situation. Restoration can therefore simply focus on proforestation; the practice of allowing forests to become old-growth overtime ([Moomaw et al., 2019](#)). It can also include active measures that remove anthropogenic stressors like roads, livestock grazing, invasive species, and the reintroduction of extirpated species, all of which would drive the evaluation scores for degradation effects down over time.

6. Hypothetical application of the degradation framework

A hypothetical example is provided to illustrate how the PCIV scorings ([Table 2](#)) can work in a focal (managed) forest of interest being impacted by logging using a “spiderweb” diagram of scoring factors ([Fig. 3](#)) that compares focal areas to reference conditions such as primary and near-natural forests. This scoring of the framework can be conducted in any forest type and region and with enough replicates would be scalable to larger areas.

7. Regional examples of forest degradation in relation to the PCIV

We provide regional examples to illustrate the utility of the degradation framework in relation to [Table 1](#) PCIV generally; however, the examples are not meant as a specific test of the approach. We recognize that subsequent studies are needed to apply the framework via statistically robust comparisons of focal sites with reference areas.

7.1. Degradation of tropical rainforest

Sustainable Forest Management (SFM) is a broad and somewhat imprecise term promoted globally since the United Nations Conference on Environment and Sustainable Development in Rio of 1992. The SFM concept is meant to guide the maintenance of a forest's ecological values while generating a sustained yield of timber ([Putz and Thompson, 2020](#)). In the tropics, SFM involves selective logging of large trees from a relatively small suite of commercially valued species that propoorts to be based on reduced-impact logging and post-logging silvicultural treatments to encourage regeneration ([Putz and Thompson, 2020](#)). However, a number of ecological factors in tropical forests conspire against truly ecologically sustainable practices. First, logging focuses on primary forests, where large old trees with a high volume of timber can still be found ([Table 1](#): structural quality-vegetation structure). However, many of the exploited trees are important for wildlife, especially host-specific pollinators, and are important for long-term carbon storage and nutrient cycling ([Table 1](#): nutrient cycling, soil compaction/productivity, ecological composition, ecosystem processes, ecosystem stability-carbon) ([Zimmerman and Kormos, 2011](#)).

Importantly, large trees generally represent a small percentage of the



Fig. 2. Deforestation on the border of Kayapo's territory, Pará, Brazil, showing stark contrast with a primary forest. Notably, edge penetrance from deforestation will creep into the juxtaposed primary forest causing spillover effects that trigger degradation in the primary forest as well (photo credits: Simone Giovine).

Table 2
Hypothetical degradation scoring factors for 4 variables in comparison to reference conditions. Scorings of 1 to 3 represent high to low integrity. Highest total scorings reflect highest degradation levels. Any and all of the PCIV in Table 1 can be included in this analysis.

	Above-ground biomass	Presence of key species	Old growth (%)	Lack of invasives	Forest degradation score
Reference forest	1	1	1	1	4
Focal forest A	2	3	2	2	9
Focal forest B	3	2	3	3	11

forest's total trees (<5 %), yet store up to 50 % of the above ground carbon (Stephenson et al., 2014; Fauset et al., 2015; Lutz et al., 2018). As a result, logged tropical forests store ~35 % less carbon than primary forests, and this amount decreases with successive logging operations (Mackey et al., 2020). Most tropical forests are also very sensitive to having their canopies opened up because that brings in secondary forest species that displace primary species, an invasion of vines and lianas, and an increase in fire proneness (Zimmerman and Kormos, 2011, Gatti et al., 2015) (Table 1: native species vs. invasive species, natural disturbance processes). Tropical forest logging therefore can have cascading effects on integrity especially when it scales up cumulatively across large landscapes (Table 1: landscape characteristics). Putz and Thompson (2020) found that the stocks of carbon and biodiversity in large primary tropical rainforests exceeded those in forests subjected to uses other than forest protection. Furthermore, because large trees tend to be slow-growing hardwood species, they require >100 years to recover from logging, if they recover at all (Mackey et al., 2020; Putz and Thompson, 2020), illustrating problems with adaptive potential and ecosystem stability (Table 1).

Even if logging intensity is lowered in tropical forests by removing only a small volume of timber, extending timber rotations, and following extensive pre- and post-logging best practices, it is typically not

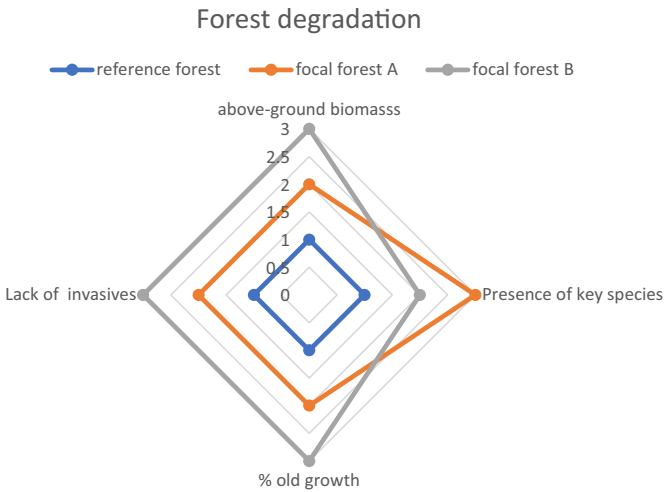


Fig. 3. Spiderweb schematic illustrating how the departure in integrity between two focal forests and a hypothetical reference condition can be scored (i. e., in comparison to primary forests, near-natural forest). The higher the overall score, the more significant the forest degradation. Statistical analyses can be applied to illustrate the main factors involved in degradation that best separate degraded sites from the reference condition.

commercially viable (Zimmerman and Kormos, 2011, Romero et al., 2024, Putz and Thompson, 2020, Vidal et al., 2020). This is why operations often fell trees illegally, exceeding their allowable cuts, and often clear-felling is used to go after the high-value, large trees (Zimmerman and Kormos, 2011, Vidal et al., 2020).

7.2. Degradation of dry fire-adapted forests of western United States

Many “fire risk reduction” and “restoration” projects include substantial and frequent biomass removals (DellaSala et al., 2022), often targeting large trees and resulting in soil compaction and excessive

understory impacts that can type-convert dense forests to open woodlands lacking native understories (Table 1: vegetation structure, nutrient cycling, soils, invasives) (Fig. 4). Impacts can accumulate across spatial scales (Table 1: landscape characteristics), affecting large areas logged and excessively burned in dry pine (*Pinus* spp.) and mixed-conifer forests, for example (Fig. 5a–c). Altered stands are then exposed to understory drying and over ventilation of forest canopies that can elevate fire spread rates and cause blow down of remaining trees (Table 1: ecosystem processes - natural disturbance). Tree mortality from removals and understory damage can also exceed that of fire disturbances (Hanson, 2022) (Table 1: ecosystem stability and adaptive potential). Moreover, excessive understory removals through mastication of shrubs and pile burning of slash can disrupt natural successional pathways with reverberating multi-functional ecosystem impacts (Ding and Eldridge, 2024), including the spread of invasive species within burn piles and soil damages (Table 1: invasive species, ecosystem processes, nutrient cycling-soils). Encroachment of woody plants, for instance, is likely to increase in many dry forest systems due to climatic shifts amplified by removal of understory plant species that may have synergistic relationships with tree establishment (Ding and Eldridge, 2024).

7.3. Degradation of boreal and temperate forests, Canada

Decades of extensive clearcut logging has led to diverse and multifaceted forest degradation that illustrates removal of important old forest structures with scalable impacts (Table 1: vegetation structure and landscape characteristics) (Fig. 6a, b). This includes: (1) habitat loss and fragmentation caused by roads and other linear features that are driving substantial declines of boreal caribou (*Rangifer tarandus caribou*; Stewart et al., 2020) (Table 1: spatial configuration - road density, ecological composition - rare, threatened, at-risk species); (2) changes in tree composition (Table 1: ecological composition-tree species composition) that have led to declines in dozens of bird species in the east coast Acadia forests - even where the amount of tree cover has remained relatively stable (Betts et al., 2022) (Table 1: adaptive potential-plant/animal richness); (3) loss of coarse woody debris and reduced nutrient cycling (Table 1: ecosystem processes-nutrient cycling); (4) declines of focal species like American marten (*Martes americana*), which is also important to many northern Indigenous peoples (Farnell et al., 2020) (Table 1: adaptive potential); (5) cumulative logging and road building that have increased extreme flooding in British Columbia's coastal and inland temperate rainforests (Pham and Alilal, 2024) (Table 1: ecosystem processes-hydrology); and (5) conversion of carbon-rich, primary forests to planted forests that decrease landscape-level carbon storage (Table 1: vegetation structure-carbon stock levels) (Malcolm et al., 2020; Mackey

et al., 2024). Such impacts accumulate spatially and temporally (Table 1: landscape characteristics-spatial and temporal).

7.4. Degradation of tall wet forests of Victoria, Australia

Although native forest logging has officially ceased in the tall wet forests of the Australian State of Victoria, various active management practices within these forests continue to degrade them.

First, so-called “firebreaks” spanning 1450-km are fragmenting tall, wet forests and cool temperate rainforests (Department of Energy, Environment and Climate Action (DECCA), 2024) (Table 1: landscape characteristics-spatial extent, configuration) even within the Yarra Ranges National Park in the Central Highlands (Fig. 7). Removing large (>1.2-m diameter, 200–350+ years old) trees is impacting the nesting and denning habitat of the Southern Greater Glider (*Petauroides volans*), recently uplisted to Nationally Endangered (Lindenmayer et al., 2017, 2024) (Table 1: at-risk species). Degradation of these keystone structures is widespread even while the extent of forest remains stable.

A second form of forest degradation is the removal of so-called “dangerous trees” for up to 40-m either side of all roads in tall, wet eucalypt forests, a treatment also frequently used in western US forests (DellaSala et al., 2022). Trees considered a risk to firefighters are extensively logged, not only during firebreak construction but also around forestry roads more generally. Such removals are contributing to the scarcity of important wildlife habitat elements with corresponding negative impacts on an array of threatened cavity-dependent fauna (Lindenmayer et al., 2024) and the fragmentation of intact areas (Table 1: landscape characteristics-spatial, temporal).

A third form of forest degradation in this region is post fire and post windstorm “salvage” logging (Fig. 8). Such logging is occurring in many State forests and even in National Parks (in US and Canada this also frequently occurs after fire and insect outbreaks, including within Yosemite National Park). In this case the ecologically beneficial effects of a natural disturbance (fire, insects, windstorms) are overridden by logging and road building that impact many plant and animal species and soils (Lindenmayer et al., 2008; Thorn et al., 2018) (Table 1: ecosystem processes, adaptive potential, nutrient cycling, landscape characteristics). Degradation from post-disturbance logging can mean that forest recovery may not occur for centuries (Lindenmayer and Ough, 2006) (Table 1: ecosystem stability, adaptive potential). Indeed, the Government of Victoria has listed post-fire salvage logging as a Key Threatening Process under its flora and fauna legislation for the State (Victoria Government Gazette, 2024).



Fig. 4. Naturally regenerating ponderosa pine stand (left, high integrity) vs. excessive “fuel reduction” (right, low integrity) deemed as “restoration” on the Santa Fe National Forest, New Mexico. Excessive canopy removals and overly frequent prescribed burning can type-convert forests to open savannahs invaded by flammable invasive species prone to fire spread from overly ventilated canopies (Table 1: adaptive potential, ecological composition) (photo: D. DellaSala).



Fig. 5. Google Earth imagery of excessive fuel treatments on the Coconino National Forest, Arizona illustrating landscape scale changes (Table 1: landscape characteristics) showing (a) pre-treatment (2017); (b) commercial thinning (right side) in 2021; and (c) commercial thin (right) and group-selection (left) in 2024. While dry pine forests were naturally open before fire suppression, the degree of biomass removal can act as an ‘ecological shock’ that type shifts communities into permanently altered states (Table 1: ecosystem stability, adaptive potential) (imagery provided by Bryant Baker, Wildland Maps).

7.5. Degradation of temperate and boreal forests in Europe

About 40 % of the terrestrial continent is forested (European Environment Agency, 2024). While forest cover has been increasing in Europe since World War II (i.e., the Tree Cover Scenario of Gasser et al., 2022), the latest State of Nature report (European Environment Agency, 2023) indicated only 14 % of forests are in “favourable conservation status” (high integrity) within the Natura 2000 network. Logged forest area increased by 49 % while forest biomass loss increased by 69 % from 2016 to 2018 (Ceccherini et al., 2020). The European Union’s Bioeconomy Strategy will likely cause further pressure on European forests generally. This is troubling because the European Environment Agency

(2024) also reported a doubling of tree canopy mortality from natural disturbances and climate stressors since the late 20th century, which is the equivalent of 1 % of the European Union-27 forest area dying annually. Defoliation rates increased by 10 % while the abundance of forest birds decreased by 3 % between 1990 and 2020 (European Environment Agency, 2024).

Some specific examples of degradation from European countries are as follows.

- Almost half of Hungary’s forests are monocultures and nearly a quarter are non-native Black locust (*Robinia pseudoacacia*) plantation (NFK, 2023). However, the Minister of Agriculture managed to get Black locust on the list of national treasures as a Hungarikum (uniqueness of Hungary, Hungarikum., 2014). Importantly, Hungary has only 347 ha of natural forest from its reported 2 M forested hectares to serve as reference sites in degradation assessments, illustrating major multiple degradation factors (Table 1: vegetation structure, nutrient cycling, optimal hydro-ecology, characteristic native species, ecosystem stability, adaptive potential, and spatial extent).
- In Austria, the length of forest roads available for logging trucks increased by 40 % since 1996, reaching a total of 218,000 km (Table 1: optimal hydrology, landscape characteristics-road density). The dense network of forest roads used by trucks has a negative impact on the microclimate, wildlife collisions, and the ability of forests to store carbon (Feldbacher-Freithofnig et al., 2024).
- In the four Nordic countries (Denmark, Finland, Norway and Sweden), the extent of forests taller than 15-m declined from logging by 2.25 M ha with the biggest decline rate of 3.5 % of total forests and 20 % of tall forests between 2001 and 2021 (Turubanova et al., 2023) (Table 1: vegetation structure and associated forest age classes).
- In Germany, logging and development resulted in nearly 2 M ha of fragments <1km², covering nearly 30 % of total forest area. Fragmentation effects contribute to maximum temperature increases that may push ecosystems to near collapse vs. remaining intact areas that may act as refugia (Mann et al., 2023) (Table 1: adaptive capacity, landscape characteristics-spatial extent). Additionally, removal of tree canopies by as little as 10 % contributed to increased forest temperatures in Scots pine (*Pinus sylvestris*) plantations and European beech (*Fagus sylvatica*) forests (Blumroeder et al., 2021) (Table 1: ecosystem complexity, climate buffering).

Notably, only 2.4 % of the European Union’s forests are primary and old-growth forests (Barredo et al., 2021), and most of these forests are not strictly protected (Sabatini et al., 2018). The Białowieża Forest along the Polish-Belarusian borderland is the best example of a temperate lowland primary forest in Europe. However, it has undergone substantial fragmentation from road development and construction of a border wall that has completely blocked movement of large mammals (Fig. 9a, b, c) (Table 1: multiple factors including barriers to wildlife movement). The border wall and associated infrastructure have been accompanied by a general increase in anthropogenic disturbances. These impacts have altered most ecological processes, including natural forest regeneration and herbivory, while jeopardizing nearly all factors in Table 1.

8. Roads as a driver of expansive forest degradation

One of the most pervasive cumulative drivers of degradation globally is the proliferation of roads (Laurance et al., 2014; Ibisch et al., 2016). Up to 25 M km of new paved roads will be constructed globally by mid-century (Dulac, 2013), enough to encircle the Earth >600 times. Roughly 90 % of these new roads will be in developing nations, often in tropical and subtropical regions with outstanding forest integrity

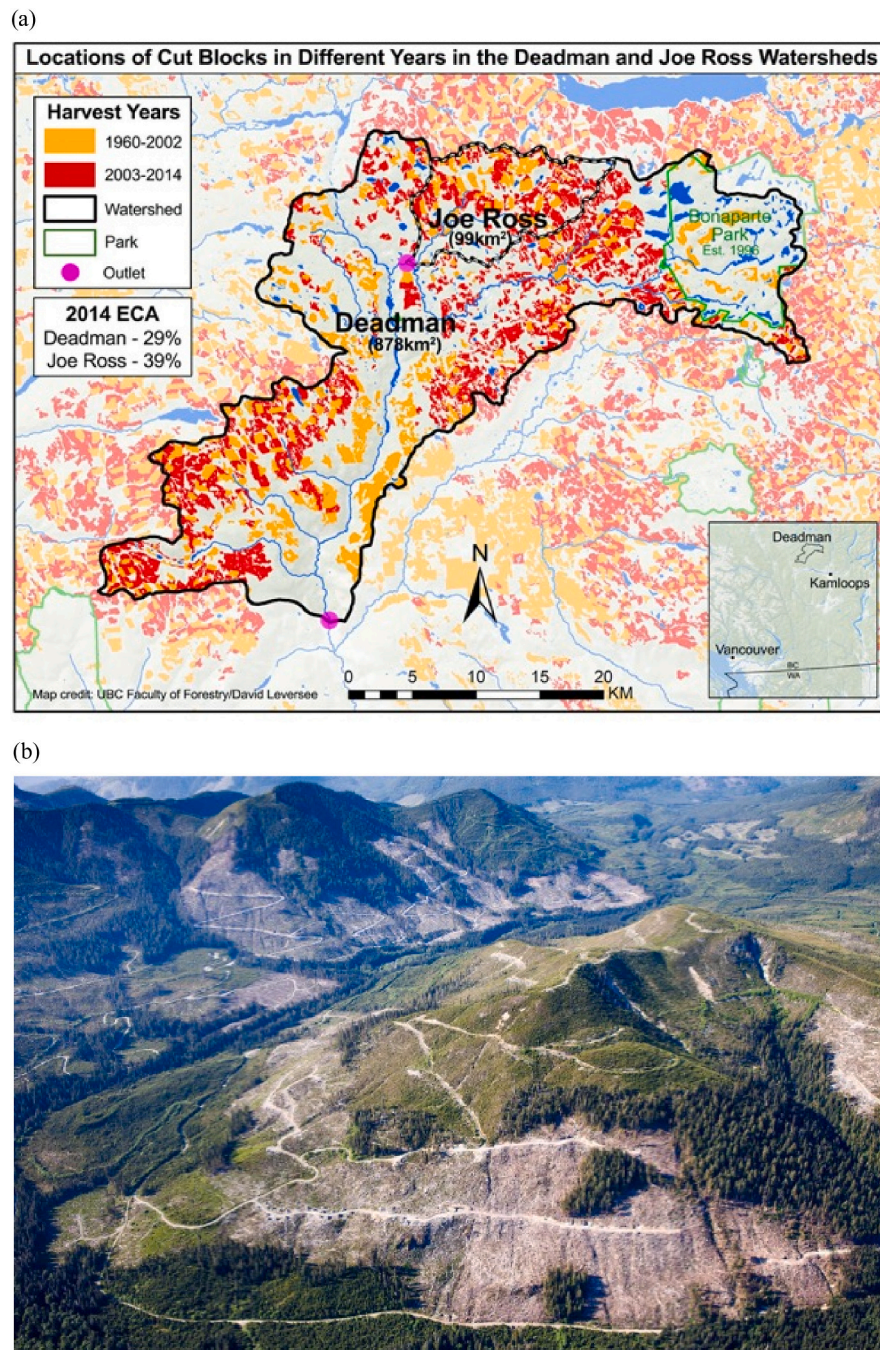


Fig. 6. (a) Extensive clearcutting with impacts that accumulate at the landscape scale, increasing the risk of extreme flooding and mass-wasting events (Table 1: ecosystem processes-hydrology; landscape characteristics). The equivalent clearcut area (ECA) is the area that has been clearcut with a reduction factor to account for the hydrological recovery due to forest regeneration and subsequent growth (map credit: D. Leversee, UBC Faculty of Forestry). (b) Clearcut logging and road building in Klanawa Valley, British Columbia, Canada showing extensive degradation via fragmentation effects (Table 1: road density) (photo credit: TJ Watt).

(Laurance et al., 2009). Many new roads are opening up primary forests—promoting influxes of illicit loggers, land grabbers, land speculators, miners, poachers, and illegal-drug producers, among others, many of which operate outside the law and with no environmental oversight (Alamgir et al., 2017; Engert et al., 2024) (Fig. 10).

The expansion of roads is clearly one of the most urgent degradation issues. For instance, China's planet-changing Belt and Road Initiative currently spans a total of 155 nations and is promoting thousands of roads and extractive-industry projects (Laurance, 2017; Ascensão et al., 2018). In Latin America, an ambitious suite of road and other infrastructure projects is advancing, penetrating remote regions and key

ecosystems (Laurance et al., 2001; Fearnside et al., 2012, 2013). In Africa, 35 massive 'development corridors' are underway or planned, crisscrossing the continent and collectively exceeding 53,000 km (Laurance et al., 2015). A proposed superhighway in Nigeria would slice through much of the remaining habitat for the critically endangered Cross River Gorilla (*Gorilla gorilla diehli*) (Mahmoud et al., 2017). That highway, which was eventually re-routed following heated public debate, would have generated only questionable economic benefits while allowing the federal government to seize extensive lands owned by traditional communities (Laurance et al., 2021).

Poorly planned road projects not only degrade a large area but can



Fig. 7. A large old tree removed as part of the commencement of the construction of a firebreak in the montane ash forests of the Central Highlands of Victoria (photo: D. Lindenmayer), illustrating the loss of important structures for at-risk species (Table 1: vegetation structure, at-risk species).



Fig. 8. Post-fire “salvage” logging operation in the tall wet forests of the Central Highlands of Victoria is a form of degradation even though trees are planted following logging (photo: D. Lindenmayer). This type of logging alters nutrient cycling, successional processes, post-disturbance structures, native species, ecosystem stability, adaptive capacity, hydro-ecology, soils and is scalable at landscape levels (Table 1).

provoke serious cost overruns, increase corruption, and cause major environmental impacts, while generating sparse or uneven economic benefits that instigate social unrest (Alamgir et al., 2017). Road projects can trigger an array of environmental and societal risks, particularly for lower-income nations where corruption and weak governance undercut efforts to promote sustainability (Laurance et al., 2009). Many developing nations are selling their minerals, timber, and other natural resources or borrowing heavily from international lenders, thereby risking economically damaging debt defaults (Ascensão et al., 2018, Laurance, 2018). There is a significant socio-economic and ecological cost to this type of degradation.

9. Conclusions and Recommendations

9.1. Degradation monitoring and research needs

It is vital that improved spatial resolution and on-the-ground monitoring of degradation receive the same support as deforestation monitoring.

Many of the PCIV factors provided herein can be obtained and monitored through remote sensing that is readily available from Landsat and high-resolution imagery from the GEDI ecosystem LiDAR program (<https://gedi.umd.edu/>; accessed October 27, 2024). Coarse-scale tracking systems are also available on tree cover, intact forest landscapes, and endangered forest locations (<https://canopyplanet.org/tools-and-resources/forest-mapper/map>; accessed October 27, 2024) along



Fig. 9. (a) Primary forests of the transboundary Białowieża World Heritage Property in Poland and Belarus showing high density of old trees and dead wood. Most of the oak (*Quercus robur*)-lime (*Tilia cordata*)-hornbeam (*Carpinus betulus*) forest on the Polish side is uneven aged, multi-species and multi-layered (photo: A. Wajrak). (b) Logging decks along roads removed in the commercial part of Białowieża Forest in Poland as a response to a bark beetle outbreak. Periodical outbreaks are a natural disturbance and an important ecological process; massive logging and removal of dead trees was ruled illegal by the EU Court of Justice in 2017 (photo: N. Selva). (c) Border wall and associated infrastructure built in 2022 (photo: R. Kowalczyk).

with change detection analyses (e.g., Global Forest Watch, <https://www.globalforestwatch.org/>; accessed October 27, 2024).

Importantly, there is an urgent need to improve mapping of primary forests to better track degradation in these high conservation value forests. Morphological Spatial Pattern Analysis from the GuidosToolbox can be used to calculate patch statistics (e.g., Vogt and Riitters, 2017) and FRAGSTAT (e.g., Keeley et al., 2021) is available to assess landscape-scale degradation determinations of primary forests. Large-

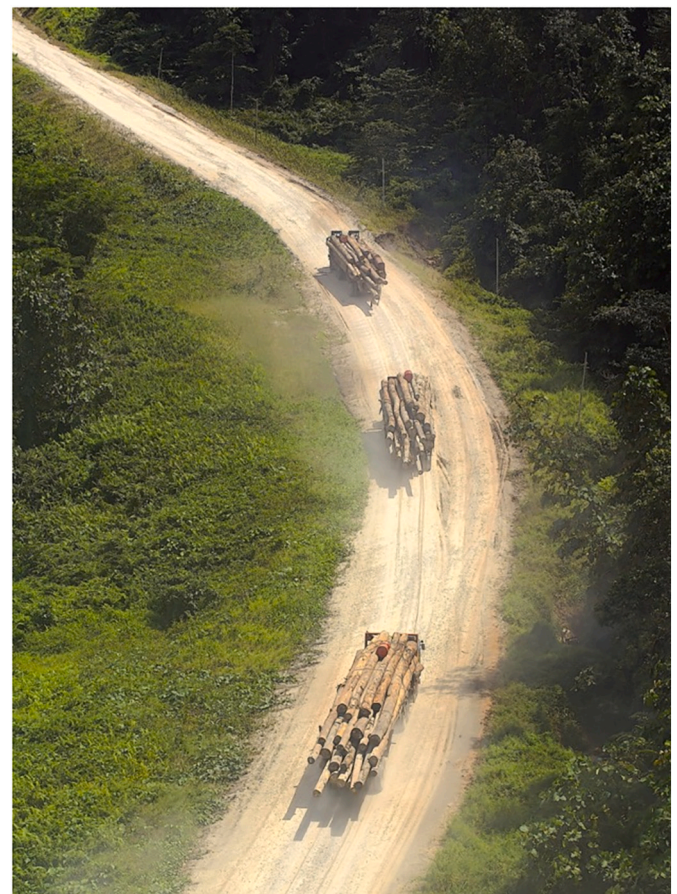


Fig. 10. New roads are opening up many of the world's last remaining intact ecosystems, as evidenced by this forest road in Sabah, Malaysian Borneo (photo: Rhett Butler). Roads have numerous impacts illustrated in Table 1 particularly to hydro-ecology, barriers to wildlife movements, and landscape characteristics related to forest fragmentation.

scale forest carbon mapping is also available in some regions (e.g., LANDCARB in the Pacific Northwest, <https://research.fs.usda.gov/pnw/products/dataandtools/tools/forest-sector-carbon-calculator>; accessed October 27, 2024).

In other cases, published forestry inventory and plot sampling (e.g., Forest Inventory and Analysis program of the USDA Forest Service) will be needed to determine forest age class and tree size distributions (e.g., as in “timber stand exams”), coarse woody debris for nutrient cycling, carbon stock levels, and soil characteristics. Citizen science can also help with focal taxa determinations (e.g., ebird; <https://ebird.org/home>; accessed October 27, 2024). Costs of obtaining the necessary information for the PCIV will vary based on whether data are raw or processed, the degree of site-specific sampling involved, and data quality and availability from published datasets. An important follow up is to test the PCIV approach in specific forest types (boreal, tropical wet/dry, wet/dry temperate) using reference versus focal sites that are replicated across scales.

9.2. Degradation avoidance

Meeting the goals of the Paris Climate Agreement and Kunming-Montreal Global Biodiversity Framework requires an urgent policy shift to include the protection and restoration of forest ecosystem integrity. We illustrate a testable process for assessing and monitoring forest degradation that uses an ecosystem integrity framework applied across scales, forest types, and regions and is useful in international agreement compliance. The PCIV framework can also determine when

degradation is approaching levels that further exacerbate the biodiversity-climate crisis, including when it is virtually indistinguishable from deforestation. When degradation is assessed as the gross loss of ecosystem integrity, advanced warning can be given to prevent tipping points and cumulative impacts. Examples are provided from forest biomes where the degradation framework can be used in forest reporting by nations, landowners, investors looking for “greener” wood sourcing, and decision makers involved in pledges and international agreements. In this case, the spatial distribution of degradation drivers extends from logging of large, old trees, to skewed young tree age class distributions at the stand and landscape level, and the fragmentation of landscapes by logging, road building, and other developments (Seigel et al., 2023).

We recommend that to better comply with 2030 biodiversity and climate targets, at a minimum, primary and near natural forests with relatively high integrity should be the reference condition that is protected from all forms of degradation and is used as a “blueprint” in restoration efforts aimed at restoring integrity. We emphasize that our framework links ecosystem integrity as fundamental to effective planning and governance (Morgan et al., 2022). As part of our framework, proforestation (Moomaw et al., 2019) could be adopted to assist in recovery of degraded ecosystems that otherwise can become old growth in just a few decades (e.g., mature forests in northeastern US forests, Australia, Europe). Restoration of near-natural forests would make a substantial, more resilient and low-risk contribution to climate mitigation as their integrity would improve over time with the removal of anthropogenic stressors like logging and roads. We also acknowledge that the demonstrated contribution of Traditional Ecological Knowledge to maintaining ecological integrity across forest ecosystems is not formally reflected in our proposed framework. Further collaborative research with Indigenous Peoples would strengthen its implementation.

Degradation, much like deforestation, threatens basic human services and quality of life, and requires integrated solutions to address socio-economic impacts such as related job losses. This can happen by shifting the wood supply out of high integrity forests and into existing purpose planted or other dedicated production forests. To accommodate this transition, investments are needed in increased capacity of existing purposed forests, retooling milling infrastructure for small logs, enabling value-added manufacturing that reduces log exports by keeping more of what is removed locally, and assisting timber reliant communities impacted by industrial automation in milling technologies. An example of where this transition is currently occurring is on the Tongass National Forest in southeast Alaska, where wood supply has been shifting from old-growth forests into previously logged and reforested areas on the designated timber base that is now available for a second rotation on a much smaller logging footprint (DellaSala and Furnish, 2020). The shift is being aided by changes in forest planning and government funding via the *Southeast Alaska Sustainability Strategy* (2023).

Finally, we provide a transparent and testable assessment framework for assessing and reporting on forest degradation, generating the information needed to meet global forest pledges, implementing forest-climate policies, and supporting relevant procurement strategies. Our framework is urgently needed to slow and even reverse the global biodiversity and climate crisis as many of the world's last primary, near natural forests, and older forests remain vulnerable to preventable anthropogenic losses despite unfulfilled pledges, international agreements, and policies that thus far have failed to sufficiently stem and reverse degradation.

CRediT authorship contribution statement

Dominick A. DellaSala: Writing – review & editing, Writing – original draft, Visualization, Project administration, Investigation, Data curation, Conceptualization. **Brendan Mackey:** Writing – review & editing, Writing – original draft, Methodology, Data curation,

Conceptualization. **Cyril F. Kormos:** Writing – review & editing, Writing – original draft, Validation, Conceptualization. **Virginia Young:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Julie J. Boan:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Jennifer L. Skene:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **David B. Lindenmayer:** Writing – review & editing, Writing – original draft, Visualization, Validation, Conceptualization. **Zoltan Kun:** Writing – review & editing, Writing – original draft, Visualization. **Nuria Selva:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Jay R. Malcolm:** Writing – review & editing, Writing – original draft, Conceptualization. **William F. Laurance:** Writing – review & editing, Writing – original draft, Visualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. This paper was supported by anonymous donors and Environment Now to D. DellaSala but none of the funders had any involvement in the project.

Data availability

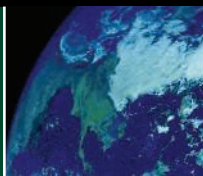
No data was used for the research described in the article.

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LETTERS

edited by Etta Kavanagh

Post-Fire Logging Debate Ignores Many Issues

RECENT CONTROVERSY CONCERNING POST-FIRE LOGGING IN OREGON is emblematic of the problems of “salvage logging” globally (1). Although tree regeneration after disturbances in forested areas is important (2–4), a narrow view of this issue ignores important ecological lessons, especially the role of disturbances in diversifying and rejuvenating landscapes. Scientific advances in recent decades demonstrate that disturbances are not catastrophes, trees in these landscapes are not wasted if they are not harvested, and post-fire logging is not forest restoration (5).

Fires (6), floods (7), volcanic eruptions (8), hurricanes (9), and



Two views of forests after the Biscuit fire of 2002 in the Siskiyou National Forest, southwest Oregon: (left) unlogged botanical reserve with legacy trees present and (right) adjacent logged area with legacy trees removed and soils damaged (blackened areas) by burning of logging slash. [Photos taken November 2005.]

insects (9) create and sustain the structure and composition of forests; disturbed areas also support species that are rare or absent from closed-canopy forests, including many that are restricted to recently burned areas (6). The extraordinary habitat mosaics of southwest Oregon’s Biscuit fire area (10) and characteristic post-disturbance communities present in forests throughout the world (11) are in large part due to periodic “catastrophic” disturbances. Relative to naturally disturbed forests, intensively managed forests and plantations lack biological legacies, including intact understory vegetation, snags (standing dead trees) and logs, and patches of undisturbed or partially disturbed forest (11). Additionally, the het-

erogeneity associated with natural disturbances typically includes areas of low tree density and high shrub cover (12), which results in structural complexity required by many elements of the forest biota (13).

Ecological damage caused by post-disturbance logging may outweigh short-term economic benefits. If conducted improperly, timber harvest of any kind damages soils and below-ground processes, spreads invasive species, increases sediment delivery to streams, and destroys or degrades key environments for terrestrial and aquatic species. With post-disturbance logging, however, these impacts occur when forest recovery is most vulnerable to the effects of additional, especially anthropogenic, disturbances, creating cumulative effects not associated with logging in undisturbed forests (14, 15). Such effects can extend for a century or more, because of the removal of long-persisting and functioning biological legacies (11). Moreover, a focus on post-disturbance logging will divert the attention of forest managers from conducting legitimate fuels reduction in fire-prone areas by, for example, thinning overly stocked trees and undergrowth, especially within at-risk rural communities, thereby exacerbating the already existing problem of declining local agency staffing and budgets.

The effects of post-disturbance logging require careful consideration of whether to log at all, and if so, how to conduct such logging to minimize negative consequences. If we must conduct post-disturbance logging for timber production, stringent ecological safeguards must be in place to minimize impacts to terrestrial (14) and aquatic (15) ecosystems. When viewed through an ecological lens, a recently disturbed landscape is not just a collection of dead trees, but a unique and biologically rich environment that also contains many of the building blocks for the rich forest that will follow the disturbance.

DOMINICK A. DELLASALA,^{1*} JAMES R. KARR,² TANIA SCHOENNAGEL,³ DAVE PERRY,⁴ REED F. NOSS,⁵ DAVID LINDENMAYER,⁶ ROBERT BESCHTA,⁷ RICHARD L. HUTTO,⁸ MARK E. SWANSON,⁹ JON EVANS¹⁰

¹National Center for Conservation Science and Policy, Ashland, OR 97520, USA. ²Professor Emeritus, University of Washington, Seattle, WA 98195, USA. ³David H. Smith Research Fellow, Department of Geography, University of Colorado, Boulder, CO 80309, USA. ⁴Professor Emeritus, Ecosystem Studies, Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA. ⁵Davis-Shine Professor of Conservation Biology, University of Central Florida, Orlando, FL 32816, USA. ⁶Centre for Resource and Environmental Studies, The Australian National University, Canberra, ACT 0200, Australia. ⁷Professor Emeritus, College of Forestry, Oregon State University, Corvallis, OR 97331, USA. ⁸Avian Science Center, Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA. ⁹Forest Ecosystem Analysis, College of Forest Resources, University of Washington, Seattle, WA 98195, USA. ¹⁰Landscape Analysis Laboratory, Department of Biology, University of the South, Seawee, TN 37383, USA.

*To whom correspondence should be addressed. E-mail: Dominick@nccsp.org

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Preventing HIV/AIDS in Adolescents

I WAS PLEASED TO SEE THAT THE UNITED Nations Population Fund (UNFPA) is cooperating with the Interreligious Committee in Honduras without compromising its own principles, particularly as regards the effectiveness of condoms in fighting HIV/AIDS

(“Mission possible: integrating the Church with HIV/AIDS efforts,” J. Cohen, Special Section on HIV/AIDS: Latin America & Caribbean, 28 July, p. 482). UNFPA has taken on a special mandate to work with the world’s staggering numbers of adolescents who need scientifically based information and the wherewithal to make responsible decisions.

In 2002, Lois Abraham and I started 34 Million Friends, a grassroots organization that raises money and awareness of UNFPA (1). I have witnessed UNFPA youth centers in Mali and Senegal where the young are enticed by sports and perhaps a cyber cafe and then are deluged with information and peer counseling about sexual matters. Lois has witnessed the same dedication toward AIDS prevention in Nicaragua. The Bush Administration has withheld \$34 million from UNFPA every year since 2002 and touts “abstinence only” policies abroad, which do not take into account forced early marriage of girls to older, more sexually experienced men and often their need to trade sex for food or school tuition. The United States should fully support the UNFPA in its human rights–based work for sexual health. UNFPA works

in 140 countries at their invitation. Last year, 171 countries contributed to UNFPA, but not the United States. For shame!

JANE ROBERTS

Redlands, CA, USA.

Reference

1. See www.34millionfriends.org.

On Purpose in Conservation

THE EMPHASIS ON THE PRESERVATION OF biodiversity as the objective of conservation (“Global biodiversity conservation priorities,” T. M. Brooks *et al.*, Review, 7 July, p. 58) has three distressing faults.

First, species contain ecotypes that are unique to their locales. As the range of the species is restricted, ecotypes are lost and the functional integrity of the natural communities in that region suffers. Although the ecotypes may be reproducible over many generations from a population residual in a protected “hot spot,” the reproduction is not guaranteed and is certain to be slow.

Second, the very best efforts in preserving species in parks will be defeated if we allow the environment to erode out from

under them. The issues are not simply climatic disruption, but also include physical, chemical, and biotic disruption.

Finally, the focus on biodiversity by well-financed and obviously influential scientists appears to be an authoritative statement that the needs of conservation are finite and can be met adequately by establishing parks to preserve species in hot spots. The fact is that these objectives are appropriate but completely inadequate and, presented without elaborated conditions, become distracting to the point of being misleading.

The objective of conservation is the preservation of a fully functional biosphere as the only human habitat. That entails preservation of the full range of genetic potential in species, the species in all of its intrinsic diversity. This argument presents a far more aggressive mission for conservation, one much closer to the objective recognized, at least nominally, by Brazil in preserving by law a high fraction of each land holding in forested regions as intact forest and by New York State's Adirondack Park, which embraces villages, towns, and businesses operating under special rules governing forested land over 6 million acres. Success also entails immediate implementation of the Framework Convention on Climate Change to stabilize the heat-trapping gas content of the atmosphere at levels safe for nature and for people. Conservation as a whole demands a new design on how to manage the world, not one based on parks alone, which are bound to fail.

GEORGE M. WOODWELL

Woods Hole Research Center, Woods Hole, MA 02543, USA.
E-mail: gmwoodwell@whrc.org

Response

WOODWELL'S DISTRESS APPEARS TO STEM from confusion about the objective, strategy, and scale of conservation addressed by our Review. As suggested by our title, our aim was to review biodiversity conservation as an objective, and prioritization as a strategy, at the global scale. First, other conservation objectives beyond biodiversity are also valid, such as cultural diversity (1) and eco-

system services (2). Happily, there are many synergies between these objectives and that of biodiversity conservation, because they have similar distributions and threats and can therefore harness similar conservation responses.

Second, Woodwell's assertion that conservation should represent the "preservation of the full range of genetic potential in species, the species in all of its intrinsic diversity" is in no way antagonistic to the strategy of prioritization, as others have mistakenly claimed (3). Representation is about conserving everything; prioritization is about what to conserve first (4).

Third, the scale of coverage of our review was global: which regions should be the first targets for flexible resources worldwide? Woodwell concentrates his criticism on the scale of individual parks; we agree with him that this is not the only scale at which biodiversity conservation must be implemented. At the broadest, planetary scale, tackling the effects of climate change (5) will require intergovernmental policy instruments to reduce greenhouse gas emissions (6). At intermediate scales, management needs to maintain the landscape/seascape-level ecological processes on which biodiversity depends (7). However, at the finer, pragmatic level of much current conservation implementation, clear targets for safeguarding individual sites of global biodiversity significance are essential. This is the case whether the appropriate conservation tactic is the establishment or better management of protected areas, or the implementation of other site-scale efforts.

The "Key Biodiversity Areas" approach, for instance, is being used to identify sites through local and national processes and ownership, but following global standards and criteria (8). This work uses two decades of experience in 170 countries in identifying "Important Bird Areas" (9) as a foundation to incorporate newly available comprehensive data for mammals, amphibians, and other taxa (10). Major efforts are now under way through the Species Survival Commission of IUCN (the World Conservation Union) to compile equivalent data sets for reptile, plant, marine, and freshwater biodiversity [e.g., (11, 12)]. A particularly urgent subset of Key Biodiversity Areas are the 595 sites identified by the "Alliance for Zero Extinction" and endorsed by more than 60 biodiversity conservation organizations (13, 14).

We respectfully refer Woodwell to the last four paragraphs of our paper, and references therein, for further discussion of these points.

T. M. BROOKS,^{1,2,3} R. A. MITTERMEIER,¹ G. A. B. DA FONSECA,^{1,4} J. GERLACH,^{5,6} M. HOFFMANN,¹

Letters to the Editor

Letters (~300 words) discuss material published in *Science* in the previous 6 months or issues of general interest. They can be submitted through the Web (www.submit2science.org) or by regular mail (1200 New York Ave., NW, Washington, DC 20005, USA). Letters are not acknowledged upon receipt, nor are authors generally consulted before publication. Whether published in full or in part, letters are subject to editing for clarity and space.

J. F. LAMOREUX,³ C. G. MITTERMEIER,¹ J. D. PILGRIM,⁷ A. S. L. RODRIGUES⁵

¹Conservation International, Washington, DC 20036, USA. ²World Agroforestry Centre (ICRAF), University of the Philippines, Los Baños, Laguna 4031, Philippines. ³Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22904, USA. ⁴Departamento de Zoologia, Universidade Federal de Minas Gerais, Belo Horizonte, MG 31270, Brazil. ⁵Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK. ⁶Nature Protection Trust of Seychelles, Post Office Box 207, Victoria, Mahé, Seychelles. ⁷BirdLife International in Indochina, 4/209 Doi Can Street, Ba Dinh, Hanoi, Vietnam.

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TECHNICAL COMMENT ABSTRACTS

COMMENT ON "Pairing and Phase Separation in a Polarized Fermi Gas"

Martin W. Zwierlein and Wolfgang Ketterle

Partridge *et al.* (Reports, 27 January 2006, p. 503) reported pairing and phase separation in a polarized Fermi gas. We argue that it is not possible to distinguish the superfluid from the normal regimes in the presented data, or to discern which clouds were phase-separated. Some of the reported conclusions are inconsistent with recent experiments.

Full text at www.sciencemag.org/cgi/content/full/314/5796/54a

RESPONSE TO COMMENT ON "Pairing and Phase Separation in a Polarized Fermi Gas"

Guthrie B. Partridge, Wenhui Li, Ramsey I. Kamar, Yean-an Liao, Randall G. Hulet

Zwierlein and Ketterle fail to establish that trap anharmonicities or other objective mechanisms affect the conclusions of our report. Instead, they make the subjective assertion that our claims are not supported by the data. In emphasizing discrepancies between our results and theirs, they ignore potentially important differences in physical parameters. We stand by the statements and claims made in our report.

Full text at www.sciencemag.org/cgi/content/full/314/5796/54b

Post-Wildfire Logging Hinders Regeneration and Increases Fire Risk

D. C. Donato,^{1*} J. B. Fontaine,² J. L. Campbell,¹ W. D. Robinson,² J. B. Kauffman,³ B. E. Law¹

¹Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA. ²Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA. ³Institute of Pacific Islands Forestry, USDA Forest Service, Pacific Southwest Research Station, 60 Nowelo Street, Hilo, HI 96720, USA.

*To whom correspondence should be addressed. E-mail: dan.donato@oregonstate.edu

Recent increases in wildfire activity in the United States have intensified controversies surrounding the management of public forests after large fires (1). The view that postfire (salvage) logging diminishes fire risk via fuel reduction, and that forests will not adequately regenerate without intervention that includes logging and planting, is widely held and commonly cited (2, 3). An alternative view maintains that postfire logging is detrimental to long-term forest development, wildlife habitat and other ecosystem functions (1). Scientific data directly informing this debate are lacking.

Here we present data from a study of early conifer regeneration and fuel loads following the 2002 Biscuit Fire, Oregon, USA, with and without postfire logging. Because of the fire's size (~200,000 hectares), historic reforestation difficulties in the region (4), and an ambitious postfire logging proposal, the Biscuit Fire has become a national icon of postfire management issues. We used a spatially nested design of logged and unlogged plots replicated across the fire area and sampled before (2004) and after (2005) logging (5).

Natural conifer regeneration on sites that experienced high-severity fire was variable but generally abundant, with a median stocking density of 767 seedlings per hectare, primarily of Douglas-fir (*Pseudotsuga menziesii*) (Fig. 1A). Such density exceeds regional standards for fully stocked sites, suggesting that active reforestation efforts may be unnecessary. Postfire logging subsequently reduced regeneration by 71%, to 224 seedlings per hectare (Fig. 1A), due to soil disturbance and physical burial by woody material during logging operations. Thus, if postfire logging is conducted in part to facilitate reforestation, replanting could result in no net gain in early conifer establishment.

Postfire logging significantly increased both fine and coarse downed woody fuel loads (Fig. 1B). This pulse was comprised of unmerchantable material (e.g., branches), and far exceeded expectations for postfire logging-generated fuel loads (5, 6). In terms of short-term fire risk, a reburn in logged stands would likely exhibit elevated rates of fire spread, fireline intensity and soil heating impacts (7).

Postfire logging alone was notably incongruent with fuel reduction goals. Fuel reduction treatments (prescribed burning or mechanical removal) are frequently intended following postfire logging, including in the Biscuit plan, but resources are often not allocated to complete them (8). Our study underscores that, after logging, mitigation of short-term fire risk is not possible without subsequent fuel reduction treatments. However, implementing these treatments is also problematic. Mechanical removal is generally precluded by its expense, leaving prescribed burning as the most feasible method. This will result in additional seedling mortality and potentially severe soil impacts due to long duration combustion of logging-generated fuel loads. Therefore, the lowest fire risk strategy may be to leave dead trees standing as long as possible (where they are less available to surface flames), allowing for aerial decay and slow, episodic input to surface fuel loads over decades.

Our data show that postfire logging, by removing naturally seeded conifers and increasing surface fuel loads, can be counterproductive to goals of forest regeneration and fuel reduction. In addition, forest regeneration is not necessarily in crisis across all burned forest landscapes. The results presented here suggest that postfire logging may conflict with ecosystem recovery goals.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/1122855/DC1

Materials and Methods

SOM text

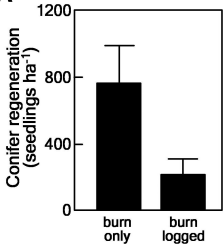
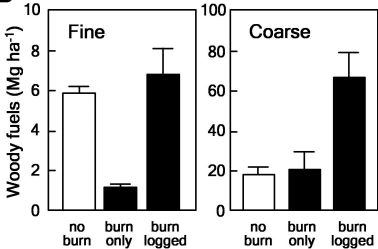
References and Notes

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Fig. 1. Natural conifer regeneration (**A**) and surface woody fuel loads (**B**) before and after postfire logging of the Biscuit Fire, Oregon, USA. (A) Regeneration was abundant following fire. Postfire logging significantly reduced seedling densities ($P < 0.01$, Wilcoxon signed rank test) from 767 seedlings ha^{-1} to 224 seedlings ha^{-1} . (B) Postfire logging significantly increased downed fine ($P < 0.01$) and coarse ($P < 0.05$) woody fuel loads (Mg ha^{-1}) relative to burn-only by Wilcoxon signed rank test. To provide context, fuel data from unburned stands are shown as reference for pre-fire conditions (fuel loads in burn-logged stands were at or well above pre-fire levels). Graphs of seedling densities and fine (≤ 7.62) and coarse (> 7.62) surface woody fuels are medians \pm SE; $n = 8$ stands for no burn, $n = 9$ for burn-only and burn-logged (5).

A**B**

Transient dynamics of invasive competition: Barred Owls, Spotted Owls, habitat, and the demons of competition present

KATIE M. DUGGER,^{1,3} ROBERT G. ANTHONY,² AND LAWRENCE S. ANDREWS²

¹Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331 USA

²Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. The recent range expansion of Barred Owls (*Strix varia*) into the Pacific Northwest, where the species now co-occurs with the endemic Northern Spotted Owl (*Strix occidentalis caurina*), resulted in a unique opportunity to investigate potential competition between two congeneric, previously allopatric species. The primary criticism of early competition research was the use of current species' distribution patterns to infer past processes; however, the recent expansion of the Barred Owl and the ability to model the processes that result in site occupancy (i.e., colonization and extinction) allowed us to address the competitive process directly rather than inferring past processes through current patterns. The purpose of our study was to determine whether Barred Owls had any negative effects on occupancy dynamics of nesting territories by Northern Spotted Owls and how these effects were influenced by habitat characteristics of Spotted Owl territories. We used single-species, multi-season occupancy models and covariates quantifying Barred Owl detections and habitat characteristics to model extinction and colonization rates of Spotted Owl pairs in southern Oregon, USA. We observed a strong, negative association between Barred Owl detections and colonization rates and a strong positive effect of Barred Owl detections on extinction rates of Spotted Owls. We observed increased extinction rates in response to decreased amounts of old forest at the territory core and higher colonization rates when old-forest habitat was less fragmented. Annual site occupancy for pairs reflected the strong effects of Barred Owls on occupancy dynamics with much lower occupancy rates predicted for territories where Barred Owls were detected. The strong Barred Owl and habitat effects on occupancy dynamics of Spotted Owls provided evidence of interference competition between the species. These effects increase the importance of conserving large amounts of contiguous, old-forest habitat to maintain Northern Spotted Owls in the landscape.

Key words: Barred Owl; colonization; competition; extinction; habitat characteristics; Northern Spotted Owl; occupancy modeling; old forest; Southern Cascades, Oregon, USA; *Strix occidentalis caurina*; *Strix varia*.

INTRODUCTION

The Northern Spotted Owl (*Strix occidentalis caurina*) was listed federally as threatened by the U.S. Fish and Wildlife Service in 1990, and that status was upheld again during a status review in 2004 (USFWS 2004). The original listing of this species was based on the owl's strong association with old conifer forest and declining trends in both old-forest habitat and owl populations (USDOI 1990). More recently, the Barred Owl (*Strix varia*), another medium-sized owl species, has expanded its range in the Pacific Northwest and has come in contact with the endemic Northern Spotted Owl (Kelly et al. 2003, Livezey 2009). The encroachment of the Barred Owl into what was historically Spotted Owl habitat is expected to pose an additional and competi-

tive threat to Spotted Owl persistence. Compared to the Spotted Owl, the Barred Owl is a larger (Hamer et al. 1994), more aggressive species (Gutiérrez et al. 2007) that uses a broad range of forested habitats, including those used by Spotted Owls (Hamer et al. 2007, Singleton et al. 2010). The Barred Owl also has a more generalist diet (review in Gutiérrez et al. 2007) and smaller home ranges, so it occurs in the landscape at higher densities than Spotted Owls in some areas (3–8 Barred Owl territories per Spotted Owl; Hamer et al. 2007, Singleton et al. 2010).

Historical studies of interspecific competition have, by necessity, been based on patterns of species distributions and abundance (Diamond 1975), with these patterns presented as evidence for the competition process because the process itself could not be tested directly without experimental removal of one species. Unfortunately, pattern does not necessarily reflect process, so quantifying the effect of competition on species distributions has been difficult and historical attempts have been strongly criticized (e.g., Connor and

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³ E-mail: katie.dugger@oregonstate.edu

Simberloff 1979). Currently, little data exists regarding the direct impact of Barred Owls on demography of Spotted Owls, but the use of recently developed occupancy models for Spotted Owls suggest Barred Owls have a negative impact on detection probabilities and colonization rates and increase extinction probabilities on Northern Spotted Owl territories (Olson et al. 2005). By investigating the effects of Barred Owl detections on Spotted Owl colonization and extinction rates on Spotted Owl territories over several years where Barred Owls increased in abundance, we had the rare opportunity to investigate the potential processes associated with interspecific competition rather than inferring a past competitive process from current patterns (i.e., the “ghost of competition past”; Connell 1980). Because Spotted Owls are habitat specialists associated with old conifer forests (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), we also wanted to investigate the combined effects of Barred Owls and vegetative characteristics around nesting territories on occupancy dynamics of territories.

Because of habitat declines, relationships between demographic parameters of Northern Spotted Owls and forest habitat characteristics have been the primary focus of recent modeling efforts (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). These published studies suggested some unifying relationships between territory quality and owl demographics, particularly the importance of old forests for higher reproduction and survival (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), but there is a lot of variation in the magnitude of the effects of habitat on demography, and these relationships have not been observed for some areas (K. M. Dugger and R. G. Anthony, *unpublished data*). Implicit in the interpretation of these studies is the assumption that Spotted Owls chose high-quality habitat to improve fitness (Fretwell and Lucas 1970), but that may not always be the case, particularly in the face of deleterious or novel habitat alterations that may not be recognized by the birds (Lloyd and Martin 2005, Shochat et al. 2005). In other words, if external factors, such as competition with Barred Owls, are affecting the quality of Spotted Owl habitat, then relationships between habitat structure and fitness may be decoupled. When habitat selection becomes decoupled from habitat quality, then negative effects on fitness and population dynamics can result in ecological traps (Dwernychuk and Boag 1972, Schlaepfer et al. 2002, Kristan 2003). This may explain why populations of Northern Spotted Owls continue to decline in some areas (Anthony et al. 2006, Forsman et al. 2011), even though large amounts of old forest have been protected throughout the subspecies’ range (FEMAT 1993).

Hypotheses regarding the effect of Barred Owls on the habitat selection of Northern Spotted Owls can also be framed in a classic meta-population context where local populations have a substantial probability of extinction and the long-term persistence of a meta-population can

only occur at a regional scale by the balance of local extinction and colonization rates (Levins 1969). This classic meta-population model was extended and generalized by Lande (1987) for application to territorial species like the Northern Spotted Owl. By identifying a unit of suitable habitat for individual territories, Lande (1987) established a correspondence between local extinction and the death of individuals inhabiting a territory, and colonization by recruitment and dispersal of individuals into a territory. Most recently, this model has been applied to territorial occupancy of two potentially competing raptor species in relation to habitat availability (Carrete et al. 2005). Their results and the models of Levins and Culver (1971) and Horn and MacArthur (1972) imply that conservation measures for two competing species should require an increase in the amount of suitable habitat in the landscape.

Herein, we describe the relationship between the occupancy dynamics of Spotted Owls in relation to a potential competitor, the Barred Owl, and forest habitat characteristics for a population in the Southern Cascades of Oregon, USA. A natural experiment in the form of dramatic increases in Barred Owl density within the range of the Northern Spotted Owl during the last 10–15 years (see Forsman et al. 2011) has allowed us to investigate the effects of Barred Owl presence on Northern Spotted Owl territory occupancy. The purpose of our study was to investigate (1) the potential competitive effects of Barred Owls on Northern Spotted Owls by determining whether there was a negative relationship between Barred Owl detections and occupancy of breeding territories by Spotted Owls, and (2) the possibility of a synergistic relationship between Barred Owls and the amount of suitable habitat on occupancy dynamics of Northern Spotted Owls. We predicted that, independent of habitat characteristics, Barred Owl detections would increase extinction rates and decrease colonization rates of Spotted Owl territories, thereby decreasing rates of site occupancy. We also predicted an additive effect between Barred Owl detections and habitat characteristics, with higher extinction rates and lower colonization rates expected even when Barred Owls were detected depending on the proportion of older forest and/or fragmentation of older forest surrounding Spotted Owl territories.

STUDY AREA

The Southern Cascades Study Area is one of eight study areas throughout the Northern Spotted Owls’ range where data is collected annually on marked individuals to determine survival and productivity as part of the Effectiveness Monitoring Program (Lint et al. 1999) associated with the Northwest Forest Plan (for recent demographic reviews see Anthony et al. 2006, Forsman et al. 2011). This study area was chosen for this analysis because we also had a reliable and accurate map of vegetation characteristics associated with owl territo-

ries on this area, so we were able to investigate associations between occupancy dynamics and both Barred Owl detections and habitat characteristics. The study area is geographically situated on federal lands within the southern terminus of the Oregon Cascades in parts of Douglas, Jackson, and Klamath counties. The climate was characterized by warm summers and cool winters (Baldwin 1973). Annual precipitation occurred mainly during the winter and spring, with summers being characteristically hot and dry. Much of the precipitation at mid to high elevations was in the form of snowfall and a persistent snow cover often extended into late spring. Owl territories were located at elevations ranging from 900 m to 2000 m.

Vegetation primarily reflects five vegetation zones including *Pinus ponderosa*, mixed conifer, *Abies concolor*, *Abies magnifica* var *shastensis*, and *Tsuga mertensiana* from lowest to highest elevation, respectively (Franklin and Dyrness 1973). The study area was ~2230 km² in size, and >60% of the landscape was covered by mature (80–200 years) or old-growth (>200 years) forest (Anthony et al. 2006).

METHODS

We collected and quantified data to test our predictions with models of occupancy, extinction, and colonization following MacKenzie et al. (2003) and Olson et al. (2005). This included Barred Owl occurrence and habitat characteristics as model covariates. The sampling units for occupancy modeling were individual Spotted Owl territories as delineated by areas with known nesting and roosting activity at any time during the study.

Survey data

Data were collected annually from 1991 to 2006 on marked owls within the Southern Cascades Study Area following a standard protocol used by researchers across the owl's range to estimate survival and productivity (Franklin et al. 1996, Lint et al. 1999). The general field methods for locating and banding of owls, determining sex and age, re-sighting previously marked owls, and determining productivity were described by Franklin et al. (1996), and adaptation of this data for occupancy analysis was described by Olson et al. (2005). Although these survey methods were designed to document survival and productivity, they also were well suited for determining occupancy rates (Olson et al. 2005, Kroll et al. 2010).

Each year, we used multiple vocal lure surveys (maximum = 7–9 per year) with Spotted Owl calls to systematically search sites for territorial owls in areas where Spotted Owl use was documented at any time during the study. Boundaries with calling points for surveys associated with each site were established a priori each year and conformed in general to the median home range size of Spotted Owls in southern Oregon. From these multiple surveys within a year we developed

detection histories for each visit to each site, and from this detection/nondetection data across multiple seasons we could estimate occupancy dynamics (MacKenzie et al. 2006). The variation in number of yearly visits corresponded to occupancy rates (i.e., fewer visits were made to sites where owls were detected), variation in nesting phenology, and nest success. However, unequal sampling effort across sites within seasons and the rare occasion when a site was not surveyed at all in a particular year (i.e., primarily due to access), can be accommodated with these open occupancy models as long as we assume occupancy dynamics are the same at sites that are and are not surveyed each year (MacKenzie et al. 2006).

We investigated pair occupancy because breeding pairs are the true ecological unit of interest and the basis for viable, breeding populations. Thus, the data set we analyzed here represents the detection of confirmed owl pairs only (Olson et al. 2005). There were 103 territories surveyed for owls and included in this occupancy analysis for the Southern Cascades Study Area between 1991 and 2006.

A Barred Owl covariate was developed to model the effect of Barred Owl presence on site occupancy dynamics. Following Olson et al. (2005), a year-specific binary covariate was coded as “1” if a Barred Owl was detected on the site during any of the surveys and “0” if not detected. This Barred Owl covariate was both year- and site-specific (Olson et al. 2005), which is an improvement over previous measures of Barred Owl occurrence used in demographic modeling (Anthony et al. 2006). Both extinction (epsilon, ϵ) and colonization probabilities (gamma, γ) (MacKenzie et al. 2003) are interval estimates encompassing the interval from time i to time $i + 1$, so there are two potential time periods at which Barred Owls might be detected (time i and time $i + 1$), which could affect extinction and colonization rates. In order to address this issue we investigated the relationship between Barred Owl presence at time i (BO) and at time $i + 1$ (BO1) in relation to extinction and colonization probabilities (Olson et al. 2005).

Data on vegetative characteristics were collected from the specific sites occupied by territorial Northern Spotted Owls within the study area, following the general approach used by Franklin et al. (2000), Olson et al. (2004), and Dugger et al. (2005) to link habitat characteristics to Spotted Owl demography. We used 730 m and 2230 m radius circles (167 ha and 1565 ha, respectively) centered on nest sites or primary roost areas (site centers) to represent the core use area and home range of owls, respectively. These areas represent the mean 50% and 95% adaptive kernel utilization distributions, respectively, for estimating home range size (Whorton 1989) as determined from analysis of movement data from a nearby area (Wagner and Anthony 1999). If a different nest tree was used in subsequent years, a new site center was established. If the owls were confirmed to be non-nesting, the site

center for that year was assigned to the previous historic nest location. Habitat attributes for sites with multiple centers were calculated as a weighted mean based on the number of years that a specific center was used. We also characterized vegetation in the 1388 ha area within the home range that was not included within the core area (home range – core = ring).

We identified three general vegetation types of interest: older forest, intermediate-aged forest and non-habitat (Appendix A). Older and intermediate-aged forest represented suitable owl habitat and were broadly classified, corresponding to stages of general forest stand development within the study area. Cover types that received essentially no use by radio-marked owls in a previous study (Wagner and Anthony 1999) and included non-forest, early seres, sapling, and moderate and heavy partial cuts, were combined into a single category called “non-habitat” (Appendix A).

Vegetation within the circles was classified by interpretation of stereo pairs of 1996 color aerial photography (1:12 000) and ground reconnaissance. Classified habitats were mapped onto USGS orthophotoquads, which were subsequently digitized and converted to ArcInfo (ESRI 1991) format. Digitized maps were used to tabulate habitat composition as a proportion of the 167-ha and 1565-ha circular areas. Digitized maps were buffered and converted from vector to grid coverage. Landscape pattern (i.e., fragmentation) indices were estimated from the 1565-ha circular areas with program FRAGSTATS (Appendix A; McGarigal and Marks 1995). General classes of habitat used in generating landscape indices were limited to older forest, and we investigated the five pattern variables that most closely reflected the amount of edge and fragmentation within an owl territory (Appendix A).

Model development

We modeled site occupancy using models developed by MacKenzie et al. (2003) for open populations. We estimated site occupancy for the first primary sampling period (ψ_1), extinction probability (ϵ), and colonization probability (γ) for primary sampling periods, and detection probability (p_{ij}) given presence in survey j (secondary samples within seasons) within primary sampling period i (MacKenzie et al. 2003). All models were generated and occupancy parameters estimated using Program MARK (White and Burnham 1999). Extinction and colonization probabilities were developed for intervals between year i and year $i + 1$, and they are conditional on status at year i (time prior to each time interval) (MacKenzie et al. 2003). Because we had a large number of habitat covariates to consider on extinction and colonization parameters, we chose to use a multi-stage approach to build models, which was similar to the approach of Olson et al. (2005). We used an information theoretic approach (Burnham and Anderson 2002) to select the best and competing models at each stage. We also calculated year-specific site

occupancy probabilities using the equation from MacKenzie et al. (2003):

$$\hat{\psi}_i = \hat{\psi}_{i-1}(1 - \hat{\epsilon}_{i-1}) + (1 - \hat{\psi}_{i-1})\hat{\gamma}_{i-1}.$$

First, we modeled detection probabilities by investigating time trends including linear (T), pseudo-threshold ($\ln T$), and quadratic (TT) trends, as well as general time-specific effects (t) on between and within year detection probabilities, and the annual presence of Barred Owls (BO , $BO1$). The best detection probability model was retained and used for the rest of the modeling. During the second stage of modeling we investigated time-specific (t) and time trend (T , $\ln T$, TT) models on extinction and colonization probabilities. Finally, Barred Owl covariates were then added to the best time-specific models, and the best model structure for time and Barred Owl effects were used to model the effects of habitat on extinction and colonization rates. A candidate model set for the habitat covariates that described predicted relationships between the habitat variables and occupancy parameters were developed from a set of a priori predictions regarding the direction of effects (Appendix A).

Other studies found relationships between owl demographic parameters and habitat variables that were not linear (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). However, we could not envision a quadratic relationship between extinction and colonization probabilities and habitat characteristics, so our models included only two structural forms (linear and pseudo-threshold) of the habitat covariates.

Model selection

We used information theoretic approaches as detailed by Burnham and Anderson (2002) to select the best models at each step. We used the corrected version of Akaike's information criterion (AIC_c) for small sample sizes and Akaike weights to rank models (Burnham and Anderson 2002:66, 75–79). The degree to which 95% confidence intervals for slope coefficients (β_i) overlapped zero was also used to evaluate the strength of evidence for the importance of variables in competing models ($<2 AIC_c$ values). During modeling we generally selected the model with the lowest AIC_c value as our “best” model unless confidence intervals on slope coefficients suggested there was more support for a closely competing model (within one AIC_c unit of the best model). For habitat modeling, we reduced the total model list by ranking all the models by AIC_c , and then retained only the “best” scale and structure for each variable. We did this to reduce the number of competitive models and redundancy that often resulted when scales and structures for individual covariates were correlated.

RESULTS

Pair occupancy data from the visit histories included a total of 125 secondary sampling periods across all years

and sites during 1991–2006 (16 primary sampling periods). Barred Owls were detected on <5% of the Spotted Owl territories until 1999, when the proportion of territories affected by Barred Owls doubled. Since that time, the proportion of Spotted Owl territories where Barred Owls were detected increased steadily and reached a high of 30% in 2006 (Fig. 1). This increase in Barred Owls provided for a natural experiment by which we were able to investigate the effects on Spotted Owls.

Detection probabilities

We found a time trend on detection probabilities within years for Spotted Owl pairs (Appendix B). The trend within years exhibited a pseudo-threshold structure (lnT), but the direction of the trend on detection probabilities varied between years (Appendix B: Fig. B1). During most of the study, detection probabilities of Spotted Owls decreased and then stabilized throughout the season, but during the later part of this study detection probabilities exhibited a positive pseudo-threshold pattern, with owl detectability increasing, and then stabilizing as the season progressed (Appendix B: Fig. B1).

Detection probabilities between years were modeled to investigate time effects in addition to the effects of Barred Owls. The best model describing detection probabilities included an interaction between the effect of Barred Owls and time ($t \times \text{BO}$; Appendix B: Fig. B1). Excluding the earliest years of this study, detection probabilities <0.20 for pairs were typical when Barred Owls were detected, compared to substantially higher rates (>0.50) when Barred Owls were not detected. This structure including an interaction between time and a Barred Owl effect between years was retained for further modeling along with the pseudo-threshold affect on within season detection probabilities ($p(t \times \text{BO}, \text{lnT})$).

Occupancy parameters

Barred Owl and time effects.—We found strong support for an association between the detection of Barred Owls and extinction and colonization rates of Spotted Owl pairs (Table 1). The detection of Barred Owls in year i was associated with increased extinction rates ($\hat{\beta} = 1.39 \pm 0.34$ [mean \pm SE], 95% CI = 0.67 to 2.11) and decreased colonization rates ($\hat{\beta} = -2.55 \pm 0.72$, 95% CI = -3.95 to -1.14) in year $i + 1$ as predicted. Our best model had strong support as it accounted for most of the AIC weight ($w_i = 0.99$); it also included general time variation (t) on extinction probabilities (Table 1).

Habitat characteristics.—The amount of old forest at the core of home ranges (cOF) most strongly influenced extinction rates for Spotted Owl pairs (Table 2). This was a strong effect, as all the top 10 models contained this effect on extinction probabilities (Table 2). As predicted, extinction rates increased with decreased amounts of old forest at the core ($\hat{\beta} = -0.01 \pm 0.003$, 95% CI = -0.02 to -0.01), and this effect was 2–3 times greater when Barred Owls were detected (Fig. 2).

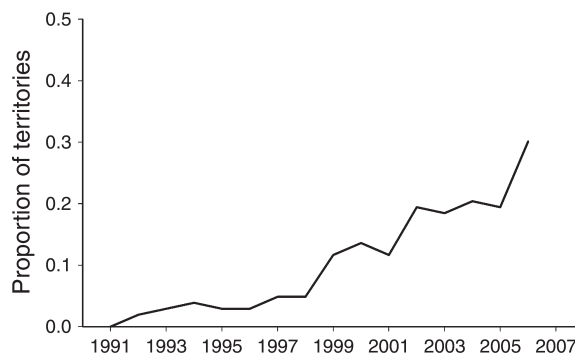


FIG. 1. Annual proportion of Northern Spotted Owl (*Strix occidentalis caurina*) territories with Barred Owl (*Strix varia*) detections (BO covariate) in this study in southern Oregon, USA, 1991–2006.

The strongest effect on colonization rate for pairs was Barred Owls and the \log_e structure of the mean nearest-neighbor distances of old-forest patches ($\text{BO} + \text{ln_MNNof}$; Table 2). The 95% confidence intervals for the habitat effect overlapped zero only slightly ($\hat{\beta} = -0.24 \pm 0.12$, 95% CI = -0.48 to 0.01), and the direction of the relationship was negative as predicted (Fig. 3). In addition, the detection of Barred Owls decreased (additive effect) the probability of colonization of vacated nesting territories as the nearest-neighbor distance between old-forest patches increased (Fig. 3). This model had an AIC weight of 0.63 and was ~ 2.5 times more likely than the second model. The second competitive model (<2 AIC_c) included an interaction between the Barred Owl effect and the distance between old-forest patches, with a stronger effect of habitat on colonization rates when Barred Owls are not present (Table 2).

Mean annual site occupancy was generally high and more variable when Barred Owls were not detected near breeding territories (Fig. 4). In contrast, we observed greatly decreased annual site occupancy rates when Barred Owls were detected, and occupancy rates were consistently low in the latter years of the study when Barred Owls were frequently detected (Fig. 4).

DISCUSSION

The strong effect of Barred Owls on the site occupancy dynamics of Northern Spotted Owls we observed in this study support the hypothesis that these two species are competitors and that the Barred Owl is currently displacing Spotted Owls from historical breeding territories. This was a retrospective study that did not include an experimental control, but rather took advantage of a natural experiment that is ongoing as Barred Owl densities increased over time within the range of the Spotted Owl. Our results indicated a negative effect of Barred Owls on the Northern Spotted Owl and evidence that competition is currently occurring between these two species.

TABLE 1. Model selection results for the 10 best models relating time and Barred Owl (*Strix varia*) covariates to extinction (ϵ) and colonization (γ) probabilities of Northern Spotted Owl (*Strix occidentalis caurina*) pairs on territories in southern Oregon, USA (1991–2006).

Model	$\Delta\text{AIC}_c^\dagger$	K	w	Deviance
$\epsilon(t + \text{BO}) \gamma(\text{BO})$	0.00	67	0.99	7811.91
$\epsilon(t) \gamma(\text{BO})$	9.98	66	0.01	7824.07
$\epsilon(t) \gamma(\ln T + \text{BO})$	12.08	67	0.00	7823.99
$\epsilon(t) \gamma(T + \text{BO})$	12.15	67	0.00	7824.06
$\epsilon(t + \text{BO}) \gamma(\cdot)$	22.31	66	0.00	7836.40
$\epsilon(t + \text{BO}) \gamma(\ln T)$	23.53	67	0.00	7835.44
$\epsilon(t + \text{BO}) \gamma(T)$	24.17	67	0.00	7836.08
$\epsilon(t) \gamma(\text{BO1})$	26.72	66	0.00	7840.82
$\epsilon(t) \gamma(\ln T + \text{BO1})$	28.47	67	0.00	7840.38
$\epsilon(t) \gamma(T + \text{BO1})$	28.81	67	0.00	7840.72
$\epsilon(t) \gamma(t)$	56.91	79	0.00	7842.41

Notes: Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c). The model deviance, number of parameters (K), ΔAIC_c , and AIC_c weights (w) are given for all models. General time effects (t), a linear time trend (T), a pseudo-threshold time trend ($\ln T$), a quadratic time trend (TT), and a Barred Owl effect (Barred Owl presence at time i [BO] and at time $i + 1$ [BO1]) were added to a base model that included no effect on $\psi(\cdot)$ and the best detection probability structure [$p(t \times \text{BO}, \ln T)$]. Plus signs denote additive effects, and \times 's denote interactions. The base model with time dependence on ϵ and γ is also included for comparison.

† Lowest $\text{AIC}_c = 7961.93$.

Our findings are consistent with, but even stronger than, those reported for Spotted Owl pairs by Olson et al. (2005), who found colonization rates affected by Barred Owl presence for one study area and extinction rates affected on the remaining two. This previous research reported on the effects of time and Barred Owl detections (Olson et al. 2005) on site occupancy dynamics in Oregon. In California, researchers investigated Spotted Owl occupancy in relation to changes in habitat (Seamans and Gutiérrez 2007); however, our study represents the first attempt to describe the

synergistic effects of Barred Owls and habitat characteristics of territories on extinction and colonization rates of Northern Spotted Owls.

We observed additive effects of both Barred Owls and habitat characteristics around nesting centers on extinction and colonization of breeding territories by Spotted Owls. The extinction probability of pairs from territories varied from 0.11 to 0.23 when Barred Owls were not detected, but then nearly tripled to 0.33–0.54 when Barred Owls were detected. Conversely, the probability of colonization of vacant territories by pairs varied from

TABLE 2. Model selection results for the 10 best models relating habitat characteristics to extinction (ϵ) and colonization (γ) probabilities of Northern Spotted Owl pairs on territories in southern Oregon (1991–2006).

Model	$\Delta\text{AIC}_c^\dagger$	K	w	Deviance
$\psi(\cdot) \epsilon(t + \text{BO} + \text{cOF}) \gamma(\text{BO} + \ln_MNNof)$	0.00	69	0.63	7794.67
$\psi(\cdot) \epsilon(t + \text{BO} + \text{cOF}) \gamma(\text{BO} \times \ln_MNNof)$	1.90	70	0.24	7794.40
$\psi(\cdot) \epsilon(t + \text{BO} \times \text{cOF}) \gamma(\text{BO} \times \ln_MNNof)$	3.50	71	0.11	7793.81
$\psi(\cdot) \epsilon(t + \text{BO}) \gamma(\text{BO} + \ln_MNNof)$	9.52	68	0.01	7806.39
$\psi(\cdot) \epsilon(t + \text{cOF}) \gamma(\text{BO} + \ln_MNNof)$	11.11	68	0.00	7807.99
$\psi(\cdot) \epsilon(t + \text{BO}) \gamma(\text{BO} \times \ln_MNNof)$	11.58	69	0.00	7806.26
$\psi(\cdot) \epsilon(t + \text{cOF}) \gamma(\text{BO} + \text{rOF})$	12.50	68	0.00	7809.38
$\psi(\cdot) \epsilon(t + \text{cOF}) \gamma(\text{BO} + \text{rNON})$	12.55	68	0.00	7809.42
$\psi(\cdot) \epsilon(t + \text{cOF}) \gamma(\text{BO} + \text{rGF})$	12.57	68	0.00	7809.45
$\psi(\cdot) \epsilon(t + \text{BO}) \gamma(\text{BO})$	12.85	67	0.00	7811.91
$\psi(\cdot) \epsilon(t + \text{cOF}) \gamma(\text{BO})$	13.07	67	0.00	7812.13

Notes: Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c). The model deviance, number of parameters (K), ΔAIC_c , and AIC_c weights (w) are given for all models. Habitat characteristics were added to a base model (included for comparison) containing a Barred Owl (BO) and general time effect (t) on extinction rates, a Barred Owl effect on colonization rates, Barred Owl and general time interaction on between-year detection probabilities and pseudo-threshold trends on within-year detection probabilities [$\psi(\cdot) \epsilon(t + \text{BO}) \gamma(\text{BO}) p(t \times \text{BO}, \ln T)$]. These 10 highest ranking models included the following habitat covariates: the pseudo-threshold structure of mean nearest-neighbor distance between old forest patches (\ln_MNNof), the amount of old forest at the ring scale (rOF ; ring = home range scale – core), the amount of non-habitat at the ring scale (rNON), and the amount of general forest at the ring scale (rGF). Plus signs denote additive effects, and \times 's denote interactions.

† Lowest $\text{AIC}_c = 7939.10$.

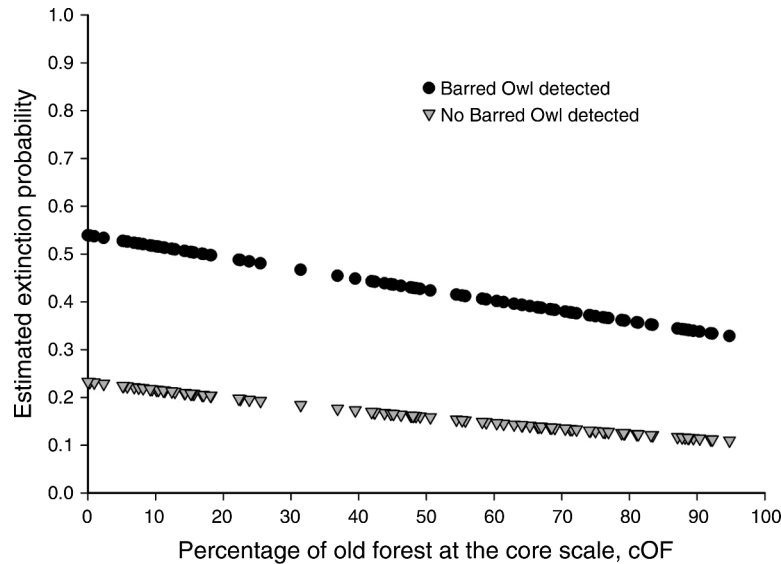


FIG. 2. Mean extinction probability (ϵ) from 1991 to 2005 for Northern Spotted Owl territories when Barred Owls were detected and not detected plotted against the percentage of old forest at the core scale (cOF). Estimates were generated from the best model [$\psi(\cdot) \epsilon(t + BO + \ln_cOF) \gamma(BO + \ln_MNNof) p(t \times BO, \ln T)$]. The best model included the following: no effects (\cdot) on initial site occupancy (ψ); general time effects (t) plus additive effects of Barred Owls and the pseudo-threshold effect of old forest at the core (\ln_cOF) on extinction rates (ϵ); the additive effects of Barred Owls and the pseudo-threshold structure of the mean nearest-neighbor distance between old forest patches (\ln_MNNof) on colonization rates (γ); a pseudo-threshold trend within seasons ($\ln T$) and an interaction between Barred Owl effects and time (t) across seasons on detection rates (p). The core use area was represented as a 167-ha circle centered on the nest site or primary roost area (site center) of each pair.

approximately 0.33 to 0.73, depending on habitat characteristics when Barred Owls were not detected, but this probability was much lower (0.03–0.20) when Barred Owls were detected. Extinction probabilities for pairs decreased as the amount of old-forest habitat (cOF) near the nest site increased. In addition, colonization probabilities were highest when the nearest-

neighbor distance between old-forest patches (\ln_MNNof) was the lowest, which corresponds to lower fragmentation of older forest.

Thus, colonization rates for Spotted Owl pairs were higher on territories with old-forest patches that were closer together, indicating owls reoccupied territories at a higher rate when there was less fragmented amounts of

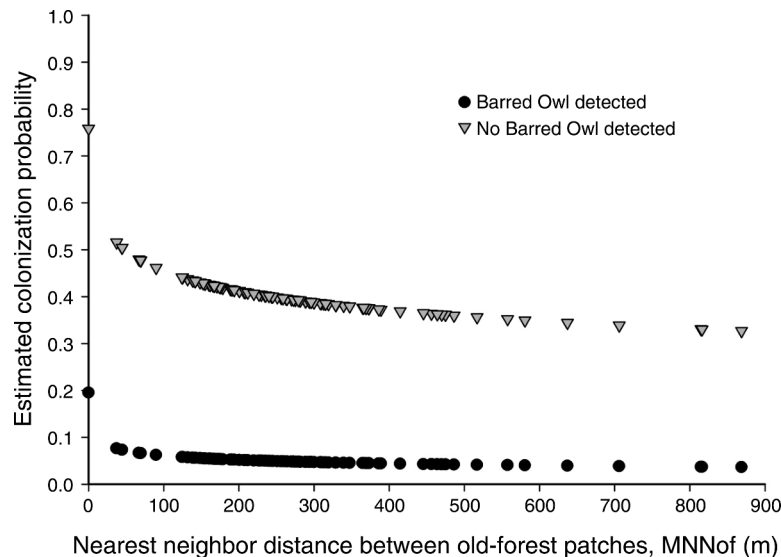


FIG. 3. Estimated colonization probabilities (γ) from 1991 to 2005 for Northern Spotted Owl territories when Barred Owls were detected and not detected plotted against the mean nearest-neighbor distances between old-forest patches (MNNof). Estimates were generated from the best model [$\psi(\cdot) \epsilon(t + BO + \ln_cOF) \gamma(BO + \ln_MNNof) p(t \times BO, \ln T)$]. See Fig. 2 for abbreviations.

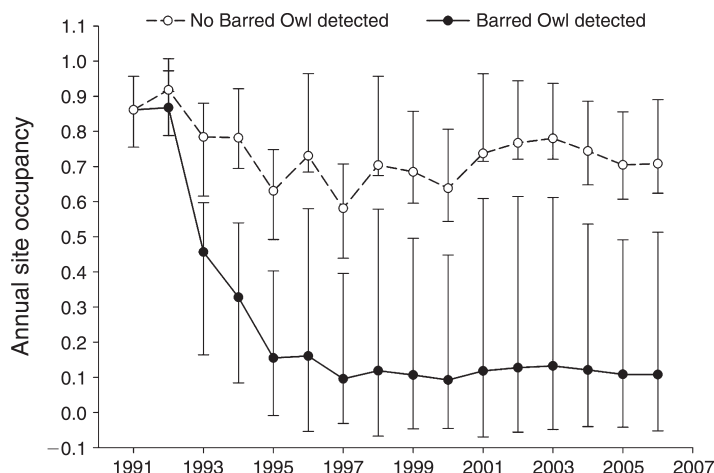


FIG. 4. Estimates of mean annual site occupancy generated across all Northern Spotted Owl territories from 1991 to 2006. Estimates incorporate each combination of territory-specific habitat characteristics and whether Barred Owls were detected or not detected, using initial occupancy, extinction, and colonization parameters from the best model [$\psi(\cdot) \varepsilon(t + \text{BO} + \ln_{\text{cOF}}) \gamma(\text{BO} + \ln_{\text{MNNof}}) p(t \times \text{BO}, \ln T)$]. See Fig. 2 for abbreviations.

old forest at the home range scale. In essence, our results suggest that a balance between extinction and colonization of territories by Spotted Owls (i.e., population stability) will likely be possible only when the amount of old forest in the core (<730 m radius from nest center) is maximized and the amount of fragmentation of this old forest within the home range (<2230 m radius of nest center) is minimized.

These results are consistent with previous demographic models for Spotted Owls in southern Oregon that identified the importance of old forest at the core of their home range on reproduction (Dugger et al. 2005) and survival (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). Old forest at the territory core is necessary for suitable nest sites (Swindle et al. 1999) and to provide prey resources for raising young close to the nest. Our results are also consistent with those reported by Seamans and Gutiérrez (2007) in California, who observed higher colonization and lower extinction rates for female California Spotted Owls on territories with more mature conifer forest.

We did investigate interactions between the best habitat covariates and Barred Owl detections on colonization and extinction rates and found some support for an interaction between Barred Owl detections and the \log_e mean nearest-neighbor distances between old-forest patches (\ln_{MNNof}) on colonization. Thus, the negative effects of forest fragmentation on colonization rates were weaker when Barred Owls were not detected, but less fragmentation did not decrease the effect of Barred Owls, possibly because high-quality, unfragmented Spotted Owl habitat on our study area is also suitable for Barred Owls.

We believe that the interactions between the species is a form of interference competition whereby Spotted Owls are driven from and excluded from their breeding territories by the larger (Hamer et al. 1994) and more aggressive Barred Owl (Gutiérrez et al. 2007). Northern Spotted Owls are food specialists, which prey on medium-sized arboreal mammals (Forsman et al. 2001,

2004), whereas Barred Owls eat a broader range of prey items (Hamer et al. 2001), which is likely the reason Barred Owl home ranges are 3–8 times smaller than those of Spotted Owls (Hamer et al. 2007, Singleton et al. 2010).

The extension by Carrete et al. (2005) of Lande's (1987) territory occupancy model to include two competing species suggests that, in order for both species to persist, there must be exclusively suitable habitat for both species (i.e., areas only used by one of the two species). There is currently little evidence suggesting that suitable Spotted Owl habitat is not also used by Barred Owls (i.e., suitable habitat exclusive to Spotted Owls is very low; Gutiérrez et al. 2007). Conversely, Barred Owls have been documented using a wider range of forest types (younger seral stages with more fragmentation) than Spotted Owls (Kelly et al. 2003, Hamer et al. 2007). Consequently, the loss of late-successional old-growth forest and increased fragmentation of these forests will decrease the amount of suitable habitat for Spotted Owls. The fact that we had no strong support for interactions between Barred Owls and habitat characteristics supports the conclusion that on our study area, exclusive suitable Spotted Owl habitat may not exist, as the degree of fragmentation and amount of old forest at the core did not ameliorate the effects of Barred Owls when they were detected. However, Barred Owls were never detected during the course of this study on 53% of the territories surveyed, so less than half the study area was impacted by Barred Owls. In addition, some Spotted Owl pairs retained their territories and continued to survive and successfully reproduce during our study even on territories where Barred Owls were detected. Thus, there may be refugia where Spotted Owls will be able to coexist with Barred Owls, but much more information is needed on the degree to which these species partition specific resources (exploitive competition) within the habitats used by both species.

In summary, we found that occupancy rates for Northern Spotted Owls were related to the amount and degree of fragmentation of older forest; occupancy increased when the proportion of old forest increased and/or the degree of fragmentation was decreased. In addition, occupancy rates decreased when Barred Owls were detected regardless of the habitat configuration of a territory. Extinction of Spotted Owl territories was lowest in areas where old forests were most abundant, and colonization was highest in less-fragmented forests. The presence of Barred Owls in Spotted Owl territories influenced these relationships, so it's vitally important to consider the effect of Barred Owls when trying to understand the relationship between habitat use/selection and occupancy of Spotted Owls. The number of Spotted Owl territories where Barred Owls are detected each year continues to increase on our study area (Fig. 1), so it's clear the two species have not yet reached equilibrium, and the habitat relationships we observed may change as Barred Owl densities continue to increase.

Finally, our results support those of Carrete et al. (2005), who recommended an increase in suitable habitat for two potentially competing raptors, the Golden Eagle (*Aquila chrysaetos*) and Bonelli's Eagle (*Hieraaetus fasciatus*) in southern Spain. Thus, increased habitat protection for Spotted Owls may be necessary to provide for sustainable populations in the presence of Barred Owls, and it is obvious from our results that these two additive stressors on Spotted Owl populations cannot be decoupled in any conservation efforts. Experimental removal of Barred Owls from Spotted Owl territories will be important to fully understand the effect of Barred Owls on the demography of Northern Spotted Owls (Buchanan et al. 2007) and the potential for interference and/or exploitive competition between the species. The final recovery plan for Spotted Owls (USFWS 2008) recommends these kinds of experiments to understand this relationship more completely, and we support such recommendations.

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APPENDIX A

Acronyms, brief descriptions, and direction of predicted effects of habitat and landscape variables used to model site occupancy dynamics including initial occupancy, extinction, and colonization probabilities of Northern Spotted Owls in southern Oregon, USA, 1991–2006 (*Ecological Archives* A021-108-A1).

APPENDIX B

Model selection results for the 10 best models relating time and Barred Owl covariates to between- and within-year detection probabilities of Northern Spotted Owl pairs on territories in southern Oregon, USA, 1991–2006 (*Ecological Archives* A021-108-A2).

Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities

Kostadin B. Georgiev^{1,2}  | Anne Chao³  | Jorge Castro⁴ | Yan-Han Chen³ | Chang-Yong Choi⁵ | Joseph B. Fontaine⁶ | Richard L. Hutto⁷ | Eun-Jae Lee⁸ | Jörg Müller^{1,2}  | Josep Rost⁹ | Michal Žmihorski¹⁰ | Simon Thorn¹ 

¹Field Station Fabriksschleichach, Biocenter, University of Würzburg, Rahenebrach, Germany; ²Bavarian Forest National Park, Grafenau, Germany; ³Institute of Statistics, National Tsing Hua University, Hsin-Chu, Taiwan; ⁴Department of Ecology, University of Granada, Granada, Spain; ⁵Research Institute of Agriculture and Life Sciences, Seoul National University, Seoul, Korea; ⁶Environmental and Conservation Sciences, Murdoch University, Murdoch, WA, Australia; ⁷Division of Biological Sciences, University of Montana, Missoula, MT, USA; ⁸Urban Planning Research Group, Daejeon Sejong Research Institute, Daejeon, Korea; ⁹Department of Environmental Sciences and Food Industries, University of Vic-Central University of Catalonia, Catalonia, Spain and ¹⁰Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland

Correspondence

Kostadin B. Georgiev

Email: kostadin.georgiev@posteo.de

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Abstract

1. Salvage logging following natural disturbances may alter the natural successional trajectories of biological communities by affecting the occurrences of species, functional groups and evolutionary lineages. However, few studies have examined whether dissimilarities between bird communities of salvaged and unsalvaged forests are more pronounced for rare species, functional groups and evolutionary lineages than for their more common counterparts.
2. We compiled data on breeding bird assemblages from nine study areas in North America, Europe and Asia, covering a 17-year period following wildfire or windstorm disturbances and subsequent salvage logging. We tested whether dissimilarities based on non-shared species, functional groups and evolutionary lineages (a) decreased or increased over time and (b) the responses of rare, common and dominant species varied, by using a unified statistical framework based on Hill numbers and null models.
3. We found that dissimilarities between bird communities caused by salvage logging persisted over time for rare, common and dominant species, evolutionary lineages and for rare functional groups. Dissimilarities of common and dominant functional groups increased 14 years post disturbance.
4. Salvage logging led to significantly larger dissimilarities than expected by chance. Functional dissimilarities between salvaged and unsalvaged sites were lower compared to taxonomic and phylogenetic dissimilarities. In general, dissimilarities were highest for rare, followed by common and dominant species.
5. *Synthesis and applications.* Our research demonstrates that salvage logging did not decrease dissimilarities of bird communities over time and taxonomic, functional and phylogenetic dissimilarities persisted for over a decade. We recommend

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resource managers and decision makers to reserve portions of disturbed forest to enable unmanaged post-disturbance succession of bird communities, particularly to conserve rare species found in unsalvaged disturbed forests.

KEYWORDS

biodiversity, breeding season, forest management, harvesting, Hill numbers, natural disturbance, successional trajectory

1 | INTRODUCTION

Naturally occurring disturbances (i.e. wildfires, windthrows and insect outbreaks) are an integral part of natural forest dynamics (Pickett & White, 1985). Disturbances can cause abrupt but long-lasting changes in forests by altering biophysical and environmental features, resource availability and ecosystem processes (Turner, 2010). Generally, forests are resilient to historic disturbance regimes and, given sufficient time, typically recover their pre-disturbance state (Gunderson, 2000). Within disturbance-affected communities, taxonomic diversity, that is, the identity and richness of species, can gradually recover to a pre-disturbance state (Purvis & Hector, 2000). However, the extent, frequency and intensity of natural disturbances have increased globally and are expected to continue to increase in the near future (Seidl et al., 2017), with possible effects on community recovery. Functionally and phylogenetically diverse species communities may hence be necessary for the provision of ecosystem services and for maintaining ecosystem stability (Cadotte, Dinnage, & Tilman, 2012; Loreau & de Mazancourt, 2013). Also, evolutionarily distinct avian species are more likely to become extinct in anthropogenically disturbed forests (Frishkoff et al., 2014). While the loss of a single species could lead to a negligible reduction of taxonomic diversity, it might represent the loss of an entire evolutionary lineage or distinct functional group (Cadotte et al., 2010; Faith, 2015). The increasing amount of natural disturbances has also led to an increase of salvage logging, that is, the removal of trees affected by disturbances, conducted in managed and protected forests worldwide (Leverkus, Lindenmayer, Thorn, & Gustafsson, 2018). It has hence become increasingly important to understand whether and how the recovery of forest biodiversity is altered by the combined effects of natural and anthropogenic disturbances.

Besides economic reasons, salvage logging is commonly justified on the basis that it contributes to forest structural restoration (reviewed in Müller et al., 2019). For instance, following a major drought and bark beetle outbreak in 2018/19, the Federal Ministry for Food and Agriculture of Germany called for a 'clear-up followed by reforestation strategy' to support the recovery of disturbed forest stands (Thorn, Müller, & Leverkus, 2019). Because salvage logging immediately follows the natural disturbance (i.e. up to 3 years), it acts as an additional disturbance (Lindenmayer, McBurney, Blair, Wood, & Banks, 2018; Morissette, Cobb, Brigham, & James, 2002),

with possible negative effects on species richness, community recovery of various species groups (Thorn et al., 2018) and ecosystem services (Leverkus et al., 2020).

Naturally occurring disturbance and salvage logging can have long-lasting effects on forest structures (Donato, Campbell, & Franklin, 2012) and forest bird communities (Thorn et al., 2018). For instance, the species richness and community composition of birds in boreal stands affected by wildfire or green-tree harvesting differed significantly during the first years after these disturbances, and differences may persist for more than 25 years (Hobson & Schieck, 1999), or even 60–70 years (Zhao, Azeria, Le Blanc, Lemaître, & Fortin, 2013). However, in contrast to the many studies investigating community convergence in disturbed versus green-tree-logged stands, there have been very few comparisons of disturbed and salvage-logged stands (reviewed in Thorn et al., 2018).

Anthropogenic disturbances, such as salvage logging, may result in the reduction of specialized species and/or increases of generalist species (Gossner et al., 2016) but also the potential extinction or extirpation of rare species (Leitão et al., 2016). Specialist bird species often respond more negatively to landscape fragmentation and disturbance than generalists (Devictor, Julliard, & Jiguet, 2008). These changes in specialist and generalist species may also apply to rare functional groups or rare evolutionary lineages (Olden, 2006). However, empirical tests of whether the strength of community response to salvage logging varies depending on the relative contribution of dominant versus rare (for abundance data) or common versus rare (for occurrence data) species are lacking (but see Thorn et al., 2020).

We compiled a large dataset of breeding bird assemblages sampled in salvaged and unsalvaged naturally disturbed forests in North America, Europe and Asia. We extended incidence-based dissimilarity metrics based on Hill numbers to include dissimilarities in species life-history traits and evolutionary ancestries (Chao et al., 2015, 2019) to test: (a) whether compositional differences between communities of salvage-logged and unsalvaged forests decrease or increase over time and (b) whether those trends differ for rare, common and dominant species. We expected that dissimilarities of non-shared species, functional groups and evolutionary lineages would decline with increasing time after the disturbance and that dissimilarities would be more pronounced for rare than for common and dominant species.

2 | MATERIALS AND METHODS

2.1 | Bird data

Data on breeding bird assemblages were compiled from nine study areas in North America ($n = 3$), Europe ($n = 4$) and Asia ($n = 2$; Figure 1; Table 1), by extending the databases compiled by two reviews on the effect of salvage logging on biodiversity and ecosystem services (Leverkus, Rey Benayas, et al., 2018; Thorn et al., 2018). The data compilation followed a systematic review protocol to warrant high standards in data selection (Leverkus, Gustafsson, Benayas, & Castro, 2015). We retained only datasets based on field surveys and excluded modelling studies. Studies provided comparisons between completely salvage-logged plots and completely unsalvaged control plots, that is, more than 75% of the trees were affected by a natural

disturbance and then completely salvage logged. Salvage-logged plots were of similar size, surveyed with the same sampling effort as unsalvaged control plots (Thorn et al., 2018). In addition to the use of the raw data from published studies (see Table 1 and *Data sources* section), the time series for the present work was extended by expanding three of the studies (Hutto & Young, 2002; Thorn et al., 2016; Zmihorski, 2010) by additional surveys, adhering in each case to the original sampling design.

The forests in the studied areas were affected first by wildfires or windstorms and then by salvage logging. Bird surveys were standardized to a specific plot area by using standardized fixed-radius point counts or fixed-width transect counts (Bibby, Burgess, Hill, & Mustoe, 2000). Bird surveys were conducted only on days without rain, with low wind speed and with clear or slightly overcast skies (Bibby et al., 2000). Our final dataset consisted of 668 salvage-logged

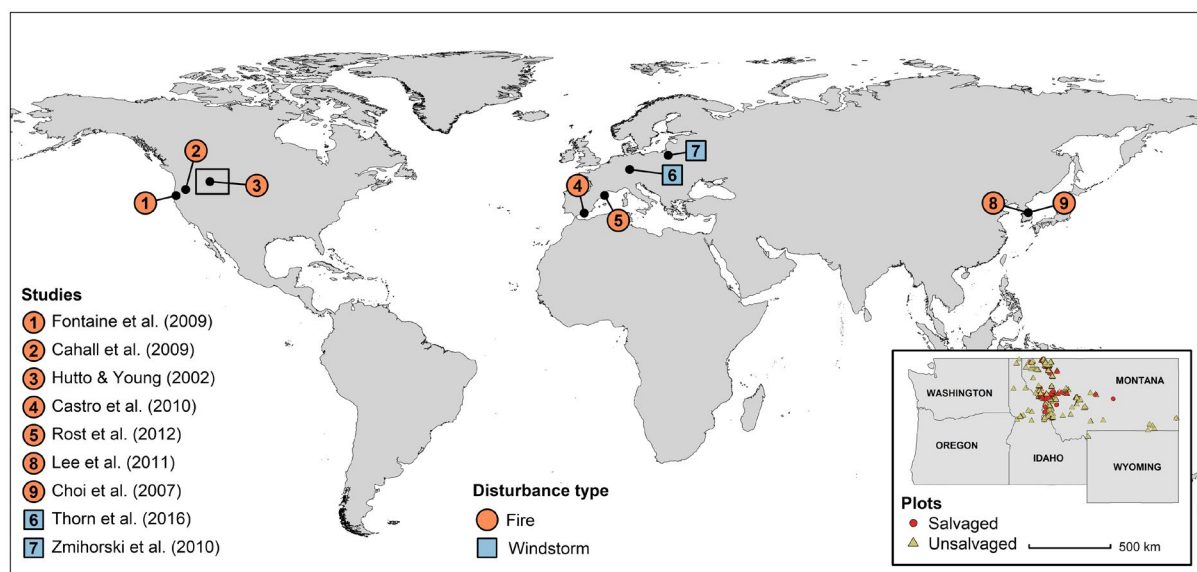


FIGURE 1 General locations of the breeding birds surveyed to investigate the effects of salvage logging on bird communities. The inset map shows the extent of the sampling plots in the study of Hutto and Young (2002)

TABLE 1 Datasets used to investigate the effect of additional disturbance on the successional trajectories of bird communities

No.	Country	Disturbance type	Number of years sampled	Study plots	Recorded species	Recorded individuals	Reference
1	USA	Wildfire	1	122	49	979	Fontaine et al. (2009)
2	USA	Wildfire	2	20	34	363	Cahall and Hayes (2009)
3	USA	Wildfire	17	4,100	145	42,091	Hutto and Young (2002)
4	Spain	Wildfire	2	27	44	724	Castro, Moreno-Rueda, and Hódar (2010)
5	Spain	Wildfire	3	58	55	971	Rost, Clavero, Brotons, and Pons (2012)
6	South Korea	Wildfire	1	38	24	105	Choi, Lee, Nam, and Lee (2007)
7	South Korea	Wildfire	2	48	42	689	Lee, Lee, Son, and Rhim (2011)
8	Germany	Windstorm	4	42	52	1,912	Thorn et al. (2016)
9	Poland	Windstorm	3	109	76	4,225	Zmihorski (2010)

plots (hereafter salvaged plots) and 3,896 disturbed (control) plots without post-disturbance logging (hereafter unsalvaged plots) and covered studies with survey duration ranging from one to 17 consecutive sampling years after the natural disturbance (Table 1).

2.2 | Functional traits and phylogeny

We followed Calba, Maris, and Devictor (2014) in the selection of 22 ecological traits reflecting avian resource and habitat use. Body mass and clutch size were continuous variables. Binary classifications were used for the main dietary component (plants, vertebrates, invertebrates), the main foraging method (pursuit, gleaning, pouncing, grazing, digging, scavenging, probing), the main foraging substrate (water, mud, ground, vegetation, air), the main foraging period (nocturnal) and the migratory status. Nest location was classified as one categorical variable (canopy, ground and hole). All traits were classified using the Cornell Laboratory of Ornithology (www.allaboutrbirds.org) and the Handbook of Birds of the World (www.hbw.com). For a full list of the traits, see Table S2. We did not account for possible regional differences in the species migratory status, since the majority of our studies were located on a similar latitude in the Northern Hemisphere (Figure 1).

Phylogenetic trees were constructed separately for the species pool in each study area by combining a relaxed molecular clock of trees containing well-supported avian clades and a fossil-calibrated backbone that included representatives from each clade (Hackett et al., 2008). For each study area, 4,000 bootstrap replicate trees were mined from the online tool at www.birdtree.org, which first trims to a subset and then samples trees from a chosen pseudo-posterior distribution (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). The bootstrap replicates were then condensed into a dated consensus tree using TreeAnnotator 1.8.2 (<http://beast.community/treeannotator>). All subsequent analyses were based on these consensus trees (phylogenetic trees may be found in Figures S9–S17).

2.3 | Quantifying dissimilarity

Dissimilarities between the bird communities of salvaged and unsalvaged plots were quantified by treating each sampled plot within each year as a sampling unit and then extracting the species incidence (presence/absence) to obtain a count of the occurrences (i.e. the incidence-based frequency) for each species. This procedure yielded a species-incidence-based frequency vector for salvaged and unsalvaged plots for each sampling year. The number of occurrences among multiple plots of each species was treated as a proxy of the abundance of that species. As shown by Colwell et al. (2012), such incidence-based occurrence records are able to account for spatial aggregation or clustering in the data. Moreover, incidence-based data support statistical approaches to diversity inferences that are just as powerful as the corresponding abundance-based approaches.

We used Hill numbers (i.e. the effective number of species; Hill, 1973), based on species proportional incidence frequencies, to quantify and decompose diversity measures. Hill numbers differ by a parameter q that reflects their respective sensitivity to the relative frequency of a species. A main advantage of using Hill numbers is that they obey the replication principle (Chao, Gotelli, et al., 2014) and can thus be decomposed into independent components of alpha- and beta-diversity. The resulting beta-diversity is then transformed to obtain two general classes of dissimilarity measures, the Jaccard-type and the Sørensen-type (Chao, Chiu, & Jost, 2014). The Jaccard-type taxonomic dissimilarity index quantifies the effective proportion of non-shared species in salvaged and unsalvaged plots pooled, whereas the Sørensen-type index quantifies the effective average proportion of non-shared species in individual plots. These two types of dissimilarity measures include most of the commonly used dissimilarity indices.

We used Jaccard-type taxonomic dissimilarity measures (Chao, Chiu, et al., 2014) to quantify the temporal change in the dissimilarity of unsalvaged versus salvaged plots. Figures S1–S8 show that the dissimilarity patterns for the Sørensen-type indices were generally consistent except for differences in magnitude. Setting $q = 0$ in the class of Jaccard-type measures yields the classic richness-based Jaccard index, which weights all species equally; setting $q = 1$ yields the Shannon-entropy-based Horn index, which weights all incidences equally, that is each species is weighted according to its incidence frequency; setting $q = 2$ yields the regional non-overlap index, which is very sensitive to dominant species but gives little weight to rare species (Chiu, Jost, & Chao, 2014). Special cases of Sørensen-type measures are described in Chao, Gotelli, et al. (2014). Because of the different weighting of the species, dissimilarity measure of $q = 0$ is disproportionately sensitive to rare species (i.e. infrequently detected species for incidence data), $q = 1$ to common species (i.e. frequently detected species for incidence data) and $q = 2$ to dominant species (i.e. highly frequently detected species for incidence data). Since our analysis is based on incidence frequencies, the classification of the species as rare ($q = 0$), common ($q = 1$) or dominant ($q = 2$) was based on each local dataset and was not linked to their global abundance. Here, 'rare' species refer to those species whose occurrence rates are relatively low in any plot.

Another advantage of using Hill numbers is that they enable a unified approach to generalizing the Jaccard- and Sørensen-type taxonomic dissimilarity measures to include species differences based on species evolutionary ancestries (i.e. phylogenetic trees; Chiu et al., 2014) or on species traits (Chao et al., 2019). In our study, the dendrogram-based approach of Chao, Gotelli, et al. (2014) was applied to quantify phylogenetic dissimilarity between salvaged and unsalvaged plots. This approach takes all species inter-relations into account, incorporating species relations not only for species pairs but also for every possible combination of any subset of species. For functional dissimilarity, we followed the approach of Chao et al. (2019), which is based on species pairwise-distances. For species traits, these distances were obtained by Gower distances (Gower, 1971). All plausible threshold levels of functional distinctiveness between any two species were considered. Interpretation of the Jaccard- and Sørensen-type phylogenetic and functional

dissimilarity indices is similar to that of their taxonomic versions. For example, the Jaccard-type phylogenetic and functional dissimilarity measures quantified, respectively, the effective proportion of non-shared evolutionary lineages (for phylogenetic dissimilarity) and non-shared functional groups (for functional dissimilarity) in salvaged and unsalvaged plots.

2.4 | Data analysis

All analyses were carried out in R 3.4.2 (R Development Core Team, 2017). Null models were used to compare the expected dissimilarities within unsalvaged plots (i.e. within the control treatment), to the dissimilarities between salvaged and unsalvaged plots (i.e. among treatments). Therefore, the dissimilarities of 999 randomly assembled communities ('simulated dissimilarities') recruited from unsalvaged plots were calculated and compared to the observed dissimilarities between salvaged and unsalvaged plots. Randomization was achieved using the independent swap algorithm (function *randomizeMatrix* from *PICANTE* package; Kembel et al., 2010), in which species occurrences, frequencies and species richness of the sample are held constant during the randomization process (Gotelli, 2000). Since, during randomization, every species can be randomly assigned to any unsalvaged plot, the results from the null model depicted the mean dissimilarities between any pair of unsalvaged plots occurring by chance.

For every study region and year after the disturbance, the mean dissimilarity value for every $q = \{0, 1, 2\}$ and every respective dissimilarity (taxonomic, functional and phylogenetic) was calculated. Changes in the mean dissimilarity in a given year between salvaged and unsalvaged plots over the course of succession were identified by fitting general additive mixed-effects models (Gaussian error distribution, function *gamm4* from *GAMM4* package; Wood & Scheipl, 2017). Separate models were fitted for all types of dissimilarities (taxonomic, functional and phylogenetic) and q numbers ($q = 0, q = 1, q = 2$), resulting in nine models (Table S1). To each of those models, we included the year after the disturbance as smoothed effect, fitted for observed and simulated communities separately, to test if successional trends in dissimilarities differ. Additionally, the null model (observed vs. simulated) was included as a fixed effect to test for differences between the observed and simulated dissimilarities. The study identity was specified as random effect to account for differences across the study sites and repetitive sampling within these sites.

The data provided by Hutto and Young (2002) covered 90% of all studied plots and 81% of all surveyed individuals in our final dataset (Table 1). To assess the effect of this study on the overall results, we repeated our analysis by excluding the data of Hutto and Young (2002). However, our results and trends were mostly similar, with overall few exceptions (Figures S5–S8). Also, we repeated the analysis by excluding the year 17, to evaluate the robustness of our results to this possible outlier. We found the same significant trends as in Figure 3 and Figure S2, with the exception that the increasing trends in dissimilarity after year 14 either disappeared or became very small (Figures S3 and S4).

3 | RESULTS

Our final dataset consisted of 299 species, represented by 51,813 individuals. The analysis showed that observed and simulated bird communities differed significantly for non-shared species (taxonomic dissimilarity), evolutionary lineages (phylogenetic dissimilarity) and functional groups (functional dissimilarity; Figure 2; Figure S1). The dissimilarities varied when the species

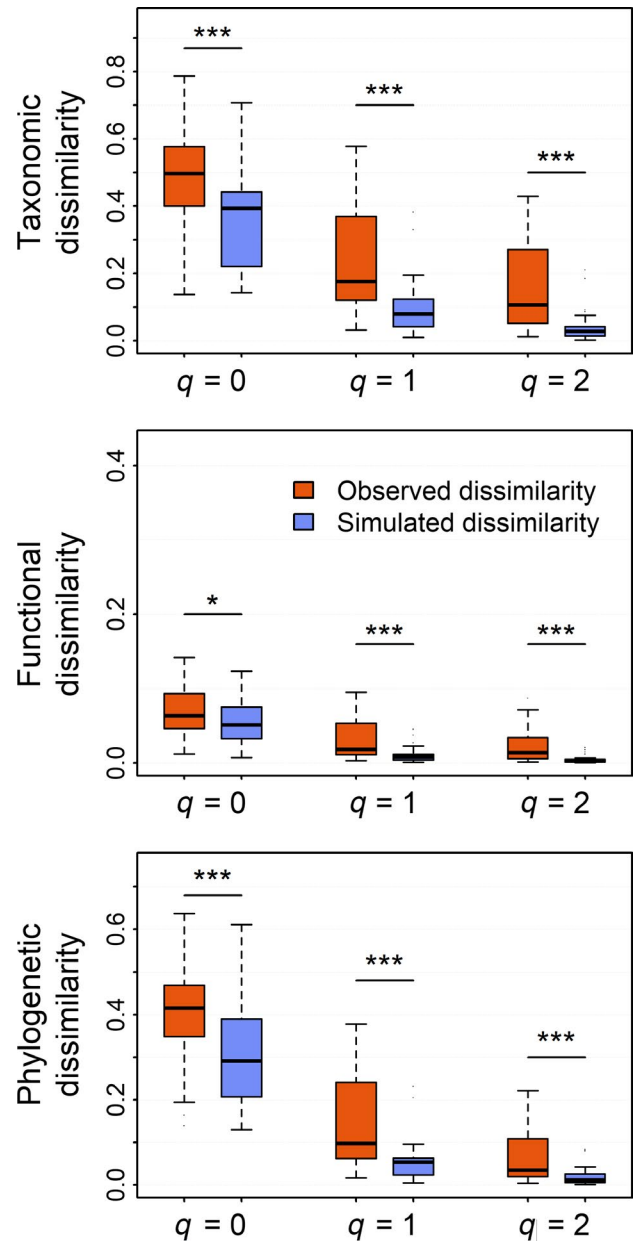


FIGURE 2 Effective proportion (Jaccard-type) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). Boxplots show the dissimilarity for rare ($q = 0$), common ($q = 1$) and dominant ($q = 2$) species. Pairwise comparisons between observed and simulated dissimilarities are based on general additive mixed-effects models. *0.05, ***0.001

were weighted according to their relative abundance. The largest dissimilarities occurred when all species, all evolutionary lineages and all functional groups were weighted equally ($q = 0$). The mean dissimilarity decreased when weighting of the species was shifted towards common ($q = 1$) and dominant ($q = 2$) species (Figure 2; Figure S1).

Over the course of 17 years, there was no significant increase or decrease in the observed community dissimilarity between salvaged and unsalvaged plots (Figure 3; Figure S2). Significant non-linear trends in the observed community dissimilarity were found only for: (a) common ($q = 1$) and dominant ($q = 2$) functional groups (Jaccard-type; Figure 3b); and (b) for dominant ($q = 2$) non-shared species

(Sørensen-type; Figure S2a), as well as for common ($q = 1$) and dominant ($q = 2$) functional groups (Sørensen-type; Figure S2b). For all of these trends, the observed community dissimilarity followed a decrease between year 1 and year 12, followed by an increase after year 14 (Figure 3; Figure S2).

For simulated communities we found a significant trend of slight decrease followed by a slight increase only for dominant species ($q = 2$; taxonomic dissimilarity; Figure 3a). However, the magnitude of changes in dissimilarities was very small (<5%).

The average dissimilarity of simulated communities was significantly lower ($p < 0.001$) than the observed dissimilarities (Table S1). Thus, the average dissimilarities between salvaged and unsalvaged

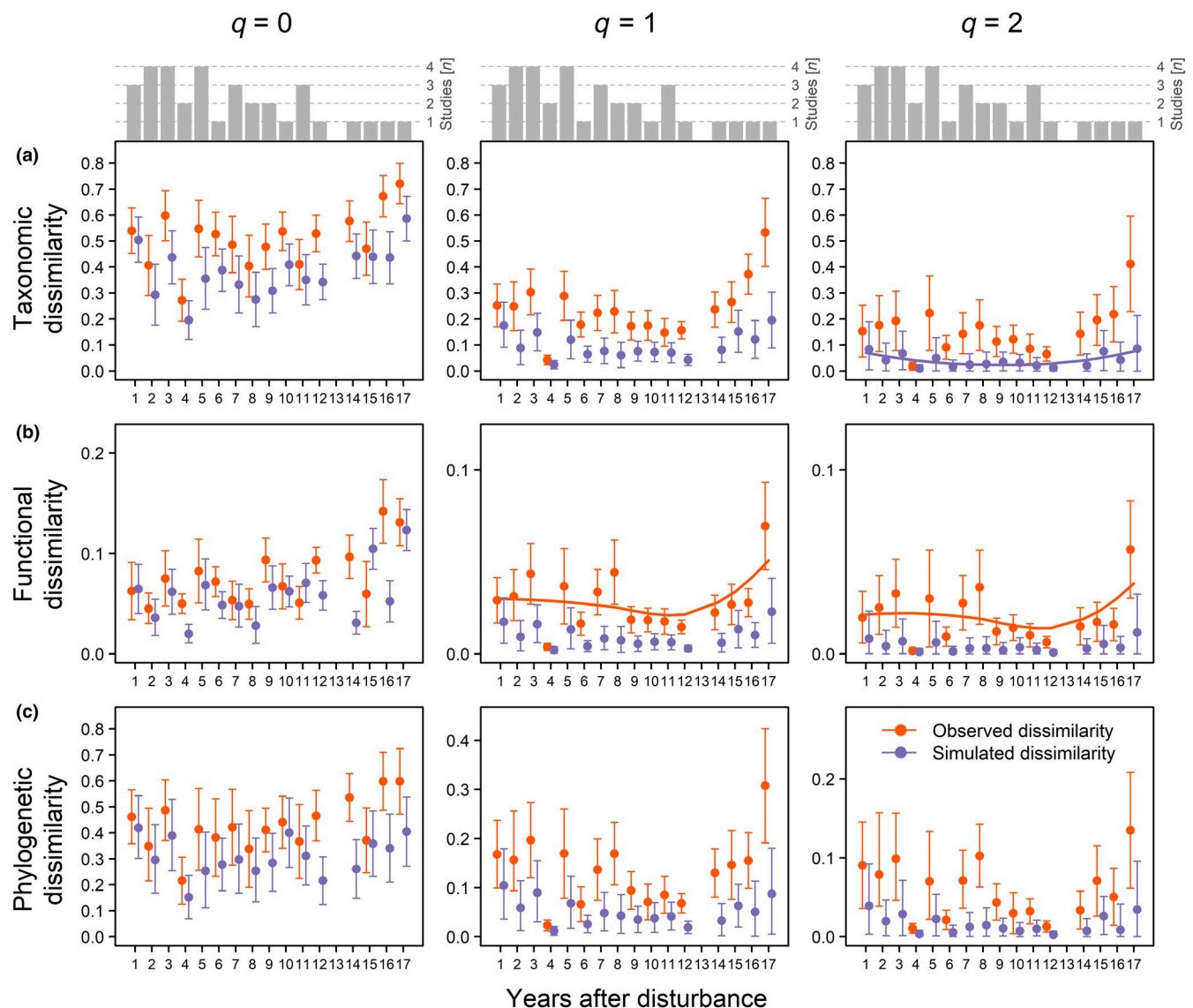


FIGURE 3 Effective proportion (Jaccard-type; mean \pm SD) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity), and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots over the studied years (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). (a) Taxonomic dissimilarity, (b) functional dissimilarity and (c) phylogenetic dissimilarity are shown. The columns represent the dissimilarities for rare ($q = 0$), common ($q = 1$) and dominant ($q = 2$) species. Significant ($p < 0.05$) trends are drawn as solid lines, showing the average dissimilarity, based on general additive mixed-effects models. Top-row bar plots indicate the number of studies used to calculate the mean dissimilarity within every single year. Note the different scales of the y-axes

plots were higher than the average dissimilarity that occurred within the unsalvaged plots by chance during the course of post-disturbance forest succession.

4 | DISCUSSION

Analysing data from nine studies covering a post-disturbance period of 17 years, we demonstrated that dissimilarities persisted or showed a u-shaped pattern. These differences exceeded the changes expected by chance, that is, without salvage logging, and were strongest for taxonomic, followed by phylogenetic and functional dissimilarity.

Comparisons of observed and simulated dissimilarities revealed that dissimilarities caused by salvage logging were higher than expected by chance (Table S1; Figure 2; Figure S1). Bird communities following naturally occurring disturbances are thought to undergo a gradual recovery, from disturbed-forest to mature-forest communities (Fontaine, Donato, Robinson, Law, & Kauffman, 2009). Our results suggested that the differences between the bird communities of salvaged and unsalvaged sites persisted within the first 17 years after a natural disturbance. It may be that 17 years are much shorter than the time required by a disturbed forest to recover. For example, differences in species richness and community composition can be detected for >60–70 years in the bird communities of boreal forests affected by wildfire and clear cutting (Zhao et al., 2013). Hence, it may be that the differences in bird communities caused by salvage logging also last for several decades.

Our results showed that dissimilarities between bird communities of salvaged and unsalvaged plots were larger for rare ($q = 0$) than for common ($q = 1$) or dominant ($q = 2$) species (Figure 2; Figure S1). Moreover, the highest taxonomic, functional and phylogenetic dissimilarities for observed and simulated communities were those of rare species (Figure 3; Figure S2). These results confirm the findings of Magurran and Henderson (2003), who in temporal studies showed that species with a low relative abundance persist only few years in the assemblage. Rare species ($q = 0$) can be habitat specialists that rely on ephemeral resources and thus occur only on a limited number of plots for short periods. A main characteristic of salvage logging is that it diminishes the structural heterogeneity caused by the natural disturbance (Swanson et al., 2011). In our case, this reduction in heterogeneity resulted in the short occurrence of rare and/or specialist species on either salvaged or unsalvaged plots, increasing the dissimilarity for rare ($q = 0$) species. For example, the corn crane *Crex crex* likely benefited from grass-dominated post-storm salvaged stands and was found only on few salvaged plots in Poland. In contrast, the common redstart *Phoenicurus phoenicurus*, which preferred remnant snags with cavities, was almost exclusively found on unsalvaged wind-disturbed plots in Germany. Conversely, common ($q = 1$) and dominant ($q = 2$) species consisted mainly of generalists that because of their broad habitat requirements and higher abundances were able to colonize salvaged and unsalvaged plots with similar success, resulting in a lower dissimilarity between the two site types.

Over the studied period, years 1–12 were characterized by a linear decrease in dissimilarity, followed after year 14 by an increase in dissimilarity for functional groups ($q = 1$ and $q = 2$; Figure 3). However, a more-detailed analysis of the included studies showed differences in the trends. For instance, after excluding Hutto and Young (2002) from the analysis no trend of increasing or decreasing dissimilarity was found, indicating that compositional differences persisted over the years (Figures S7 and S8). This result might be attributed to the sensitivity of the bird communities to salvage logging among different regions. For example, post-fire salvage logging in the Rocky Mountains can have a greater impact on bird communities than in the Mediterranean Basin because it affects a higher proportion of the bird community that occurs in burned forests (Rost, Hutto, Brotons, & Pons, 2013). Also, in the Rocky Mountains salvage logging has detrimental effects to fire specialists, like the Black-backed Woodpecker *Picoides arcticus* or the American Three-toed Woodpecker *Picoides tridactylus*, while in the Mediterranean Basin salvage logging affects only common forest birds species with wide distributions across European forests (Rost et al., 2013).

The dissimilarities between bird communities of salvaged and unsalvaged plots were lowest for functional groups (Figure 2; Figure S1). This suggests that bird communities of salvaged and unsalvaged plots share most functional groups but relatively smaller proportion of their species and evolutionary lineages. As salvage logging diminishes structural heterogeneity by reducing biological legacies (Swanson et al., 2011), communities of salvaged plots may have a high functional redundancy, in contrast to the low functional redundancy of the communities of unsalvaged plots. Although communities of salvaged plots may consist of functionally different groups (Azeria et al., 2011), we found a high similarity of rare, common and dominant functional groups in bird communities of salvaged and unsalvaged plots (Figure 2; Figure S1). Gerisch, Agostinelli, Henle, and Dziöck (2012) showed that a high taxonomic diversity was not associated with a high functional diversity. We suggest that the observed pattern of functional, taxonomic and phylogenetic dissimilarity was driven by common or dominant species from genera like *Sylvia*, *Phylloscopus* and *Setophaga*, which while taxonomically and phylogenetically distant, are functionally similar. These species are mainly generalists that colonize both unsalvaged and salvaged plots. It is thus likely that these genera drive not only the determined taxonomic and phylogenetic dissimilarity but also the high functional redundancy between communities. Indeed, larger difference can be detected when comparing salvaged and unsalvaged plots to undisturbed forests (Thorn et al., 2016; Zmihorski, 2010), where phylogenetic and functionally distantly related genera occur with higher frequency.

Current knowledge about the effects of salvage logging has mainly come from local, short-term (1–5 years) studies (reviewed in Thorn et al., 2018). Our study, conducted at a wider spatial and temporal scale, provides a mid-term comparison of disturbed and salvage-logged forests but it is still relatively short compared to the

time a forest needs to recover. Hence, future studies might address whether initial changes in successional trajectories persist to later stages and how these changes vary across changing and interacting disturbance regimes (Leverkus, Lindenmayer, et al., 2018; Seidl et al., 2017).

5 | CONCLUSIONS

Our study provides evidence that salvage logging leads to short- to mid-term changes in bird community composition that are significantly greater than those occurring over the course of natural succession. Our results therefore demonstrate that salvage logging can lead to changes in community composition for non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity). In addition, because of the reduction of structural heterogeneity that salvage logging causes, it affects rare and/or specialized the most. The global increase in natural disturbances caused by climate change will trigger high levels of salvage logging world-wide. Hence, we argue that salvage logging may lead to widespread changes in the successional trajectories of forest bird community. Therefore, we recommend resource managers and decision makers to reserve portions of disturbed forest to enable unmanaged post-disturbance succession of bird communities, particularly to conserve rare species found in unsalvaged disturbed forests.

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AUTHORS' CONTRIBUTIONS

K.B.G., J.M. and S.T. conceived the idea and designed the study; A.C., K.B.G., Y.-H.C. and S.T. analysed the data; C.-Y.C., E.-J.L., J.B.F., J.C., J.R., M.Ž., R.L.H., S.T. and K.B.G. collected the data; K.B.G. wrote the first draft of the manuscript. All authors contributed significantly to later drafts and revisions.

DATA AVAILABILITY STATEMENT

All data are from previously published articles, listed in the *Data sources* section. Data from these articles can be made available upon reasonable request to original data owners.

ORCID

Kostadin B. Georgiev  <https://orcid.org/0000-0003-0475-9439>

Anne Chao  <https://orcid.org/0000-0002-4364-8101>

Jörg Müller  <https://orcid.org/0000-0002-1409-1586>

Simon Thorn  <https://orcid.org/0000-0002-3062-3060>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Effects of post-fire logging on California spotted owl occupancy

Chad T. Hanson¹, Monica L. Bond², Derek E. Lee²

1 Earth Island Institute, 2150 Allston Way, Suite #460, Berkeley, CA 94704, USA **2** Wild Nature Institute, 15 North Main Street #208, Concord, NH 03302, USA

Corresponding author: Chad T. Hanson (cthanson1@gmail.com)

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Abstract

In fire-adapted forest ecosystems around the world, there has been growing concern about adverse impacts of post-fire logging on native biodiversity and ecological processes. This is also true in conifer forests of California, U.S.A. which are home to a rare and declining owl subspecies, the California spotted owl (*Strix occidentalis occidentalis*). While there has been recent concern about the California spotted owl occupancy in large fire areas where some territories have substantial high-severity fire effects, the influence of post-fire logging on the California spotted owl occupancy has been investigated very little, leading to some uncertainty about interpretation of conflicting results in different large fires. Research has found these owls preferentially select high-severity fire areas, characterised by high levels of snags and native shrubs, for foraging in forests that were not logged after fire, suggesting that removal of this foraging habitat might impact occupancy. The authors assessed the effect of post-fire logging and high-severity fire, on occupancy of this subspecies in eight large fire areas, within spotted owl sites with two different levels of high-severity fire effects. They found a significant adverse effect of such logging and no effect of high-severity fire alone. These results indicate it is post-fire logging, not large fires themselves, that poses a conservation threat to this imperilled species.

Keywords

wildland fire, spotted owl, forests, logging, post-fire logging, fire severity

Introduction

In fire-adapted forests around the world, a growing body of research indicates reasons for conservation concerns about the impacts of post-fire logging on native biodiversity and ecological processes (Lindenmayer and Noss 2006, Lindenmayer and Ough 2006, DellaSala et al. 2015, Heneberg 2015). The conifer forests of western North America are no exception (Hutto 2006, Swanson et al. 2011, DellaSala et al. 2015).

For a rare owl subspecies, the California spotted owl (*Strix occidentalis occidentalis*) which lives in the low/middle-montane conifer forests of the Sierra Nevada mountains of California, U.S.A. and the mountains of southern California, the effects of post-fire logging have been little studied. Some research suggests reduced site occupancy which has been observed in at least one large recent fire, the King fire of 2014 in the central Sierra Nevada, may occur due to predominantly high-severity fire effects (Jones et al. 2016). However, distinguishing the effects of fire alone from those of post-fire logging remains a challenge.

Populations of this subspecies are declining (Conner et al. 2013) and a petition for listing under the U.S. Endangered Species Act is pending (Bond and Hanson 2014). Thus, it is important to understand the extent to which forest management activities such as post-fire logging may be affecting spotted owl populations.

California spotted owls have been found to preferentially select unlogged high-severity fire areas characterised by high snag basal area and shrub cover for foraging (Bond et al. 2009) or to forage in this forest type in proportion to its availability (Bond et al. 2016, Eyes et al. 2017). This is likely due to the small mammal prey base found in this “complex early seral forest” habitat (DellaSala and Hanson 2015). One study, conducted in the San Bernardino mountains of southern California, found that removal of burned foraging habitat due to post-fire logging adversely impacted spotted owl site occupancy (Lee et al. 2013). However, this issue has not been addressed in the Sierra Nevada, where most California spotted owls live.

In this study, this issue was investigated by analysing the effect of post-fire logging on occupancy of California spotted owl sites, burned in large fires throughout the range of the subspecies, as well as the effect of high-severity fires.

Methods

First, to address how large fires affect California spotted owl site occupancy, fires with the following characteristics were analysed: (1) over 10,000 hectares in size, (2) occurring primarily on U.S. Forest Service lands post-2000, (3) included multiple spotted owl sites burned in the fire and (4) occupancy data were gathered by or for the U.S. Forest Service on national forest lands within the fire’s perimeter. The sampling unit was the site (1500 m radius around the historical centre of the territory). Locations of historical site centres come from U.S. Forest Service survey data, as described below.

All sites analysed in this study were located in mature mixed-conifer forest that had recently burned. This forest type is comprised of yellow pine (*Pinus ponderosa* or *Pinus jeffreyi*) mixed with sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*) and California black oak (*Quercus kelloggii*).

High-severity fires were defined as forest with RdNBR (Relativised differenced Normalised Burn Ratio) values >572 (Jones et al. 2016), equating to a median level of basal area mortality of trees of ~80% (Miller et al. 2009, Miller and Quayle 2015). RdNBR values are based on satellite imagery and pertain to the difference between pre-fire and post-fire reflectance of green foliage (Miller and Thode 2007). The Rapid Assessment of Vegetation Condition (RAVG) satellite imagery database employed by the U.S. Forest Service was used to assess fire severity (<https://www.fs.fed.us/postfirevegcondition/whatis.shtml>). The RAVG database did not include the four oldest fires, the McNally fire, the Old fire, the Butler2-Slide fire and the Moonlight-Antelope fire, so the Monitoring Trends in Burn Severity (MTBS) satellite imagery database (www.mtbs.gov) was used for these fires, adjusting the 572 threshold value in the RAVG system by multiplying it by 0.875 (i.e. yielding an RdNBR value of 500) to obtain the equivalent percentage of high-severity fire in the MTBS system as was used in RAVG (Miller and Quayle 2015).

The U.S. Forest Service's Region 5 biologists conducted or oversaw surveys for California spotted owls at known sites using an established protocol (USFS 1995). Protocol for a given visit to a site involved trained observers playing calls to elicit responses from territorial spotted owls at night at multiple call points at fixed locations, with each call point surveyed for >10 minutes. At each site, to infer non-occupancy, the protocol required six visits with no detections during one breeding season (this was the case for all but one of the owl sites), or three visits with no detections in each of two consecutive breeding seasons (this was the case for site TUO027). Protocol further required that surveyors temporarily discontinue or reschedule surveys during inclement weather, such as high wind or rain. The authors excluded sites that otherwise met these study criteria but did not have a sufficient number of visits (possibly due to access issues) to meet protocol requirements.

Occupancy data from these surveys were obtained both before and after post-fire logging from the U.S. Forest Service for the following fires that met the above criteria: the McNally fire of 2002 (Sequoia National Forest); the Old fire of 2003 (San Bernardino National Forest); the Moonlight-Antelope fire of 2007 (Plumas National Forest); the Butler2-Slide fire of 2007 (San Bernardino National Forest); the Chips fire of 2012 (Plumas National Forest), not including the western half of the fire area which re-burned the Storrie fire of 2000 and that had extensive post-fire logging more than a decade ago, a fact which could confound these results; the Rim fire of 2013 (Stanislaus National Forest); the King fire of 2014 (Eldorado National Forest); and the Lake fire of 2015 (San Bernardino National Forest) (Figure 1).

Sites that were occupied in the most recent spotted owl survey year prior to post-fire logging were analysed. For example, the most recent surveys on the San Bernardino

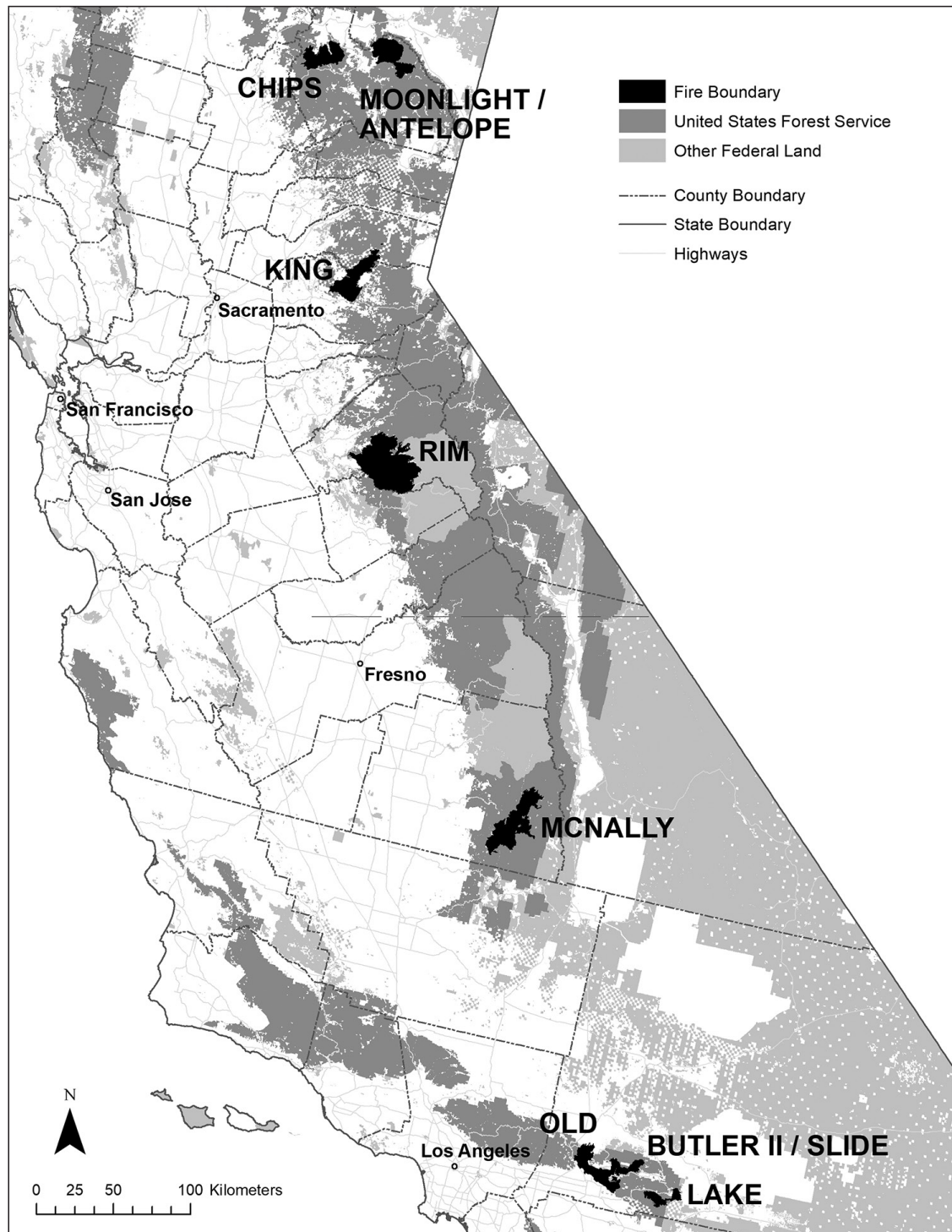


Figure 1. Large fires, in occupied California spotted owl habitat that were studied in this analysis.

National Forest (prior to the Lake fire of 2015) occurred in 2011, whereas in the Rim fire of 2013, surveys were sporadic prior to the fire, but were extensive beginning in the spring of 2014, prior to post-fire logging on national forest lands. The dates of fires, pre-logging and post-logging surveys and logging are shown in Table 1.

Table 1. Years in which the fires, pre-logging and post-logging surveys and logging occurred in each of the fires in this analysis.

Fire Name	Fire Year	Pre-/Post-Logging Surveys ¹	Logging
McNally	2002	2001/2004	Not applicable
Old	2003	2003/2005	Late 2003 through 2004
Moonlight-Antelope	2007	2006/2009	Late 2007 through 2008
Chips	2012	2012/2014	Late 2012 through early 2014
Rim	2013	2014/2016	Late 2014 through 2015
King	2014	2014/2015	Late 2014 through early 2015
Lake	2015	2011/2016	Not applicable
Butler2-Slide	2007	2007/2011	Late 2007 through 2010

¹ In the McNally and Lake fires, there was no post-fire logging in any of the spotted owl sites analysed in this study.

The authors considered a site to be occupied in a given year when at least one owl was detected (Lee et al. 2012, Lee and Bond 2015a, b, Jones et al. 2016). Detection indicated an owl utilised the site for any component of its life history, including foraging, roosting, nesting or territorial defence (Jones et al. 2016). Given the concern indicated in Jones et al. (2016) regarding lost occupancy in sites with substantial high-severity fire effects, the authors analysed naïve occupancy (detections versus no detections as recorded by surveyors, without extrapolating to adjust for probability of detection) of California spotted owl sites with 20–49% and 50–80% high-severity fire (as defined below). Occupancy of such sites was analysed within a 1500 m radius around site centres (nest or core roost locations at the centre of the site; Lee et al. 2012) at two different levels of post-fire logging, <5% and ≥5%, pertaining to the percentage of the total area within the 1500 m radius around the site's centre that was post-fire logged.

The radius distance of 1500 m around site centres was used as it has been found to be important to this subspecies for foraging (Bond et al. 2009). The authors chose 5% as the threshold for analysis of post-fire logging because this threshold, for logging in general, has previously been found to be associated with reduced California spotted owl occupancy (Seamans and Gutiérrez 2007). The effects of post-fire logging was not analysed for spotted owl sites with <20% high-severity fire because post-fire logging often does not occur in such sites. Conversely, the effects of post-fire logging were not analysed for sites with >80% high-severity fire because nearly all of these sites have ≥5% post-fire logging and there was not a sufficient number of such sites with <5% post-fire logging for the analysis.

To determine post-fire-logged areas, the U.S. Forest Service's FACTS database (<http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327833>) was used which contains spatially explicit GIS data of post-fire logging activity in any given fire during any time period. The authors also used GIS data on fire severity (<https://www.fs.fed.us/postfirevegcondition/whatis.shtml>) and land ownership, where forested moderate- and high-severity fire areas on private lands are consistently post-fire logged, with rare exceptions. Post-fire logging in California's forests is a slightly

modified form of clear-cutting, wherein nearly all fire-killed/scorched trees are removed (generally retaining ~10 snags/ha), except in low-severity fire areas which are typically not post-fire logged. Low-severity fire areas were excluded from post-fire logging polygons, with low-severity defined as RdNBR values <316 (Miller and Thode 2007). Google Earth was used, as well as physical inspections of the sites, to confirm post-fire logging. A remote private inholding in a large unroaded area in the Lake fire, which would otherwise have met the criteria described above and a private recreation inholding in the Rim fire were excluded, as no logging had occurred in either area. Similarly, some moderate/high-severity fire areas on larger private residential/recreational parcels had no post-fire logging in the Old fire and Butler2-Slide fire and such areas were not included in post-fire logging percentages.

In each of the two high-severity fire categories, the authors analysed whether post-fire logging affected spotted owl site occupancy using Chi-square tests for change in binomial proportions (Rosner 2000). A Chi-square test for change in binomial proportions was also used to analyse whether high-severity fire, without the influence of post-fire logging, affects site occupancy, restricting the analysis to sites with <5% post-fire logging and comparing occupancy of such sites with 20–49% high-severity fire to those with 50–80% high-severity fire.

Results

In sites with 20–49% high-severity fire (in terms of the percentage of the total area within a 1500 m radius around site centres with high-severity fire) and which were all occupied prior to post-fire logging, with <5% post-fire logging of the total area within a 1500 m radius of site centres, 12 of 15 spotted owl sites were occupied (80% occupancy). With 20–49% high-severity fire and $\geq 5\%$ post-fire logging, 2 of 6 sites were occupied (33% occupancy) (Table 2). This difference was statistically significant ($\chi^2 = 4.23$, $P = 0.040$, $DF = 1$, $N = 21$ sites). To verify that this effect on site occupancy did not result from differences in high-severity fire, an *a posteriori* t-test for two independent means was conducted. In terms of percent high-severity fire, there were no differences between the <5% post-fire logging category (mean = 34.9%, $SD = 7.7\%$, $N = 15$) and the $\geq 5\%$ post-fire logging category (mean = 35.7%, $SD = 11.0\%$, $N = 6$). This indicates that the difference in site occupancy was not due to different levels of high-severity fire ($t = -0.175$, $P = 0.863$). Amongst the sites with $\geq 5\%$ post-fire logging, the mean amount of such logging of the area within a 1500 m radius of site centres was 17.5% ($SD = 8.3\%$).

In sites with 50–80% high-severity fire and which were all occupied prior to post-fire logging, with <5% post-fire logging of the total area within a 1500 m radius of site centres, 10 of 13 spotted owl sites were occupied (77% occupancy). With 50–80% high-severity fire and $\geq 5\%$ post-fire logging, only 4 of 20 sites were occupied (20% occupancy) (Table 3). This difference was statistically significant ($\chi^2 = 10.40$, $P = 0.001$, $DF = 1$, $N = 33$ sites). In terms of percent high-severity fire, there were no differences

Table 2. Occupancy of California spotted owl sites with 20–49% high-severity fire. Sites have varying levels of post-fire logging, within a 1500 m radius of territory centres, in large fires >10,000 ha in size since 2001. Within each fire, all sites were occupied in a single survey year prior to post-fire logging.

Fire	Site	% Post-fire Logging Category	% Post-fire Logging	% High- Severity Fire	Occupied?
Old	SB116	≥5%	24	49	N
Moonlight-Antelope	PL253	≥5%	26	40	N
Chips	Sta. 221/222	≥5%	8	26	Y
Chips	Sta. 223	<5%	0	27	Y
Chips	Sta. 207	≥5%	25	31	N
Rim	TUO010	<5%	3	40	Y
Rim	TUO011	<5%	4	39	Y
Rim	TUO024	<5%	2	36	Y
Rim	TUO026	<5%	4	25	Y
Rim	TUO039	<5%	4	33	Y
Rim	TUO040	<5%	2	44	Y
Rim	TUO078	<5%	2	30	Y
Rim	TUO085	<5%	3	45	Y
King	ELD009	<5%	4	23	N
King	PLA080	<5%	2	43	Y
King	S. Fork	<5%	4	24	N
King	PLA016	≥5%	10	22	Y
Lake	SB123	<5%	0	38	Y
Butler2-Slide	SB013	<5%	3	34	Y
Butler2-Slide	SB003	≥5%	12	46	N
Butler2-Slide	SB074	<5%	4	43	N

Table 3. Occupancy of California spotted owl sites with 50–80% high-severity fire. Sites have varying levels of post-fire logging, within a 1500 m radius of territory centres, in large fires >10,000 ha in size since 2001. Within each fire, all sites were occupied in a single survey year prior to post-fire logging.

Fire	Site	% Post-fire Logging Category	% Post-fire Logging	% High- Severity Fire	Occupied?
McNally	TU045	<5%	0	57	Y
McNally	TU047	<5%	0	59	Y
Old	SB084	≥5%	7	61	N
Old	SB089	≥5%	7	69	N
Old	SB065	≥5%	10	50	Y
Old	SB026	≥5%	27	79	N
Old	SB053	≥5%	12	66	N
Old	SB066	≥5%	18	53	N
Moonlight-Antelope	PL122	≥5%	15	53	N
Moonlight-Antelope	PL006	≥5%	17	65	N
Moonlight-Antelope	PL229	≥5%	11	66	N
Moonlight-Antelope	PL284	≥5%	23	71	N
Moonlight-Antelope	PL107	<5%	0	51	Y
Moonlight-Antelope	PL123	≥5%	11	59	N
Moonlight-Antelope	PL042	≥5%	8	71	N
Moonlight-Antelope	PL073	≥5%	10	57	N

Fire	Site	% Post-fire Logging Category	% Post-fire Logging	% High- Severity Fire	Occupied?
Moonlight-Antelope	PL125	≥5%	17	72	N
Chips	Mosquito	<5%	4	60	Y
Rim	TUO027	≥5%	39	59	N
Rim	TUO028	≥5%	24	77	Y
Rim	TUO177	≥5%	25	64	Y
King	ELD051	<5%	2	50	Y
King	PLA039	<5%	0	60	Y
King	ELD085	<5%	4	75	Y
King	ELD058	<5%	0	67	N
King	ELD057	<5%	1	63	N
King	Rd. 12N46	≥5%	30	52	N
Lake	SB021	<5%	0	77	Y
Lake	SB041	<5%	0	78	N
Lake	SB138	<5%	0	65	Y
Butler2-Slide	SB137	≥5%	9	55	Y
Butler2-Slide	SB060	<5%	2	57	Y
Butler2-Slide	SB014	≥5%	14	57	N

between the <5% post-fire logging category (mean = 63.0%, SD = 9.2%, $N = 13$) and the ≥5% post-fire logging category (mean = 62.8%, SD = 8.5%, $N = 20$), as determined *a posteriori* using a t-test for two independent means ($t = 0.064$, $P = 0.949$). This indicates that the difference in site occupancy did not result from different levels of high-severity fire. Amongst the sites with ≥5% post-fire logging, the mean amount of such logging of the area within a 1500 m radius of site centres was 16.7% (SD = 8.7%).

For sites with <5% post-fire logging within a 1500 m radius of site centres, there was no difference in occupancy between such sites with 20–49% high-severity fire and those with 50–80% high-severity fire ($c^2 = 0.034$, $P = 0.854$, DF = 1, $N = 28$ sites).

Discussion

These results indicate that substantial declines in California spotted owl occupancy following large fires are primarily driven by post-fire logging of complex early seral forest—a forest habitat type created by high-severity fire effects in mature conifer forests and which this subspecies has been found to select for foraging (Bond et al. 2009). Spotted owls likely forage in complex early seral forests because abundant dead trees for perch sites are available for this sit-and-wait predator (Carey and Peeler 1995) and the small mammal prey base can increase in such habitat, particularly deer mice (*Peromyscus maniculatus*; Zwolak 2009, Fontaine and Kennedy 2012, Borchert et al. 2014). Under this study design, all spotted owl sites were confirmed occupied prior to post-fire logging. While none of the categories analysed had 100% occupancy following post-fire logging, this is expected given that spotted owls often temporarily abandon sites occupied in the

previous year, even where no logging or fire has occurred (USDA 1995). Thus, a portion of sites occupied in one year will not be occupied in the next. Conversely, a portion of sites not occupied in a given year may be re-colonised and occupied in the next year.

Concern has recently been expressed regarding the effect of large forest fires in the central Sierra Nevada on occupancy of the California spotted owl, particularly in sites with predominantly high-severity fire effects (Jones et al. 2016). Jones et al. (2016), who analysed the northern half of the 39,311 ha King fire of 2014, dismissed post-fire logging as a factor in the reduced spotted owl occupancy that they reported one year after the fire.

These results differ from those of Jones et al. (2016) in the King fire. There are some likely reasons for this difference. First, Jones et al. (2016) reported that a median of only 2% of the area within 1100 m circles around the site centres experienced post-fire logging based upon data obtained from privately owned forest management companies (Sierra Pacific Industries and Mason, Bruce & Girard Inc.). A mean of 6% post-fire logging within 1500 m circles was found (and a mean of 12% post-fire logging when sites with >80% high-severity fire are added), based on the methods described above, the FACTS database, Google Earth and physical inspection of the areas. This indicates a more pronounced role of post-fire logging when a larger portion of spotted owls' biological home range (Bond et al. 2009) is analysed. Second, Jones et al. (2016) reported that 8 sites, out of a total of 13 (Jones et al. 2016: figure 2) with >50% high-severity fire, experienced "site extinction" (i.e. were rendered unoccupied) due to the King fire. In fact these sites (PLA007, PLA065, PLA015, PLA109, PLA012, ELD060, PLA049 and PLA043) had not been occupied prior to the fire (based on spotted owl surveys conducted for the Forest Service, which were obtained from the agency). Many spotted owl sites have lost occupancy in recent years in this area likely due to extensive logging (Tempel et al. 2014). Thus, the conclusion by Jones et al. (2016), that the King fire caused the loss of occupancy in these sites, is not sound.

Jones et al. (2016) also reported that, for the foraging behaviour component of their study, spotted owls avoided high-severity fire areas, contrary to the findings of Bond et al. (2009). Jones et al. (2016) suggested that avoidance of high-severity fire areas may have explained reduced occupancy in sites with high levels of high-severity fire. However, Jones et al. (2016) did not account for distance from site centres for this central-place forager (Carey and Peeler 1995, Rosenberg and McKelvey 2009). They also included recent pre- and post-fire clearcut areas in their analysis of selection/avoidance of high-severity fire areas for foraging, rather than analysing foraging of intact, unlogged high-severity fire areas, as in Bond et al. (2009). Thus, the foraging behaviour results of Bond et al. (2009) and Jones et al. (2016) can be reconciled, given the owls' tendency to avoid clearcut areas (Call et al. 1992, Comfort et al. 2016), while selecting intact, unlogged high-severity fire areas dominated by an abundance of snags (standing dead trees) and shrubs (Bond et al. 2009).

Tempel et al. (2014) also reported an adverse effect of high-severity fires on California spotted owl site occupancy, mostly due to four sites that generally became unoccupied, or infrequently occupied, following the Star fire of 2001 on the Eldorado and Tahoe National Forests, amongst a sample size of 12 sites inside wildland fire areas.

However, these sites were heavily post-fire logged on both private timberlands and National Forest lands (Bond and Hanson 2014: Appendix C), a fact that was not reported by Tempel et al. (2014).

A common assumption has been that the occurrence of high-severity fires is increasing and is a major threat to the owl. This assumption is accompanied by recommendations for increased logging—especially “mechanical thinning”—on National Forest lands, intended to create low-density forests and reduce the potential for high-severity fires (Jones et al. 2016, Stephens et al. 2016). Post-fire logging and tree plantation establishment have also been promoted by the U.S. Forest Service in high-severity fire areas in an attempt to recover and restore mature, green forest cover (Peterson et al. 2015). However, these results and other research (Lee et al. 2013), indicate that post-fire logging of complex early seral forests is not consistent with California spotted owl conservation and mechanical thinning has been associated with dramatic and rapid population declines for this subspecies in the Sierra Nevada (Stephens et al. 2014). Further, multiple studies have indicated that there is no long-term increasing trend in high-severity fires in the Sierra Nevada (Hanson and Odion 2015, Keyser and Westerling 2017), or in the vast majority of the western U.S. (Keyser and Westerling 2017) since 1984.

The authors’ finding, that spotted owl sites with predominantly high-severity fire effects had 77% occupancy when <5% of the area within a 1500 m radius of territory centres was subjected to post-fire logging, is notable in the sense that it compares favourably with current California spotted owl occupancy levels in unburned, mature forest (Lee et al. 2012). More post-fire research is needed pertaining to spotted owls, including investigations of time-since-fire. This is especially true for spotted owl sites with higher levels of fire severity, such as those with >80% high-severity fire within a 1500 m radius of site centres, which are uncommon compared to those with lower levels of high-severity fire. However, most of the relatively few owl sites with such high-severity fire levels in larger fires are subjected to substantial post-fire logging on both private and public lands, undermining potential for scientific understanding of the owl’s relationship with such fire events. This will need to change in the future if one is to have sufficient data to analyse the effects of fire, versus the effects of post-fire logging, in sites with such levels of high-severity fire.

Conclusions

Adverse impacts to California spotted owl occupancy in large fires appear to be strongly influenced by post-fire logging, rather than fire alone. Increased logging of unburned forests has been proposed as a measure to curb fire behaviour (Jones et al. 2016), but such logging has been associated with a substantial and rapid loss of site occupancy (Stephens et al. 2014). Based on these results here and other research, it is suggested that such increased logging and the weakening of environmental protections that would be needed to facilitate it, are not a scientifically sound path forward towards recovery and conservation of declining California spotted owl populations.

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

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LETTER

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

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Mark E Harmon

Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, United States of America

E-mail: Mark.Harmon@oregonstate.edu

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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. Schladinger 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 analyses 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].

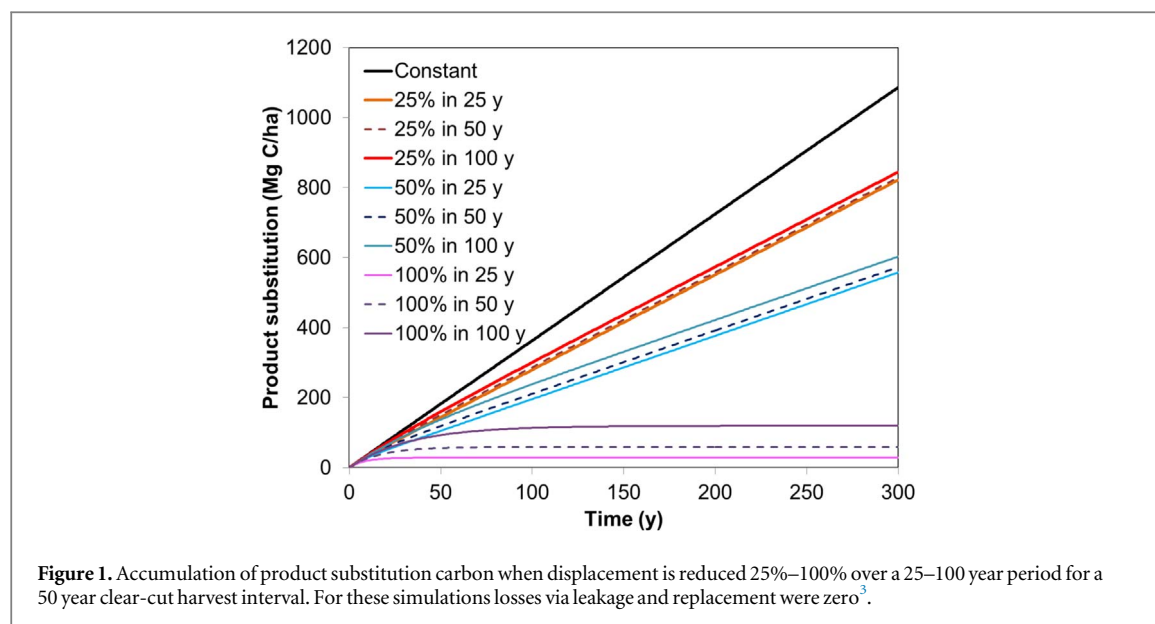
Methods

Each of the three assumptions was examined individually and then jointly for three contrasting initial conditions using a simple landscape model¹ 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.

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



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 estimates². 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 $\approx 89\%$.

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.

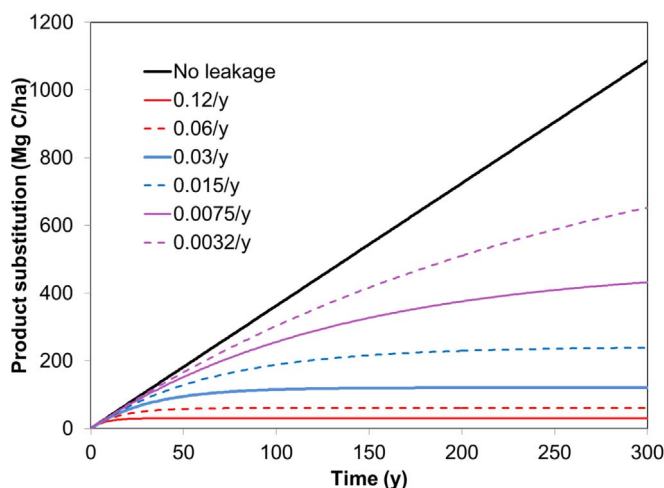


Figure 2. Accumulation of product substitution carbon when the time for displacement to be lost via leakage varies from 25 to 800 years for a 50 year clear-cut harvest interval. Displacement was assumed constant and replacement losses zero³.

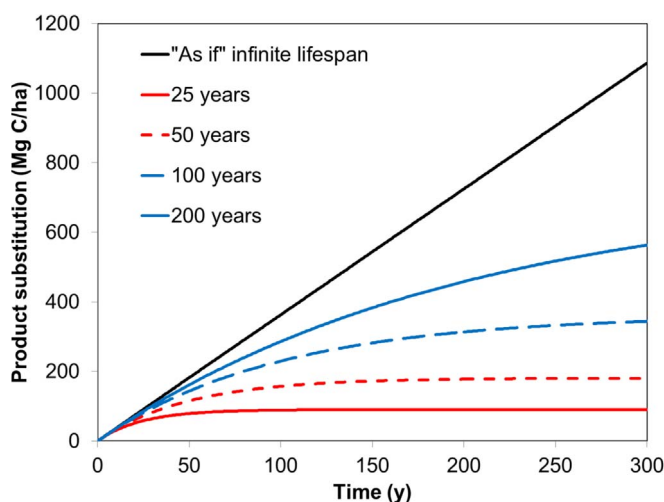


Figure 3. Accumulation of product substitution carbon when the average longevity of building varies for a 50 year clear-cut harvest interval. For these simulations displacement was constant and there were no leakage losses³.

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 $0.375\% \text{ yr}^{-1}$ (\approx one-third the current estimate of the minimum depletion rate [27]) the store at 300 years was $\approx 40\%$ lower than when there was no leakage. If the leakage rate-constant was $12\% \text{ yr}^{-1}$, then $\approx 97\%$ 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.

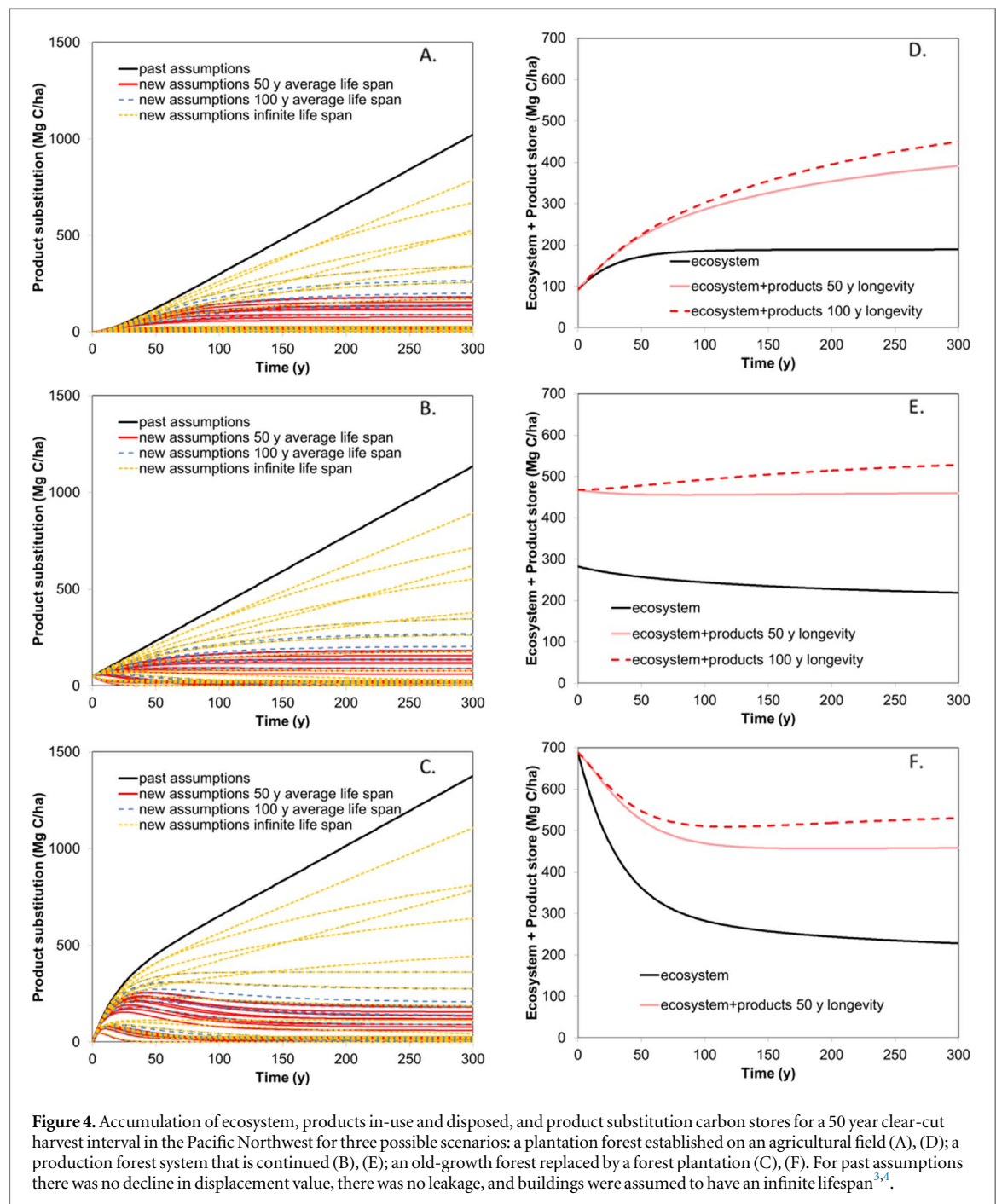
Replacement losses

For an average building longevity of 50 years the product substitution store at 300 years was $\approx 17\%$ 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 $\approx 52\%$ 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



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

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 fraction of harvested carbon, these underlying relationships would not be altered for these new situations⁴.

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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ORCID iDs

Mark E Harmon  <https://orcid.org/0000-0002-4195-8288>

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Article

Combustion of Aboveground Wood from Live Trees in Megafires, CA, USA

Mark E. Harmon ^{1,*}, Chad T. Hanson ² and Dominick A. DellaSala ³

¹ Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

² The John Muir Project, Earth Island Institute, Big Bear City, CA 92314, USA; chanson1@gmail.com

³ Wild Heritage, a Project of Earth Island Institute, 222 Joseph Drive, Talent, OR 97540, USA; dominick@wild-heritage.org

* Correspondence: mark.harmon@oregonstate.edu

Abstract: Biomass combustion is a major biogeochemical process, but uncertain in magnitude. We examined multiple levels of organization (twigs, branches, trees, stands, and landscapes) in large, severe forest fires to see how combustion rates for live aboveground woody parts varied with tree species, size, and fire severity in Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and mixed conifer-dominated forests of the Sierra Nevada, California, USA. In high severity fire patches, most combustion loss was from branches < 2 cm diameter; in low to moderate severity patches, most was from bole charring. Combustion rates decreased as fire severity declined and with increasing tree size. *Pinus* species had little branch combustion, leading them to have ≈50% the combustion rate of other taxa. Combustion rates could be 100% for small branch segments and up to 57% for small tree aboveground woody biomass in high severity fire patches. However, combustion rates are very low overall at the stand (0.1%–3.2%) and landscape level (0.6%–1.8%), because large trees with low combustion rates comprise the majority of biomass, and high severity fire patches are less than half of the area burned. Our findings of low live wood combustion rates have important implications for policies related to wildfire emissions and forest management.

Keywords: bole combustion; branch combustion; fire severity; mixed conifer forests; multi-level analysis; Sierra Nevada Mountains; wildfire combustion rates; wildfire effects; wildfire emissions



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1. Introduction

Combustion of biomass is a major biogeochemical process by which carbon is returned to the atmosphere from terrestrial ecosystems [1,2]. Fire has been an important process on Earth from at least the Silurian period over 400 million years ago [3]; since that period, this process has influenced the evolution of organisms [4,5], the successional state of ecosystems [6], and biogeochemical cycles including the concentration of oxygen and carbon dioxide in the atmosphere [7]. Although combustion is clearly a natural process that has occurred for much of Earth's history, there is also a current concern that the incidence of wildfires, due to changes in fuel loads and climate, has and will continue to increase in the future [8,9]. Increased combustion could thus serve as a positive feedback to climate change. However, there is also a concern that past estimates of vegetation combustion have been biased upward, with one study indicating that the amount of carbon released by live tree combustion has likely been overestimated by 59% to 83% [10].

The fraction of a fuel combusted in wildfire depends on the interaction of particle size, packing, moisture, distance from heat source, and rate of energy release [11–16]. Although most studies of fuel combustion are on dead biomass, theoretically they can be applied to live fuels and suggest the following mechanisms. As fire intensity (i.e., rate of energy release) increases, so do the temperatures, combustion, and woody plant mortality rates associated with fires. Fine twigs are in close proximity to leaves and other twigs (i.e., within tens of centimeters), leading to more exchange of energy than more distant plant parts;

hence, they are likely to be combusted. Moreover, their small diameter increases their surface area-to-volume ratio, allowing them to dry out and absorb energy faster than larger branches and stems. In contrast, large branch segments are not in such close proximity (i.e., separated by 10 to >100 cm), have a lower surface area-to-volume ratio, dry more slowly, and are less effective at absorbing energy from other burning particles. Tree stems or boles are separated by even more distance (i.e., often >1 m) and have a very low surface area-to-volume ratio when compared to twigs or branches; hence, they are the least likely to be combusted. As a result, the smallest diameter woody fuels are theoretically the most likely to be combusted in a wildfire [17].

Empirical estimates of the fraction of aboveground live woody vegetation combusted (as opposed to killed) by wildfires are highly uncertain, ranging from very little [10,17] to the majority [18]. It is unclear just how much of this variability in estimates is related to methodological differences as opposed to natural variation. We posit that smaller trees would have higher combustion rates than larger ones; moreover, high severity fire areas should have more combustion than low severity fire areas. Thus, natural variation in both vegetation structure and fire severity could lead to a large range in the combustion rate. However, when visual (either ground-based or remote) estimates of combustion after the fire are used, variation either among observers or methods can also introduce uncertainty.

Direct destructive methods are not practical, given the size of woody vegetation such as trees, and because combustion estimates require comparing biomass before and after a fire. Furthermore, there are hazards in working near an advancing fire front. Therefore, the most practical ways to estimate combustion rates are ground-based, post-fire estimates that can then be used to adjust existing biomass equations at the tree level (e.g., Miesel et al. [17]), make stand-level estimates of the proportion combusted (e.g., Campbell et al. [19]), and create similar types of estimates at larger spatial scales (e.g., Knorr et al. [1,2]). One challenge in making these estimates is to reconstruct the plant parts that were combusted. Another is to relate combustion estimates at one level (e.g., branches) to others (trees, stands, and landscapes); although there clearly has to be a relationship among these levels, most published estimates neither explicitly explore nor use this relationship.

Wildfires in California such as the Rim and Creek Fires have been used as an example of “fires of the future” in which wildfires become more intense, severe, and larger [20]. One of the many concerns related to such fires is the amount of carbon added to the atmosphere via combustion. Published estimates of combustion rates of aboveground live biomass from the Rim Fire, based on remote sensing, vary from 16% for low severity patches to 85% for high severity patches [18], whereas ground-based estimates from other fires [10], theoretical considerations (Figures S1 and S2), and ground-based observations (Figure S3) suggest much lower combustion rates. Therefore, our objective was to use ground-based methods to assess the fraction of aboveground woody carbon that is lost via combustion in low, moderate, and high severity patches in large fire complexes, and at multiple levels (twigs, branches and boles, individual trees, stands of trees, and the entire area in which a fire occurs), to test the following five hypotheses:

1. Smaller woody structures (e.g., twigs) would more likely to be completely combusted than larger ones (e.g., boles);
2. Combustion loss rates at the individual tree level would increase with fire severity and decrease with tree size (i.e., diameter and height);
3. High combustion rates in small trees would be countered by lower rates in the largest trees, reducing stand-level average combustion rates, because at the stand-level, larger trees contribute substantially more biomass than small ones;
4. Low and moderate severity patches are proportionally large enough and their combustion rates sufficiently low enough to reduce a fire’s average combustion rate at the landscape-level relative to that estimated for high severity patches.
5. Given Hypotheses 1–4, aboveground woody combustion at the stand to landscape levels would be an order of magnitude less than previously estimated at the Rim Fire (e.g., Garcia et al. [18]).

To address these hypotheses, we developed a more robust ground-based method to determine the fraction of live aboveground woody biomass combusted during wildfire based on a reconstruction of the biomass that was combusted from branches and from the bole (i.e., main stem), as evidenced by charring. We examined a range of fire severities and tree sizes to determine the proportional loss of branch and bole carbon. We then developed species- and size-specific models of combustion rates and applied them to a range of stand diameter distributions and fire severity spatial databases to estimate carbon losses at the stand and landscape level for multiple large fires that have been described as either high severity or catastrophic.

2. Materials and Methods

2.1. Study Area

Our field study areas were composed of mixed-conifer and *Pinus ponderosa* (Dougl. ex Laws.), which dominated forests in the Rim Fire of 2013 and the Creek Fire of 2020 within the central and southern Sierra Nevada Mountains of California, USA (Figure 1). The 104,176 ha Rim Fire was active from 17 August through 4 November of 2013 on the Stanislaus National Forest, some private lands, and the western portion of Yosemite National Park. The 153,738 ha Creek Fire was active from 4 September through 24 December of 2020, mainly on the Sierra National Forest, but including some private lands. Our field data collection locations ranged from 1370 to 1490 m elevation in the Rim Fire, and from 1520 to 2180 m elevation in the Creek Fire.

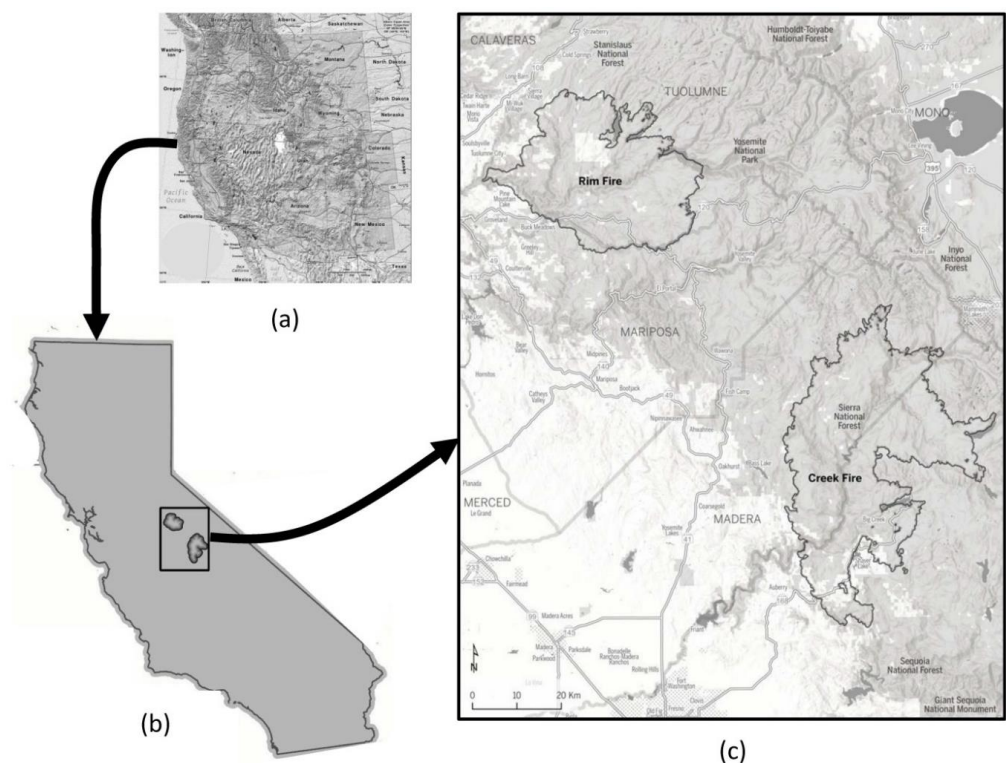


Figure 1. Location of study area in (a) western United States, (b) California, and (c) perimeters of 2020 Creek and 2013 Rim Fires in the Sierra Nevada Mountains, California.

At the lower elevations, these forests primarily consist of Ponderosa pine (*P. ponderosa*), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), sugar pine (*P. lambertiana* Dougl.), and California black oak (*Quercus kelloggii* Newb.), with shrubs mainly consisting of mountain whitethorn (*Ceanothus cordulatus* Kellogg), deer brush (*C. integerrimus* Hook. & Arn.), and greenleaf manzanita (*Arctostaphylos patula* Greene). At

the higher elevations in our study sites, the forests primarily consist of Jeffrey pine (*P. jeffreyi* Grev. & Balf.) and *A. concolor*, with some *C. decurrens* and occasional red fir (*A. magnifica* A. Murr.) at the highest elevations, and shrubs comprising mainly *C. cordulatus*.

2.2. Branch Models

Our branch models were based on branch orders, with first order branches representing the smallest twigs and second order branches representing branches where two first order branches joined, etc. (Figure S4). The benefit of this system is that it can be used to reconstruct the branch orders missing from those that remain given that higher order segments are more likely to remain than lower order ones.

2.2.1. Field Data for Branch Models

There were two phases of field data collection in the development of the branch models. First, branches from recently downed live trees or live tree tops of the main species present in the Rim and Creek Fires (*A. concolor*, *C. decurrens*, *P. lambertiana*, *P. ponderosa*, and *P. menziesii*) were dissected to determine the number, diameter, and length of the branch orders on individual branches. Mid-point diameter and the length were determined on a subsample of up to 10 of each branch order segments of each dissected branch; when there were <10, all segments were measured.

Second, we visually examined intact, standing trees of each of the five species listed above in each of six diameter at breast height (DBH) size classes (1.0–4.9, 5.0–9.9, 10.0–24.9, 25.0–49.9, 50.0–99.9, >100 cm) to determine branch structure, as defined by the highest branch order present on a tree, the maximum branch diameter, length of the highest branch order segment, and the total branch length of the highest branch order. Maximum branch order was determined by starting with the outmost twigs and visually assessing where they joined to form a second order, and where second orders joined to form third orders, and so on. Maximum branch diameter and lengths were estimated visually; however, these estimates were repeatedly checked against a caliper and meter stick when branches were low enough on the tree to be measured directly.

2.2.2. Branch-Level Models

The average maximum branch order, diameter, and length data, combined with the average bifurcation ratio (i.e., the number of lower order branches divided by the number of branches for the next higher order; see Figure S4), as well as segment diameter and length from the branch dissections, were used to develop tree species- and DBH size class-specific branch-level models. For lengths and diameters of orders not dissected, we interpolated between the highest order dissected and the highest order visually estimated. The volume of each branch order was calculated as the product of the branch segment area (as determined from the mid-length diameter), the length, and the number of segments. The total branch volume was determined by summing up all the branch order volumes and the relative branch order contribution was calculated as the ratio of the branch order volume to the total branch volume.

2.2.3. Tree-Level Branch Models

At the tree-level we developed three sets of models, with different weighting of the branches (Figure S5). The simplest used the relative contribution of orders found on the highest order branches of each species and DBH size class. We termed this the maximum branch order model. However, trees also contained branches that terminated at a lower order than those closest to the ground. We accounted for this by either using the total estimated volume of each branch for each DBH size class as a weighting factor (i.e., the volume-weighted model) or using an additional weighting factor related to the bole length each branch represented (i.e., the volume and length-weighted model).

2.3. Tree-Level Combustion Indicator Sampling

We collected field data in the spring of 2018 and 2021 for the Rim and Creek Fires, respectively. In both fire areas, we gathered data in each fire severity patch type (low, moderate, high) at five points separated by 50 m as determined by a laser hypsometer along straight-line transects through the middle of the patches. To determine the location of the fire severity categories, we used the U.S. Forest Service's "Rapid Assessment of Vegetation Condition after Wildfire" (RAVG) fire severity mapping system (<https://fsapps.nwcg.gov/ravg/data-access>, accessed on 1 May 2021). If we encountered a point location along transects that was a different fire severity category than targeted in the specific sample area, we skipped that location and proceeded to the next location, 50 m further along. Additionally, if the transect came to the end of a patch within a particular fire severity category, we changed the direction of the transect 90 degrees to stay within the patch.

At each point location, we recorded the GPS coordinates and data on individual conifer trees in six size classes (see above), using the closest tree from each size class to the point location. This theoretically resulted in 30 trees being sampled per transect. However, in some cases, certain DBH size classes were not present near a plot center. To replace these "missing" trees, we sampled others as we traveled between points within the fire severity patch. Although we did not sample by species per se, we generally found the full range of DBH size classes for the main species we encountered. In the case of *P. ponderosa*, our method did not provide sufficient numbers of small DBH trees in high severity fire patches. We therefore sampled an additional transect in a high severity patch that was dominated by *P. ponderosa* in small DBH size classes to supplement the database. In addition, because trees >100 cm DBH were uncommon, some of our point locations did not include any trees of this DBH size class. In such cases, for the Creek Fire, we sampled >100 DBH trees as we traveled between point locations.

For each tree in the Rim fire, we recorded species, DBH, height, live/dead status, distance from point location, char depth of bole, maximum bole char height, whether there was any consumption of branches (yes or no), percentage of crown length killed, diameter of the smallest branches remaining, diameter of the largest branches consumed, and percentage consumption of each order of branches. The diameter of each tree was determined using either a DBH tape or a large caliper to the nearest 1 cm. The heights of DBH size classes 3–6 were visually estimated (with periodic checks using a clinometer and tape or hypsometer), whereas those of the smaller DBH size-classes were estimated using a meter stick. The maximum height or relative height (depending on the distance) of charring was determined, as we had assumed there would be a fixed relationship between the maximum and minimum char height. The char depth on the bole was visually estimated after a subset of trees had been examined by cutting into them with either a knife or hatchet. If crown consumption was noted we visually estimated the smallest branch diameter remaining and the largest one combusted, periodically checking these estimates with a caliper. The fraction of each branch order combusted was visually estimated when crown combustion had occurred as 5%, 10%, 25%, 50%, 75%, 90%, 95%, or 100% combustion. Given that the Rim Fire occurred several years before sampling, we distinguished between branches lost via decomposition-related fragmentation and combustion (Figure S6).

In the Creek Fire, we generally followed these same methods at each point with some changes to improve precision. At the Creek Fire, all tree heights were determined either using a clinometer and hypsometer or, if they were short enough, with a meter stick. We determined the minimum and maximum char height (percentage of tree height), given our observations on the Rim Fire that the char height often varied substantially on one side of the tree versus the other side. A detailed examination of char depth at the Rim Fire indicated that the char depth was variable enough that it needed to be determined on each tree. Therefore, at the Creek Fire we used a hatchet to chop into each bole on at least two places to determine the depth of char (generally in 0.5 cm increments).

2.4. Estimate of Wildfire Intensity

We used van Wagner's scorch height model [21] to estimate I , the fire line intensity ($\text{kcal m}^{-1} \text{s}^{-1}$) of the sampled areas:

$$\text{Scorch height} = 0.385 \times I^{0.66} \quad (1)$$

with the maximum height of bole char (m) serving as the scorch height. For high severity fire patches, we used the maximum height observed on transects to indicate fire intensity. We did this for moderate and low severity fire patches as well; however, also we calculated the average fire intensity using all the trees in those transects because for these two severities it may be more representative than the maximum.

2.5. Tree-Level Combustion

The Jenkins et al. [22] general softwood equations were used to predict the proportion of aboveground woody mass in boles versus branches as a function of DBH (Figure S1). Data on the proportion of branch volume combusted were then combined with this to determine the fraction of each tree's total aboveground woody biomass lost to branch combustion.

We also used the data on bole char height and depth to estimate proportion of aboveground woody biomass lost to combustion. For the Rim Fire we made several estimates, since only the maximum height of bole char was noted. First, we assumed that the minimum and maximum char heights were equal, giving a maximum bole combustion estimate. Second, we used the relationship between the minimum and maximum bole char height found for a subsample of trees examined in detail on the Rim Fire (Figure S15). This gave the minimum bole combustion estimate. The data on bark char depth collected at each fire were then used to estimate the volume of char, assuming that the char depth declined as one went up the tree, reaching zero where the char ended. We assumed that 46% of the bark's C was lost via pyrolysis [23] during bole charring, based on the average of Czimczik et al. [24].

Individual tree estimates of the fraction combusted for each fire intensity class were used to develop non-linear regression models using SAS procedure NLIN with the Gauss method and parameter bounds [25] that would predict the proportion of branches, boles, and aboveground woody biomass consumed as a function of tree DBH. We estimated models for each fire severity class and species group (i.e., all species together, *Pinus* species, and other species). Species groups were based on a preliminary analysis, which indicated that species in the genus *Pinus* appeared to have substantially lower combustion rates (particularly of branches) than the other conifer species. Although we analyzed all six sets of estimates based on the branch and bole scorch models used, we largely present results for the estimates based on volume weighting of branches and maximum bole char height models.

The tree-level combustion models used were interrelated and based on negative exponential functions with multiple components. The most complicated was a negative exponential model with an asymptote that separated the response into three components:

$$\text{Combustion}_{\text{DBH}} = \text{Combustion}_1 e^{-k_1} + \text{Combustion}_2 e^{-k_2} + \text{Combustion}_3 \quad (2)$$

where Combustion_1 , Combustion_2 , and Combustion_3 pertain to the combustion maximums (percentage) for component 1, 2, and 3, respectively; k_1 and k_2 (cm^{-1}) determine the rate the first two components decline with increasing DBH. We also ran simpler models including a dual component negative exponential (i.e., Combustion_3 was zero):

$$\text{Combustion}_{\text{DBH}} = \text{Combustion}_1 e^{-k_1} + \text{Combustion}_2 e^{-k_2} \quad (3)$$

a single component, negative exponential decline to an asymptote (i.e., k_2 was zero):

$$\text{Combustion}_{\text{DBH}} = \text{Combustion}_1 e^{-k_1} + \text{Combustion}_2 \quad (4)$$

and a single component negative exponential (i.e., Combustion₂ was zero)

$$\text{Combustion}_{\text{DBH}} = \text{Combustion}_1 e^{-k_1} \quad (5)$$

As Proc NLIN automatically reduced the number of parameters when a simpler model was sufficient to fit the data, the Akaike Information Criteria (AIC) was not necessary to select the simplest model. Therefore, our primary method to identify the “best” model was goodness of fit, which was calculated as:

$$r^2 = 1 - \text{SS}_{\text{error}} / \text{SS}_{\text{corrected total}} \quad (6)$$

where SS is the sums of squared deviations for either the error term or the corrected total. We also examined residuals to determine if there was a bias at any point in the DBH range examined and selected the model with the minimum bias.

2.6. Stand-Level Combustion

We estimated the total stand-level combustion losses for each of the fire severity classes from our combustion regression models and published data on DBH size class structure for mixed conifer forests in the California Sierra Mountains [20,26–29]. While some of the publications reported DBH size structure for species or *Pinus* versus other species, some did not [28,29]. However, the latter did report the relative contribution of species to basal area. We therefore apportioned the number of stems in each DBH size class by the proportion of basal area of species.

Total aboveground biomass was estimated from DBH using equations for species groups developed by Chojnacky et al. [30]. Biomass in branches and boles were calculated from total aboveground biomass using the Jenkins et al. [22] general softwood equations, predicting the proportion of aboveground woody mass in boles versus branches as a function of DBH. To calculate the combustion loss for each tree in a fire severity class (e.g., low severity) the appropriate biomass term (e.g., branch) was multiplied by the combustion rate, predicted from the corresponding combustion–DBH model (e.g., branch–low severity). We also estimated the fraction of combustion coming from branches versus boles.

2.7. Landscape-Level Combustion

To explore the consequences of the distribution of fire severities at the landscape-level (i.e., the entire area burned) we weighted the losses for each fire severity class at the stand-level by the abundance of the severity class on the landscape for the five largest Sierra Nevada fires occurring during 2011–2020 in conifer forests on national forest lands that were composed >50% by *P. ponderosa*, *P. jeffreyi*, and mixed-conifer forest types. In addition to the Creek Fire and Rim Fire, this included the 61386 ha Rough Fire of 2015, the 129068 ha Bear Fire of 2020, and the 70487 ha Castle Fire of 2020, all within the Sierra Nevada region. The Rapid Assessment of Vegetation Condition after Wildfire (RAVG) dataset (<https://fsapps.nwcg.gov/ravg/data-access>, accessed 15 November 2021) was used to determine distributions for conifer forests on national forest lands in three severity classes: low (<25% basal area mortality), moderate (25%–75% basal area mortality), and high (>75% basal area mortality).

3. Results

3.1. Tree Mortality

A total of 511 trees were examined on transects: 177 from the Creek Fire and 334 from the Rim Fire. For the high severity fire patches sampled, 99.4% of the 175 trees examined were killed by fire. For moderate severity fire patches, 68.4% of 165 the trees examined were killed, and for low severity fire patches, 47.9% of 171 trees were killed (mostly in the smallest size classes). Mortality rates, based on tree numbers, were quite similar between the two fires, with the maximum difference for low severity fire patches: 38–43% mortality of stems on the Creek Fire and 39%–52% on the Rim Fire (Table 1).

Table 1. Mortality, maximum scorch and tree height, and estimated fire intensities for Creek and Rim fires in California’s Sierra Mountains.

Severity Class	Transect	Mortality ¹ (%)	Maximum Scorch Height (m)	Maximum Tree Height (m)	Fire intensity Maximum (kcal m ⁻¹ s ⁻¹)	Average (kcal m ⁻¹ s ⁻¹)
Creek Fire						
High	1	100	53	53	≥1740	NA ²
High	2	100	45	45	≥1358	NA
Moderate	1	63	25	31	557	71
Moderate	2	72	32	61	826	156
Low	1	38	25	56	557	79
Low	2	43	25	53	557	83
Rim Fire						
High	1	100	30	30	≥735	NA
High	2	96	30	30	≥735	NA
High	3	100	39	43	1081	NA
High	4	100	40	40	≥1136	NA
Moderate	1	68	22	31	459	87
Moderate	2	75	18	33	339	80
Moderate	3	64	10	30	139	47
Moderate	4	58	13	50	207	38
Low	1	39	10	36	139	26
Low	2	52	10	39	139	27
Low	3	50	17	38	311	30
Low	4	50	15	40	257	34

Notes: ¹ On a percentage of trees examined basis; ² An average is not applicable for high severity fire patches because scorch height is limited by tree height; hence, only the tallest trees can indicate the scorch height.

3.2. Estimates of Fire Intensity

High severity fire patches had at least an order of magnitude higher intensity than moderate and low severity fire patches; however, for the most severe fire patches, the intensity estimate was limited by the heights of trees present at a site (Table 1; Figure S13). Specifically, for high severity fire patches, fire intensity estimates ranged from 735 to 1740 kcal m⁻¹ s⁻¹, but for most of these patches the maximum tree height and maximum scorch height were the same. Since maximum tree height ranged from 30 to 53 m, it is likely that fire intensity was considerably higher for some of the high severity patches that we examined. Fire intensity estimates based on maximum tree height ranged from 139–826 kcal m⁻¹ s⁻¹ to 139–557 kcal m⁻¹ s⁻¹ for moderate and low severity, respectively. Average fire intensity ranged from 38–156 kcal m⁻¹ s⁻¹ to 26–83 kcal m⁻¹ s⁻¹ for moderate and low severity fire patches, respectively.

3.3. Branch Models

Diameter and length of dissected branch segments increased with order for each species (Figure S7). First order branch segment diameters ranged from 2.0 ± 0.1 (mean ± standard error) to 12.3 ± 0.3 mm for *A. concolor* and *P. ponderosa*, respectively (Table S1). Diameters of the highest branch orders on the largest DBH size class ranged from 80 ± 33 to 150 ± 3 mm, for *A. concolor* and *P. menziesii*, respectively (Figure S8b). The length of first order branch segments also varied among species, ranging from 11.2 ± 0.7 (*A. concolor*) to 36.6 ± 2.5 cm (*Pinus*) (Table S1). Average length of the highest branch order segment for the largest two DBH size classes ranged from 110 ± 4 cm for *C. decurrens* to 330 ± 30 cm for *P. lambertiana* (Figure S8d). Based on these dimensions, the highest order branch segments contained 374–62,241 times more volume than first order ones.

The bifurcation ratio on dissected branches varied among branch orders within a species, ranging from 2 to 25 (Table S2). In some species (*P. ponderosa* and *C. decurrens*),

the bifurcation ratio decreased as branch order increased; however, in others (*A. concolor*, *P. lambertiana*, and *P. menziesii*), the maximum bifurcation ratio occurred between orders two and three. The highest branch order on a tree significantly varied with DBH size class and species (Figure S8a). The maximum branch order observed also varied, the lowest being 3.8 ± 0.2 for *P. ponderosa* and the highest being 6.4 ± 0.2 for *C. decurrens*. Based on the bifurcation ratios observed, first order branch segments for the largest DBH size class were 52–2755 more numerous than the highest order segments.

The relative contribution of branch orders differed among species and DBH size classes with *A. concolor* and *P. ponderosa* exhibiting the most divergent patterns (Figure 2). In general, as DBH size class increased, the contribution of the highest order branches increased and that of order one decreased. Specifically, branch order one of DBH size class one comprised 25% to 55% of the branches; however, for DBH size class six, branch order one comprised 0.5%–8.6% of the branches.

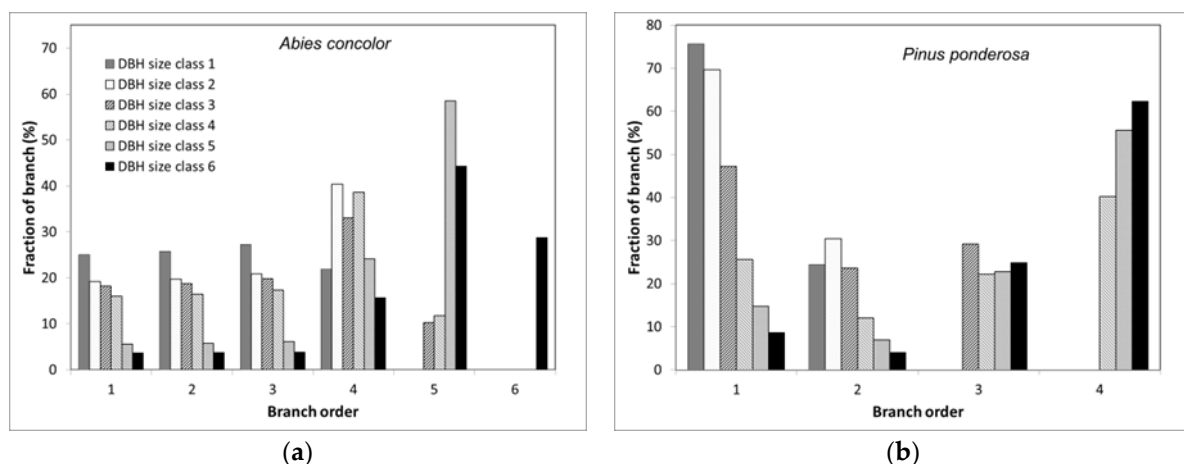


Figure 2. Relative contribution of branch orders to branch volume for (a) *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. and (b) *Pinus ponderosa* Dougl. ex Laws. for range of DBH size classes. These values are from the model that used the highest order branches found on a species-DBH size class combination.

The maximum order method estimated the lowest contribution of branch orders one to three in larger DBH size classes, whereas weighting by volume estimated the highest. However, the way that branches were weighted to produce tree-level branch models had limited effect on the relative contributions of branch orders and did not influence the overall pattern observed (Figure S9). For example, in the case of *C. decurrens* of DBH size class six, order one branch segments comprised 4% of the branches when the maximum order branch present model was used, but 5% when weighted by branch volume or when weighted by branch volume and bole length.

3.4. Branch Segment Sizes Consumed

Observations of the maximum branch segment diameter consumed by fire suggested that only the lowest few orders of branch segments were consumed even in the most severe fire patches, a finding consistent with Hypothesis 1. The largest diameter of branch segments consumed by fire was 2 cm and 1.5 cm at the Rim and Creek fires, respectively. However, the average maximum branch diameter consumed was 0.8 cm and 0.6 cm at the Rim and Creek fires, respectively. These observations of branch consumption were predominately in high severity fire patches (152 of a total of 197 branch consumption observations). Our findings suggest major limits on how much of a tree's aboveground woody biomass can be combusted (Figures S10 and S11).

The smallest diameter branch segments remaining averaged 0.1 cm and 0.3 cm on the Rim Fire and Creek Fire, respectively. As with maximum diameter consumed, the

majority of these observations were on high severity fire patches, given that consumption of branches was uncommon in low and moderate severity fire areas. Although very few small diameter branch segments remained on trees in high severity patches, there were always some to be found, particularly on larger trees. For example, in high severity fire patches, 90% of the first order branches of DBH size class one were combusted on average; in contrast, <50% of first order branch segments were combusted for DBH size classes five and six. This indicated that branch combustion was far from complete even in these extreme settings.

3.5. Bole Charring

The maximum char height on tree boles was a function of both DBH and fire severity (Figure S13). For high severity fire patches, the maximum char height generally followed tree height regardless of DBH. For low fire severity, char height was generally <10 m, although some exceptions occurred. This meant that the majority of trees in low severity patches had less than half of their bole length charred.

Although we had initially assumed that fire would have consumed some of the diameter at the trees' base, we rarely saw evidence of this, except on very small diameter trees and a few large *C. decurrens*. Instead, we mostly found evidence of charring. At the Creek Fire, with a few exceptions, the range of char depth was from 0.1 to 2 cm (Figure S14); although the range was generally similar to that at the Rim Fire, more individuals in the low severity patches at the Rim Fire were assigned a char depth of zero. To some degree this may reflect the presence of unburned spots, but it also might reflect a bias caused by not chopping into each tree to distinguish between charring and surficial soot deposition. To estimate bole combustion, we therefore assigned a nominal char depth of 0.1 cm for any tree from the low severity patches of the Rim Fire that had bole scorch.

3.6. Branch Combustion

Combustion of branches declined substantially as fire severity decreased, with the maximum consumption of 100%, 71%, and 45% for the smallest DBH trees in high, moderate, and low severity fire patches, respectively (Figure S12). The average for the smallest DBH size class was lower: 71%, 11%, and 2.6% for high, moderate, and low severity fire patches, respectively. Consistent with Hypothesis 2, branch combustion declined as DBH increased, with the largest DBH size class having an average of 2% branch combustion for high severity fire patches. *Pinus* species had substantially less branch consumption than other species regardless of fire severity; this was likely due to their larger diameter in the lowest branch orders (i.e., 1–3) when compared to the other species.

Nonlinear regressions supported these conclusions, with the sum of the Combustion_{1-3} parameters being lower as fire severity decreased and lower for *Pinus* species than other species (Table S3). The combustion maximums of the regressions could be substantially lower than the highest combustion estimates reported above, as not all trees in the smaller DBH's had high combustion rates. Although the majority of non-linear regressions were significant, the goodness of fit declined with fire severity from 0.3 to 0.6 and 0.06 to 0.08 for high and low severity fire patches, respectively. This was likely due to the fact that as fire severity decreased, the number of trees without branch consumption also increased. *Pinus* species in moderate to low severity patches had the only non-significant regressions; however, this was likely due to the fact that few branches on *Pinus* species were consumed at these two fire severity levels. In general, the number of parameters needed to fit the observations declined as fire severity decreased, with high severity best fit by a dual negative exponential, but low severity best fit by a single negative exponential or in some cases a constant.

3.7. Bole Combustion

Consistent with Hypothesis 2, combustion of boles also declined as fire severity decreased, with a maximum estimate of consumption of 24.6%, 13.5%, and 13.5% for

the smallest DBH trees in high, moderate, and low severity fire patches, respectively (Figure S12). For the smallest DBH size class, the average bole combustion rate was 9.4%, 2.8%, and 2% in high, moderate, and low severity fire patches, respectively. For the largest DBH size class, bole combustion averaged 1.3% for high severity patches and 0.1% for low severity patches, indicating a decline by roughly an order of magnitude from the smallest to the largest trees. The differences between *Pinus* and other species in bole combustion rates was less evident than for branch combustion rates; however, the maximum bole combustion (as indicated by the sum of Combustion_{1–3}) for *Pinus* species was substantially lower than that of the other species, which was likely related to the thinner depth of char for *P. ponderosa* (Figure S15b).

The majority of non-linear regressions for bole combustion were highly significant, but as with branch consumption the goodness of fit declined as fire severity decreased (Table S4). Specifically, the goodness of fit for high severity patches was 0.66–0.75, whereas for low severity patches it was 0.14–0.34. As with branches, consumption was predicted to decrease as DBH increased. *Pinus* species regressions had higher maximum combustion values than the other species; however, the rate that combustion declined with increasing DBH was higher, leading to a prediction of lower combustion rates for *Pinus* species over most of the DBH range.

3.8. Tree-Level Combustion

Consistent with Hypothesis 2, combustion of aboveground woody parts declined as DBH increased and fire severity decreased, with the maximum consumption observed to be 56.7%, 57%, and 30.2% for the smallest DBH trees in high, moderate, and low severity fire patches, respectively (Figure 3). The average, as opposed to the maximum, consumption for the smallest DBH size class was 34.9%, 7.2%, and 2.3% in high, moderate, and low severity fire patches, respectively. As with branches and boles, there was a substantial decline in aboveground woody consumption as DBH increased, so much so that even for high severity patches the largest DBH size class averaged 1.4% consumption. *Pinus* species generally had lower consumption rates than the other tree species, with the largest differences for smaller DBH's in high severity fire patches.

The non-linear regressions for the different species groups and fire severities were highly significant (Table 2). The sum of the Combustion_{1–3} parameters declined as fire severity declined; in the case of species other than *Pinus* it was 74.3%, 26.5%, and 5.3% for high, moderate, and low severity fire patches, respectively. Although these are higher than reported above, the regression equations predict a maximum of 58.7%, 16.7%, and 4.1% for trees with a DBH of 1 cm. *Pinus* species had lower combustion than the other species, but the Combustion_{1–3} parameter sums for *Pinus* species sometimes exceeded that of other species. However, *Pinus* species generally had steeper declines with an increase in DBH, leading to a lower predicted consumption rate for most of the diameter range. As with branches and boles, the goodness of fit declined as fire severity decreased; this was specifically from 0.72 to 0.80 and 0.07 to 0.20 for high and low severity fire patches, respectively.

Although Figure 3 displays the results for the volume weighted–maximum bole scorch method, the other five methods produced very similar, if somewhat lower estimates of combustion (Figure 3d). As anticipated, the maximum order–minimum bole scorch method produced the lowest estimates of combustion. The largest difference was 5% lower than the for volume weighted–maximum bole scorch method for intermediate levels of combustion, but for low and high combustion levels it was considerably less (<2%). Therefore, we conclude that the regression models in Table 2 predict the highest level of combustion of any of the methods used.

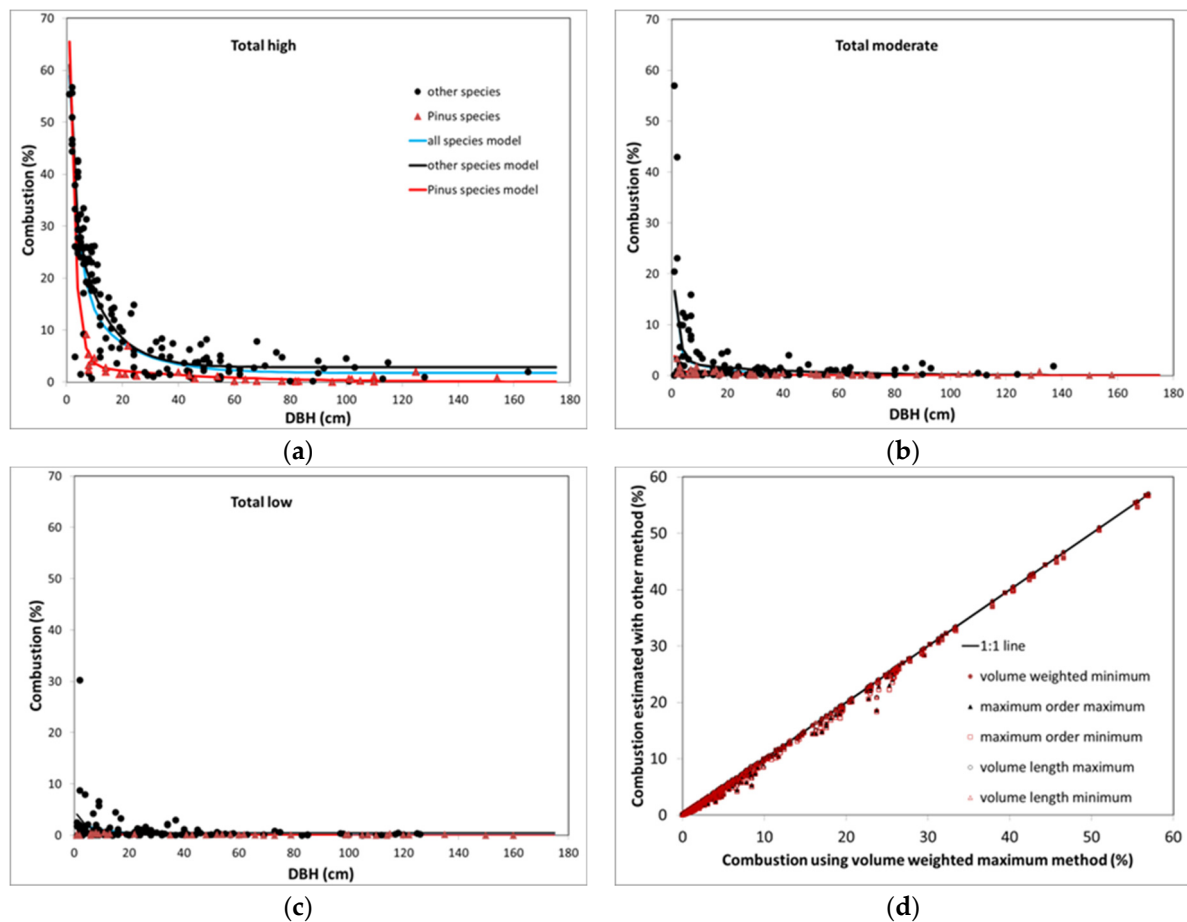


Figure 3. Total aboveground consumption as a function of fire severity and diameter at breast height (DBH) at Rim and Creek fires in California’s Sierra Mountains: (a) high severity; (b) moderate severity; (c) low severity; and (d) estimates of total combustion using other methods when compared to estimates weighting branches by volume and assuming maximum bole scorch.

Table 2. Non-linear regressions predicting aboveground woody consumption in Creek and Rim Fires as a function of DBH for different fire severity classes and species groups.

Species Group ¹	Combustion ₁	Combustion ₂	k1	k2	r ²	DF	n	Significance ²
High severity								
All	55.4(8.7)	19.2(9.4) 1.7(1.2) ³	−0.35(0.11)	−0.06(0.03)	0.80	4	173	***
Other	50.6(16.6)	34.8(8.0) 2.8(1.0) ³	−0.65(0.31)	−0.09(0.02)	0.72	4	139	***
Pinus	100(0)	3.5(1.2)	−0.48(0.05)	−0.02(0.01)	0.72	3	33	***
Moderate severity								
All	28.8(12.3)	3.7(3.0)	−0.81(0.43)	−0.06(0.06)	0.25	4	162	***
Other	24.0(8.1)	2.5(2.6)	−0.53(0.27)	−0.02(0.04)	0.25	4	110	***
Pinus	8.8(17.7)	0.9(0.3)	−1.07(1.01)	−0.04(0.02)	0.43	4	51	***
Low severity								
All	2.6(0.7)	0.5 (0.3)	−0.09(0.04)		0.07	2	169	***
Other	4.7(2.1)		−0.28(0.17)		0.09	2	130	**
Pinus	0.2(0.1)		−0.01(0.01)		0.20	2	38	***

Notes: ¹ The Pinus species group included *Pinus jeffreyi*, *P. lambertina*, and *P. ponderosa*; the other species included *Abies concolor*, *A. procera*, *Calocedrus decurrens*, and *Pseudotsuga menziesii*. ² Significance levels: NS-not significant; ** −0.01 > *p* > 0.001 >; *** -> *p* > 0.001. ³ This regression involved an additional asymptotic parameter, Combustion₃.

3.9. Stand-Level Combustion

Our stand-level results were consistent with Hypothesis 3. Applying the tree level combustion models to published DBH distributions indicated that stands within high severity fire patches combusts 1.2%–3.2% of the aboveground woody biomass (Figure 4a). In contrast, the same stand structure in a low severity fire patch combusted 0.1%–0.2%. The estimates for moderate fire patches were closer to low than high severity, with 0.2%–0.5% combusted. This indicates combustion rates do not correlate linearly with mortality rates.

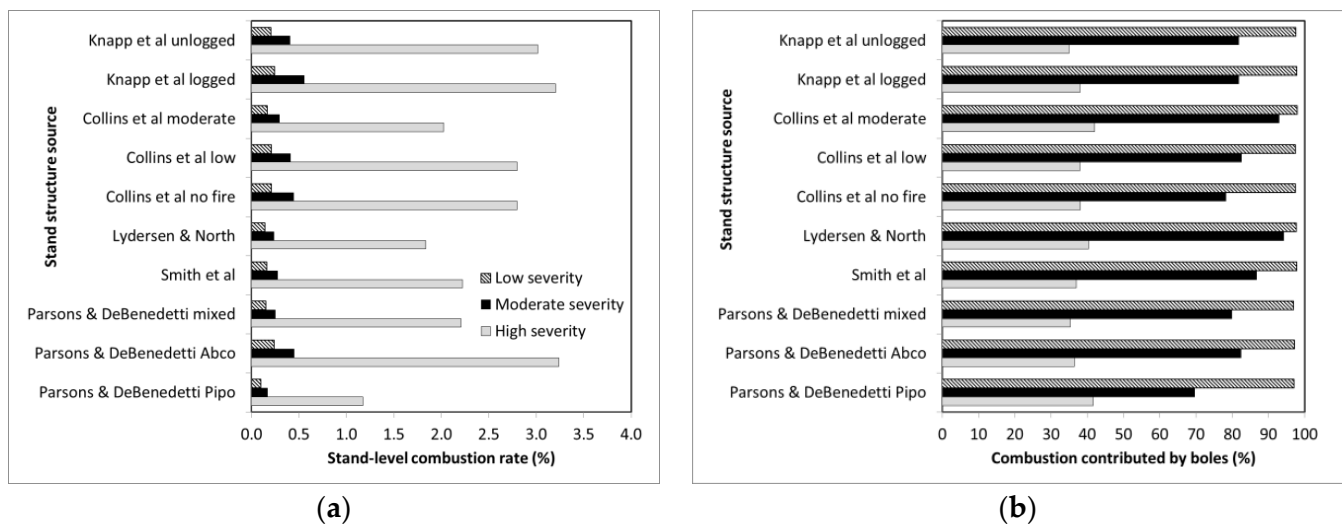


Figure 4. Stand-level combustion for published DBH size distributions for mixed conifer forests in the Sierra Nevada Mountains, California: (a) total combustion for high, moderate, and low severity fires; and (b) portion of combustion contributed by boles for high, moderate, and low severity fires. Collins et al. moderate and low severity refers to stands that had been disturbed by moderate and low severity fires in the past, respectively.

For moderate and low severity patches the majority of combustion losses (70%–98%) were related to bole combustion (Figure 4b). For high severity patches, combustion losses were predicted to largely come from branch consumption, as bole consumption was 35%–42%. This non-linear transition in combustion sources as one proceeds from high to moderate severity patches is likely the cause of the response of stand-level combustion to changes in fire severity.

3.10. Landscape-Level Combustion

For the five large fires examined RAVG indicated high severity patches comprised 45%–52% of the area, being lowest for the Rim Fire and highest on the Bear Fire (Table 3). Low severity patches (37%–44%) were more abundant than moderate severity ones (11%–16%).

Table 3. Distribution of fire severity classes as determined by RAVG for five large wildfires occurring between 2013 and 2020 in California's Sierra Mountains.

Fire Name	Year	Total Area (ha)	Low Severity ¹	Moderate Severity	High Severity
Rim	2013	104,176	0.436	0.143	0.421
Rough	2015	61,386	0.404	0.161	0.435
Bear	2020	129,068	0.373	0.111	0.516
Castle	2020	70,487	0.366	0.160	0.474
Creek	2020	153,738	0.416	0.132	0.452

Notes: ¹ Low severity (<25% basal area mortality), moderate severity (25%–75% basal area mortality), and high severity (>75% basal area mortality) as determined by RAVG.

When these severity distributions were used to estimate the landscape average, we found combustion rates ranged from 0.6% to 1.8% (Figure 5). Within a given fire, the difference between the minimum and maximum combustion rate associated with different DBH structures and species composition was 1.0%–1.1%. This difference increased as the proportion of high severity patches increased. Moreover, the lowest values were for older *P. ponderosa* dominated stands and the highest combustion rate was for logged mixed conifer stands. When the mid-point value was used to represent a mix of species and DBH structures, then the landscape combustion rate would have been 1.0%–1.2%, a result consistent with Hypothesis 4.

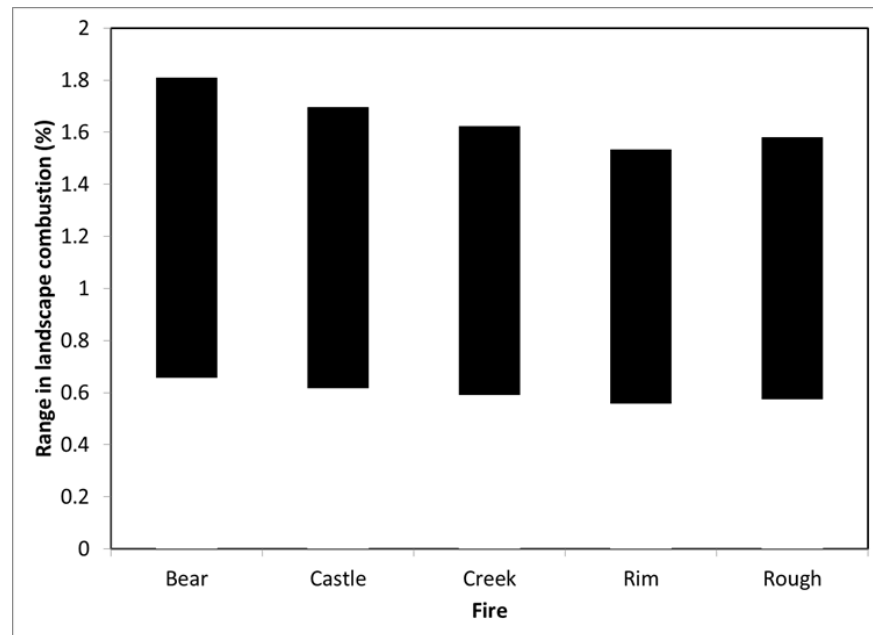


Figure 5. Landscape-level estimates for aboveground woody biomass combustion for five large, severe fires in the California Sierra Mountains. The range presented is for the various stand structures presented in Figure 4.

4. Discussion

4.1. Evaluation of Hypotheses

We employed a novel, field-based method to estimate the fraction of aboveground woody biomass combusted in large wildfires and evaluated five hypotheses that span multiple levels, ranging from tree parts to landscapes. The advantage of our method is that findings at one level can be related to another. For example, although we did find high rates of biomass combustion for some portions of branches and for small trees in high severity fire patches, a number of factors led the average combustion rate at higher levels of organization (i.e., trees, stands, and landscapes) to be substantially lower. Below, we evaluate each of our hypotheses in turn.

4.1.1. Hypothesis 1

Our findings for branches and to some degree for boles were consistent with Hypothesis 1. We did not observe any live branches >2 cm diameter that were fully combusted in even the most severe fire patches; it is likely that 2 cm represents an approximate combustion threshold in terms of the proximity, surface area-to-volume ratio, and drying rates of branch segments. Moreover, the 2 cm diameter limit suggests that for the species we examined, only branch orders one to three are of potentially combustible size. This places significant constraints on how much of a branch or tree can be combusted (Figures S10 and S11).

We found that, while all sizes of trees had losses from bark charring, this loss was proportionally highest for the smallest diameter trees. However, this may have been more related to proximity to ground fuels and the distribution of energy release than diameter per se. This suggests that proximity to heat source is also important to consider.

4.1.2. Hypothesis 2

We found multiple lines of evidence to support Hypothesis 2. Specifically, our branch models predicted that as DBH increased the proportion of branches susceptible to combustion declined. Using *A. concolor* as an example, orders one to three (the most susceptible to combustion) comprise 78% and 11% of branches for DBH size classes one and six, respectively (Figure S10). At the level of trees, the proportion of branches in total aboveground woody biomass declined as DBH increased, which meant that even if the combustion rate of branches was constant, the fraction of total woody biomass combusted would be reduced 60% from the smallest to the largest DBH trees. Combining these two DBH-related effects suggests that 1.8%–31% of aboveground woody mass could be consumed for this species, with the highest value for the smallest trees (Figure S11). These estimates pertain to *A. concolor* in high severity fire patches; very little branch consumption occurred in low and moderate severity fire patches. Specifically, in moderate severity patches, only 17% of the trees had evidence of crown consumption. In low severity patches, even fewer trees (6%) had evidence of crown consumption. This suggests that on moderate and low severity fires, one could expect that 0.3%–5.3% and 0.1%–1.9% of aboveground woody biomass would be consumed at the level of trees, respectively, with the higher values pertaining to the smallest trees.

We found that the rate of bole combustion related to charring also declined as tree size increased. Although char depth increased to some degree with fire severity, the main effect was to char more of the bole length as fire severity increased (Figure S13). In contrast to Hypothesis 2, tree species had a larger effect on bole combustion than tree size. The differences in char depth among species seemed to be related to bark density, with less dense bark exhibiting a deeper char layer (Figure S15b).

4.1.3. Hypothesis 3

At the stand-level, consistent with Hypothesis 3, higher combustion rates (i.e., 34.9% in high severity fire patches) in the smallest trees were strongly offset by the lower ones (i.e., 1.4% also in high severity fire patches) in larger trees because biomass increases exponentially with DBH. Consider that it would take $\approx 190,000$ 1 cm DBH trees to equal the biomass of a single 100 cm DBH tree (or $\approx 30,000$ to equal a 50 cm DBH tree). Thus, while small DBH trees might be orders of magnitude more abundant than larger ones, they are not sufficiently abundant to counter the effects that a few larger DBH trees have on stand-level combustion rates. In addition, increasing the proportion of biomass in *Pinus* species greatly decreased stand-level combustion rates, because branches of these species were rarely combusted. This suggests that estimates of stand level combustion rate need to account for differences in taxa as well as tree sizes.

4.1.4. Hypothesis 4

Consistent with Hypothesis 4, we found that, at the landscape level, the very low rates of combustion in low and moderate severity fire patches diluted the effects of higher combustion rates in high severity fire patches. The much lower rates of combustion observed in low and moderate severity fire patches is likely due to the fact that branch combustion in these two severity classes is extremely low. Despite being classified as high severity fires, a large share (48% to 58%) of the fires we examined was of low and moderate severity according to RAVG. Moreover, as noted below, the proportion of moderate severity fire patches is underestimated by RAVG, so it is highly likely that high severity fire patches comprise the minority of even “highly severe” wildfires. Thus, the overall combustion rate

in “high” severity fires is likely to be less than half that observed in those portions that were actually high severity.

4.1.5. Hypothesis 5

Our estimates of stand- to landscape-level combustion rates are more than an order of magnitude less than reported by some remote sensing-based studies (Table 4). For example, Garcia et al. [18] estimated that 32%, 52%, and 85% of the aboveground biomass was consumed by the Rim fire in low, moderate, and high severity fire patches, respectively. De Santis et al. [31] estimated that conifers in low, moderate, and high severity fire patches had average biomass combustion rates of 25%, 47%, and 65%, respectively. Applied to the RAVG fire severity distribution for the Rim Fire, these values suggest a landscape average combustion rate of 45%–57% in contrast to the 1%–1.2% we found when our combustion models were applied to various stand structures. For high severity fire patches, we estimated that 1.2%–3.2% of aboveground woody biomass was combusted by fire. Even when foliage was accounted for (see below) our ranges were far below that of Garcia et al. [18] and De Santis et al. [31]. In contrast, our estimates are more in line with the 1%–3% that can be inferred from Miesel et al. [17] for a range of fire severities in mixed conifer forests of California. They are also consistent with field-based research of high-severity fire patches in multiple large fires in the Eastern Cascades of Oregon, where <3% of live conifer tree biomass was consumed [32]. Thus, we cannot reconcile Garcia et al.’s or De Santis et al.’s outcomes with our field data, or with that from other field-based studies, which also find that the vast majority of the carbon remains in trees, even in moderate- and high-severity fire patches in large wildfires [10,19,32,33].

Table 4. Comparison of combustion rates (percentage) at stand- and landscape-level at Rim Fire.

Source	Fire Severity			Landscape
	Low	Moderate	High	Average ¹
Garcia et al. [18]	32	52	85	57
De Santis et al. [31]	25	47	65	45
This study	0.1–0.2	0.2–0.5	1.2–3.2	1.0–1.2

Notes: ¹ We used the distribution of fire severities from RAVG to weight the stand-level combustion rates for different fire severities.

4.2. Evaluation of Uncertainty

Our models predicting the relative volume of branch orders were preliminary and additional efforts should be made to improve them, particularly regarding estimates of bifurcation ratios. However, it is doubtful that these improvements would alter the relative relationships we found, specifically, that as tree DBH increases the maximum order present, diameter, and length of branches increases. Regardless of bifurcation ratios, these trends led to the highest order branch segments to be much larger than the lowest order ones. Hence, for the largest trees, the volume of the highest order branch segment was 374–62,241 times larger than for the first order ones. For the highest order and first order branch segments to have equal volume, then first order branch segments would have to be similarly more abundant than the highest order branch segments. Our models predicted that first order branch segments were less abundant than this by a factor of 5.5–66. It is highly unlikely that our estimates of bifurcation ratios could have been off by that much, but even if they were it may not have made a difference. In the case in which branch segment orders are equally abundant, the relative contribution of each order would be the reciprocal of the maximum order present; with six orders present, the contribution of the first three orders would be 50% to branches or 8% of aboveground woody mass of the largest trees. Therefore, given the limitations of branch mass on trees, even exceedingly high amounts of order one to three branch segments would not allow the majority of aboveground woody biomass to be consumed by fire.

Uncertainty was also introduced by our visual estimates of the fraction of branch orders consumed; however, this was unlikely to have altered our basic findings. In the case of small diameter trees in high fire severity patches, consumption of branch orders one to three were often complete, leading to little uncertainty in estimating the fraction consumed. Similarly, for trees in which no crown consumption occurred (the vast majority of trees), no uncertainty would have been introduced. Therefore, this source of uncertainty is highest for the largest trees in high severity fire patches, but even here it was unlikely to have been substantial. For example, if first order branch segments were 10% of branches and branches were 16% of aboveground woody mass (as is typical for large DBH trees), then estimating 50% consumption of first order branch segments would mean that 0.8% of aboveground woody biomass would have been consumed. Had 25 or 75% of the first order branch segments been consumed it would mean that 0.4% and 1.2% of the aboveground woody mass would have been consumed, respectively. Although these numbers certainly differ, all are small proportions of the aboveground woody biomass.

There were also uncertainties associated with combustion related to bole charring. We assumed that char thickness decreased as one proceeds up the stem. More needs to be learned about the longitudinal pattern of char depth. If the char depth is constant (which seems unlikely), then perhaps bole char losses would have been twice what we estimated. This would have had the largest impact on our estimates of combustion for low and moderate fire severity patches, because bole charring contributed to most of the combustion losses in these areas. However, char height was also limited in these patches. In addition to better understanding longitudinal variation in char depth, the amount of carbon lost via pyrolysis needs to be more precisely determined. Our use of a constant fraction of carbon loss of $\approx 46\%$ likely overestimated losses from low severity fires and potentially underestimated it for high severity ones. As charring was the most important carbon loss mechanism in low to moderate severity fire patches, it is worthy of further attention.

Our stand-level estimates are preliminary, but additional DBH distribution data would be unlikely to alter our basic finding that combustion losses from the largest trees dominate stand-level calculations (Figure S16). Substantial improvements in stand-level estimates would most likely be related to better estimates of the proportion of stands comprised of *Pinus* versus other species, given that the former have $\approx 50\%$ the combustion rates of the latter. Additionally, our analysis did not address interactions between stand structure and fire severity; however, while this interaction influences fire severity distributions, it would not change the fundamental relationships between tree size, biomass, and combustion rates.

At the level of entire fires (i.e., landscapes), uncertainty was related to the distribution of fire severity classes used. Specifically, we used RAVG to determine the areal extent of fire severity classes. Although RAVG provides an early (30–60 days) estimate of fire severities, it also tends to classify areas that eventually become moderate severity into the high severity class [34,35]. Therefore, our estimate of average landscape consumption rates may be higher than actually occurred. We can assess the degree this would have influenced our estimates of aboveground woody consumption for the Rim Fire. Potter [36] estimated that 33% of the Rim Fire was high severity; estimates based on MTBS (Monitoring Trends in Burn Severity) indicate that 20% was high severity. Using these fire severity distributions suggests that our landscape range for the Rim Fire would have been 0.5%–1.3% for Potter and 0.3%–0.9% for MTBS versus the 0.6%–1.5% we determined using RAVG.

4.3. Other Combustion Losses

We did not estimate fire consumption of either foliage or roots; however, the former, at least for high severity patches, could be substantial. If we assume that consumption of first order branch segments is the same as foliage consumption (Figure S17), then our stand level estimates of aboveground consumption for high severity patches would have been 3.2%–5.7%. At the landscape level, the average total aboveground consumption rate would have been much lower because there was very little foliage consumption for low

and moderate severity patches. Specifically, the total aboveground biomass consumed at the landscape level, adjusted for foliage combustion, would have ranged from 1.4% to 3%. Although some of the fine roots in the lower portions of the organic soil horizons may have been consumed, particularly in high severity fire patches, there was little evidence that coarse roots of live trees were consumed. Assuming that combustion of live roots was minimal, and roots comprised 20% of total live biomass, the total stand-level live biomass combustion for high severity patches would be 2.6%–4.6%. Adjusting the landscape-level combustion rate to account for root biomass gives a range of 1.1%–2.4%. Although these combustion rates are low, they are 1.3–1.9 times our estimate for aboveground woody combustion and suggest that a more detailed accounting of foliage and root combustion is warranted in future studies.

We also did not evaluate combustion losses from either understory plants or aboveground, dead organic matter. During our field work in high severity fire patches, we observed that the forest floor and many downed tree boles, stumps, and associated dead coarse roots were largely consumed. In contrast, sound, large-standing dead trees could be deeply charred, but largely remained even in high severity fire patches. We can use the published distribution of carbon pools (e.g., found in Miesel et al. [17]) combined with our live woody biomass combustion rates, and assume the complete combustion of the understory plants and aboveground dead pools (i.e., coarse woody debris and the forest floor) to estimate pool-specific losses for high severity fire patches. This indicates that combustion of aboveground live woody biomass could account for 4%–10% of the total ecosystem combustion losses. Alternatively, if we assume that 50% of the coarse woody debris was combusted, then live aboveground woody biomass would have contributed 5%–12% of the total ecosystem combustion losses. These estimates contrast markedly with the live tree contribution if the values from Garcia et al. [18] were used: live combustion rates of 85% would mean 74% to 78% of the ecosystem combustion losses would have been associated with live tree combustion.

4.4. Policy Implications

Our findings have significant implications for a wide range of policy analyses related to wildfire combustion. The fraction of live woody biomass combusted varies not only with fire severity level; but also, depending on the organizational level being examined, a number of other factors, including the size structure of woody parts and trees, the species composition of trees present, and mixture of fire severity levels within fires. This suggests that great care must be taken in selecting the combustion rate(s) to be used in either modeling combustion or calibrating remote sensing-based estimates. Furthermore, until an improved multi-level (e.g., branches to landscapes) understanding of combustion rates has been attained, we recommend that such research be tied to field-based, level-relevant data to the extent possible. A key improvement includes determining the limits within which realistic combustion rates can be expected for a given level of analysis.

These findings also suggest that assumptions about combustion in past policy-related analyzes (e.g., [37,38]) should be re-evaluated. Based on our results and those of others [10], combustion-related emissions may have been overestimated. In contrast, fire-related losses via decomposition of fire-killed trees and the amount of fuel generated by fire disturbance may have been underestimated. Hence, the consequences of management actions may not be adequately understood until a more robust understanding of live woody combustion develops.

5. Conclusions

Our field-based examination of the amount of live aboveground woody biomass combusted indicated that while rates for small branch segments can be quite high (i.e., 100%), these rates do not translate in to major losses at the stand or landscape level. This is because high combustion rates in smaller structures are countered by other factors as one proceeds from branches to trees to stands, and to landscapes. The end result in the forests we exam-

ined is that even very severe fires combust <2% of live aboveground woody biomass on average. Our work as well as that of others [10] suggests that additional field research is needed to determine how wildfires release carbon to the atmosphere in a wide range of forest structures and fire-weather conditions. We suggest that researchers and policy makers avoid using estimators that are not field-based, because they currently appear to overstate the wildfire emissions used in carbon emissions reporting. As such, they have the potential to misdirect climate mitigation policy. The fact that the vast majority of aboveground woody biomass is not combusted raises the question of when fire-killed trees actually release their carbon. If dead trees are allowed to remain in place, the natural decomposition process could take many decades to centuries to release fire-killed carbon [39]. In contrast, if logged and removed for biomass energy, much of this carbon could be released relatively quickly [40]. Therefore, additional research is also needed to determine the degree that post-fire forest management influences the temporal profile of carbon release.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13030391/s1>, Figure S1. Relationship for conifers between the proportion of aboveground woody parts in branches and tree diameter at breast height (based on equations in [22]; Figure S2. Amount of stem volume remaining for a given level of cumulative stem height lost or percentage of diameter lost along boles; Figure S3. Images of the Rim Fire from (a) December 2017 and (b) May 2018 indicate that substantial amounts of aboveground woody biomass remained even in high severity fire patches where all the trees were killed; Figure S4. Schematic depiction of branch orders and bifurcation ratios; Figure S5. Schematic depiction of branch weighting to create a whole tree estimate abundance of branch order segments for trees of different DBH size classes: (a) the maximum order method; (b) the volume weighed method; (c) the volume-length weighted method; and (d) the length weighted method; Figure S6. Examples of characteristics used to separate branches lost via combustion versus decomposition-related fragmentation: (a) branches with rectangular profiles without charring lost via decomposition-related fragmentation; (b) charring of branch stubs that had been broken off prior to fire; (c) thorn-like remnants of branches consumed in fire; Figure S7. Mean dimensions of branch orders of dissected branches for different tree species (a) mid-length diameter; and (b) segment length; Figure S8. Changes in branch structure among species and DBH size classes ((1: 1.0–4.9, 2: 5.0–9.9, 3: 10.0–24.9, 4: 25.0–49.9, 5: 0.0–99.9, 6: >100 cm)) adjacent to the Rim Fire, California: (a) highest branch order; (b) diameter of highest branch order present; (c) total length of highest order branches; and (d) length of highest order branch segment; Figure S9. Comparison of the different models used to estimate branch order contributions for *C. decurrens*. (a) maximum order model; (b) simple, unweighted average; (c) volume weighted model; and (d) volume and length weighted model; Figure S10 Theoretical maximum branch combustion possible based on: (a) branch orders observed to be consumed or (b) the maximum branch diameters to be consumed; Figure S11. Proportion of tree aboveground woody biomass in: (a) branch order segments 1–3; and (b) branch segments <2 cm diameter; Figure S12. Branch and bole consumption as a function of fire severity and diameter at breast height for the Creek and Rim Fires, California: (a) branch consumption for high severity fire patches; (b) bole consumption for high severity patches; (c) branch consumption moderate severity; (d) bole consumption moderate severity; (e) branch consumption low severity; and (f) bole consumption low severity; Figure S13. Bole char heights on trees compared to total tree height at: (a) Rim; and (b) Creek Fires; Figure S14. Radial char depth at base of tree bole based on: (a) chopping into and measuring char depth on each tree at Creek Fire; and (b) visual estimates from the Rim Fire; Figure S15. Bole char heights and depths for a subsample of trees on the Rim Fire: (a) the maximum versus minimum proportion of the bole charred; and (b) means depth of char at base of trees of three common species; Figure S16. Stand-level combustion for theoretical and published DBH size distributions: (a) total combustion of high severity fires for different DBH distribution types; and (b) total combustion of high severity fires for differing coefficients of variation for normal distribution (e.g., CV100 = coefficient of variation of 100%); Figure S17. Relationship between diameter at breast height (DBH) of trees and the amount of foliage consumed by high severity fire patches in the Rim and Creek Fires; Table S1. Dimensions of dissected branch segments for five species in Rim Fire, Sierra Nevada Mountains, CA; Table S2. Bifurcation ratios for dissected tree branches for five species in Rim Fire, Sierra Nevada Mountains, CA; Table S3. Non-linear regressions predicting branch consumption as a function of DBH for different fire

severity classes and species groups; Table S4. Non-linear regressions predicting bole consumption as a function of DBH for different fire severity classes and species groups.

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

N. L. Harris^{1,5*}, S. C. Hagen^{2†}, S. S. Saatchi³, T. R. H. Pearson¹, C. W. Woodall⁴, G. M. Domke⁴, B. H. Braswell², B. F. Walters⁴, S. Brown¹, W. Salas², A. Fore³ and Y. Yu³

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 $-460 \pm 48 \text{ Tg C year}^{-1}$, while C losses from disturbance averaged $191 \pm 10 \text{ Tg C year}^{-1}$. Combining estimates of net C losses and gains results in net carbon change of $-269 \pm 49 \text{ Tg C year}^{-1}$. New forests gained $-8 \pm 1 \text{ Tg C year}^{-1}$, while deforestation resulted in losses of $6 \pm 1 \text{ Tg C year}^{-1}$. Forest land remaining forest land lost $185 \pm 10 \text{ Tg C year}^{-1}$ to various disturbances; these losses were compensated by net carbon gains of $-452 \pm 48 \text{ Tg C year}^{-1}$. C loss in the southern US was highest ($105 \pm 6 \text{ Tg C year}^{-1}$) with the highest fractional contributions from harvest (92%) and wind (5%). C loss in the western US ($44 \pm 3 \text{ Tg C year}^{-1}$) was due predominantly to harvest (66%), fire (15%), and insect damage (13%). The northern US had the lowest C loss ($41 \pm 2 \text{ Tg C year}^{-1}$) 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

*Correspondence: nharris@wri.org

†N. L. Harris and S. C. Hagen contributed equally to this work

⁵ Present Address: Forests Program, World Resources Institute, 10 G Street NE Suite 800, Washington, DC 20002, USA

Full list of author information is available at the end of the article

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 km². 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

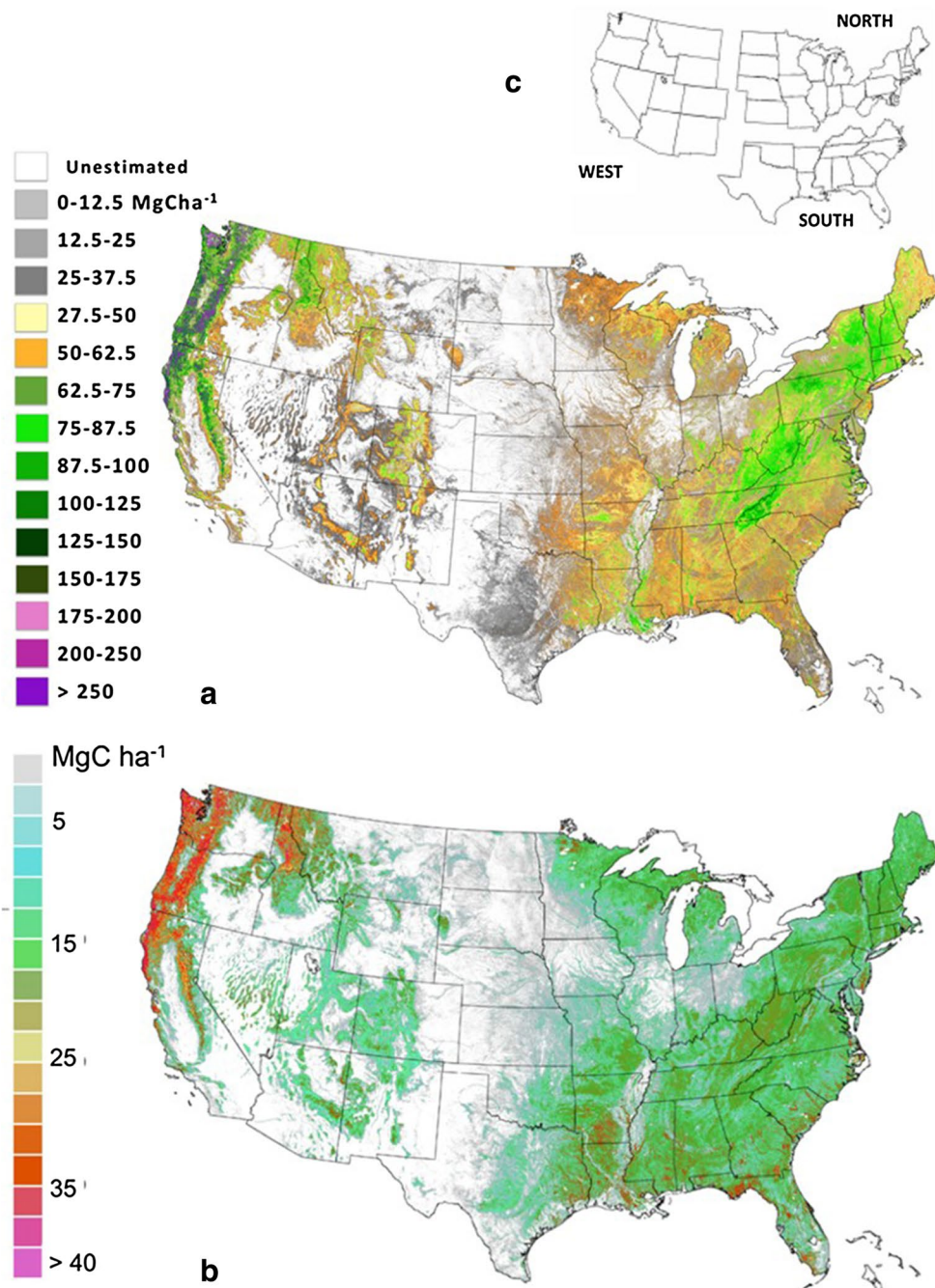


Fig. 1 **a** Map of aboveground live woody biomass carbon density (Mg C ha^{-1}) and **b** uncertainty across forest lands of the conterminous US at 1-ha resolution for circa the year 2005. **c** The regional analysis was performed by dividing the US into three sub-regions as recommended by Heath and 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/ORNLDAA/1313>)

hardwood or softwood in the NLCD 2006 dataset¹ 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 Mg ha⁻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 Mg ha⁻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:

$$\text{Error} = \sqrt{\varepsilon_{\text{measurement}}^2 + \varepsilon_{\text{allometry}}^2 + \varepsilon_{\text{sampling}}^2 + \varepsilon_{\text{prediction}}^2}$$

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

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 re-measured 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 (above-ground 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

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/ORN-LDAAC/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 class³ 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

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:

$$\begin{aligned}\Delta C_{\text{net}} = & \Delta C_{\text{undist}} + \Delta C_{\text{A/R}} + \Delta C_{\text{conversion}} \\ & + \Delta C_{\text{timberlands}} + \Delta C_{\text{insect}} + \Delta C_{\text{fire}} \\ & + \Delta C_{\text{wind}} + \Delta C_{\text{drought}}\end{aligned}$$

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. $\Delta C_{\text{A/R}}$ is the net C change in new forest land. $\Delta C_{\text{conversion}}$, 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. $\Delta C_{\text{drought}}$ is the net C reduction in sequestration in forest land experiencing drought from what was expected during non-drought periods. $\Delta C_{\text{timberlands}}$ 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:

$$\text{uncertainty}\% = \frac{\frac{\sigma}{\sqrt{n}} * 1.96}{\mu} * 100$$

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

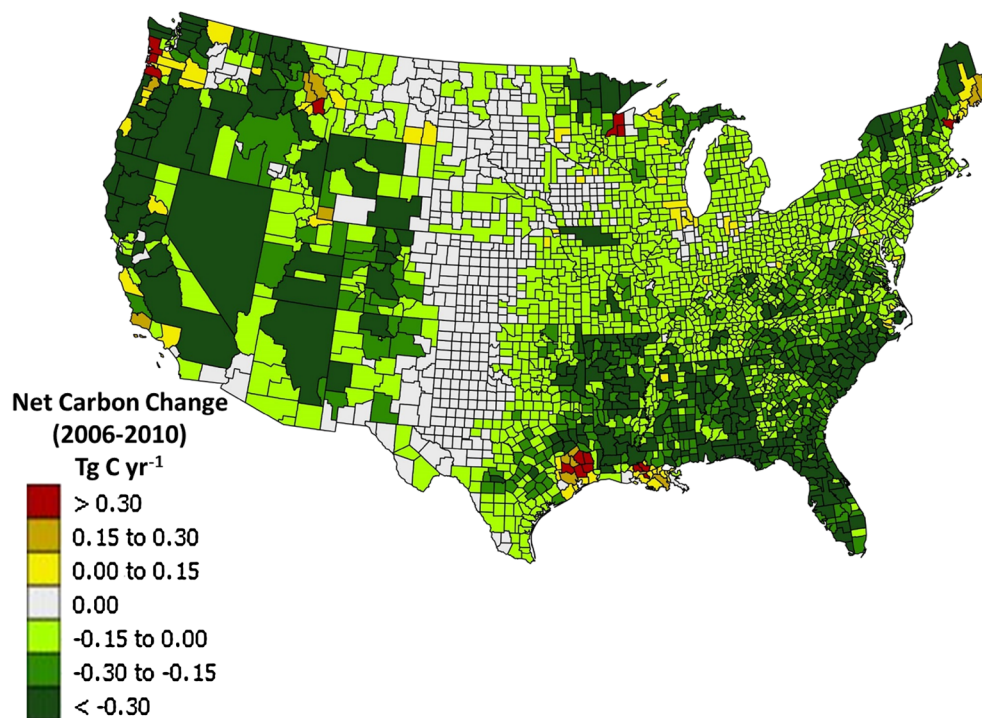


Fig. 2 Average annual net carbon change (Tg C year^{-1}) at the combined county scale across the CONUS. Most combined counties (91%) are net C sinks while areas with extensive forest disturbance can be net C sources to the atmosphere

consistent with estimates reported in the US. GHG inventory for forests in 2010 ($-293 \text{ Tg C year}^{-1}$, [33]) but we estimate a larger net sink than reported in Zheng et al. [28] ($-181 \text{ Tg C year}^{-1}$), 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 $-8 \pm 1 \text{ Tg C year}^{-1}$, while deforestation, averaging 0.1 million ha per year, resulted in C losses of $6 \pm 1 \text{ Tg C year}^{-1}$. Forest land remaining forest land lost $184 \pm 10 \text{ Tg C year}^{-1}$ to disturbance (13% from natural disturbance, 87% from harvest); these were compensated by net carbon gains of $452 \pm 48 \text{ Tg C year}^{-1}$, 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 ($-271 \pm 28 \text{ Tg C year}^{-1}$) than the North ($-97 \pm 10 \text{ Tg C year}^{-1}$) or the West ($-92 \pm 11 \text{ Tg C year}^{-1}$), while at the same time losing more C to the atmosphere from disturbances ($105 \pm 6 \text{ Tg C year}^{-1}$) than the other regions

($41 \pm 2 \text{ Tg C year}^{-1}$ for the North and $44 \pm 3 \text{ Tg C year}^{-1}$ 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 $11 \text{ Tg C year}^{-1}$ (Table 5). Georgia, Florida, Alabama, Mississippi, and North Carolina gained the most forest C in the time period, with each sequestering at least $24 \text{ Tg C year}^{-1}$. 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 ($162 \pm 9.9 \text{ Tg C year}^{-1}$) were more than five times higher than losses from all other processes combined ($30 \pm 2.6 \text{ Tg C year}^{-1}$). Fire ($7 \pm 1.0 \text{ Tg C year}^{-1}$), wind ($5 \pm 0.7 \text{ Tg C year}^{-1}$), insect infestation ($10 \pm 1.3 \text{ Tg C year}^{-1}$), and deforestation ($6 \pm 0.7 \text{ Tg C year}^{-1}$) 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 Zepfel [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

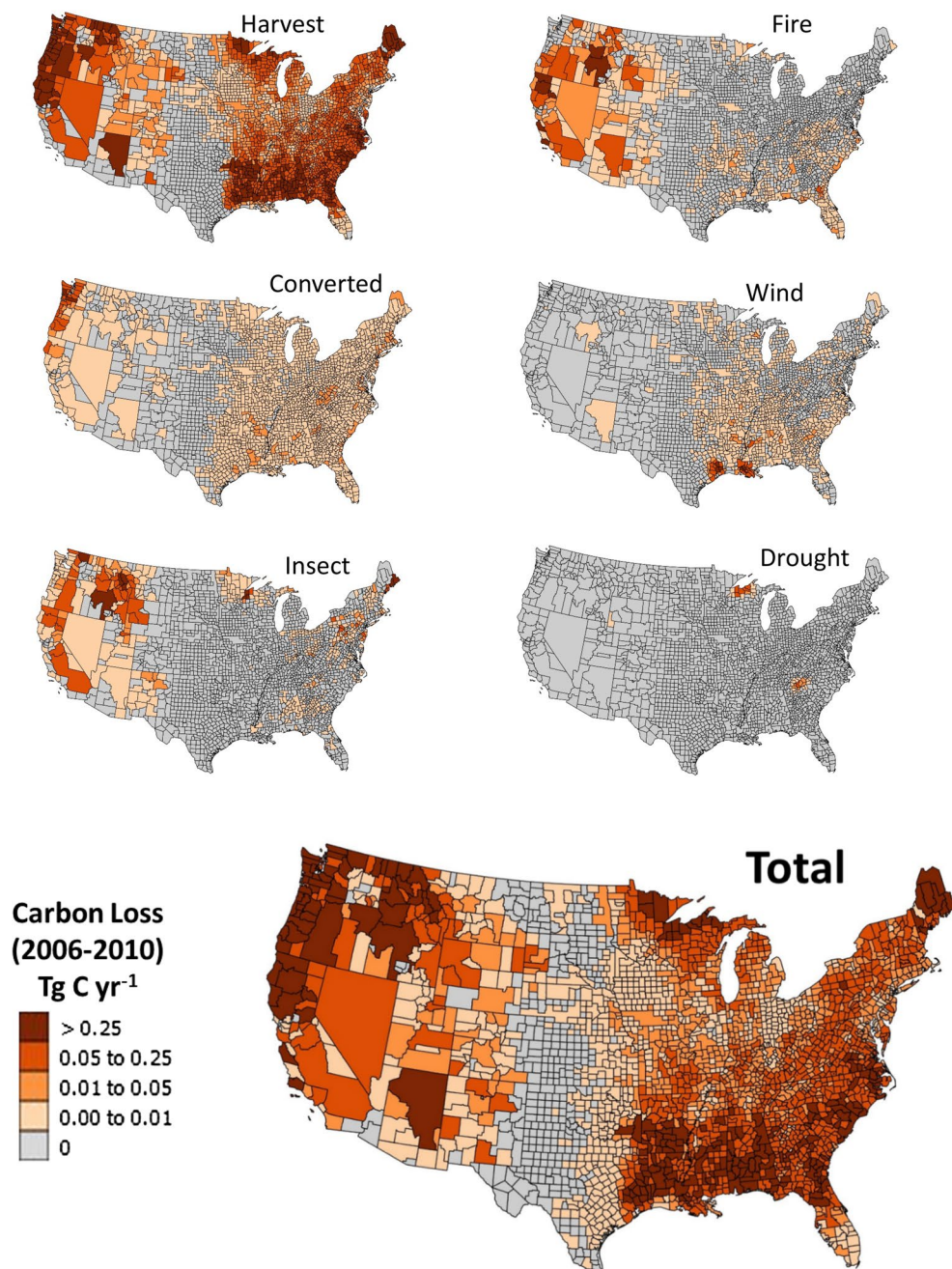


Fig. 3 Average annual net carbon loss (Tg C year⁻¹) attributed to the most likely disturbance type and estimated at the combined county scale for harvest, fire, land use conversion, wind, insect, and drought. Combining these six sources results in estimates of total annual net C loss from disturbance 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.

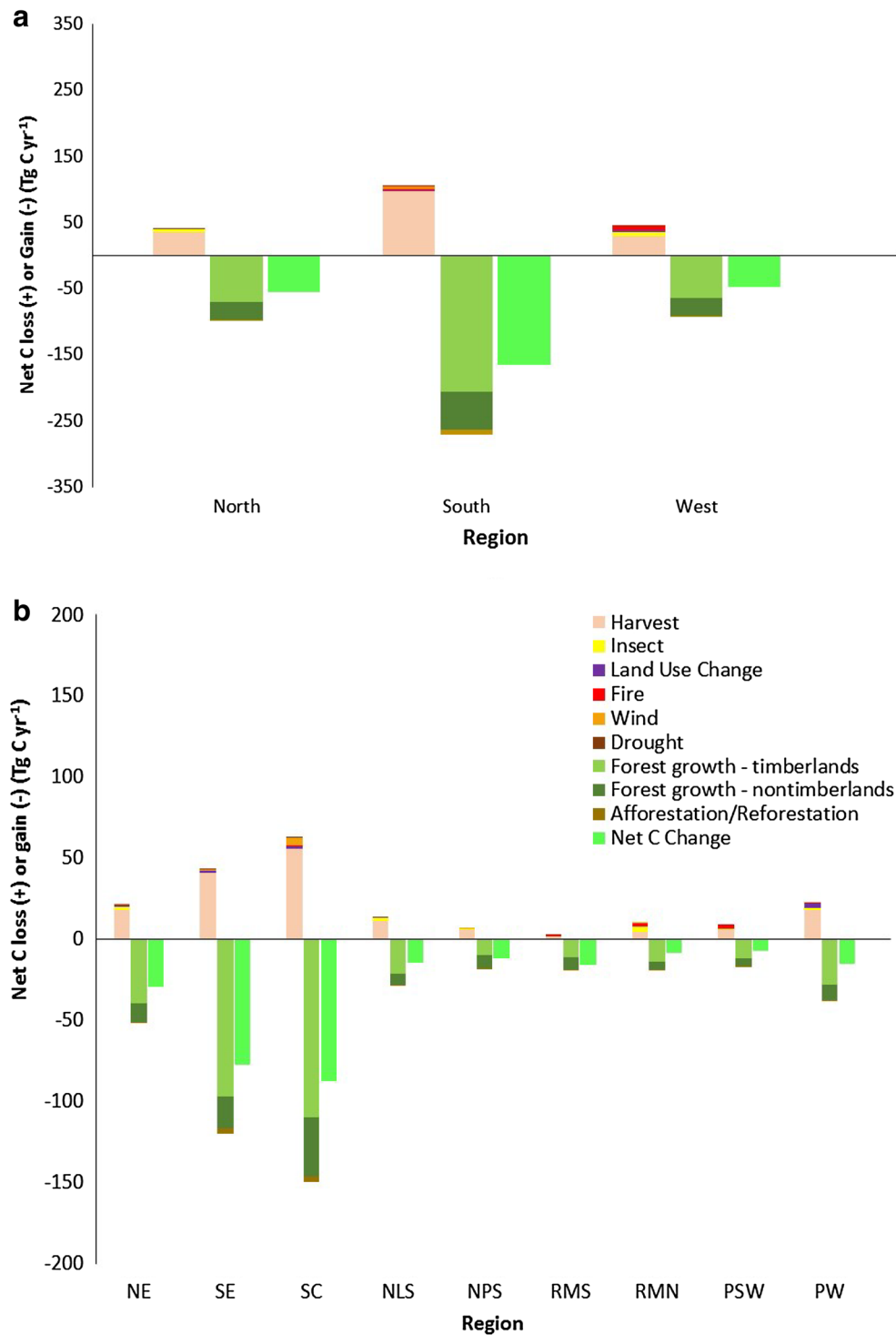
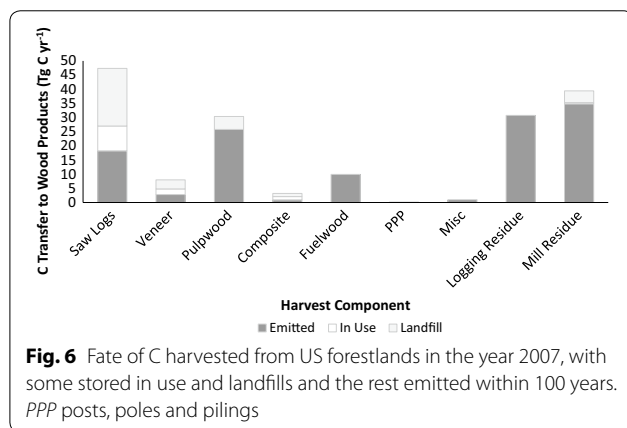
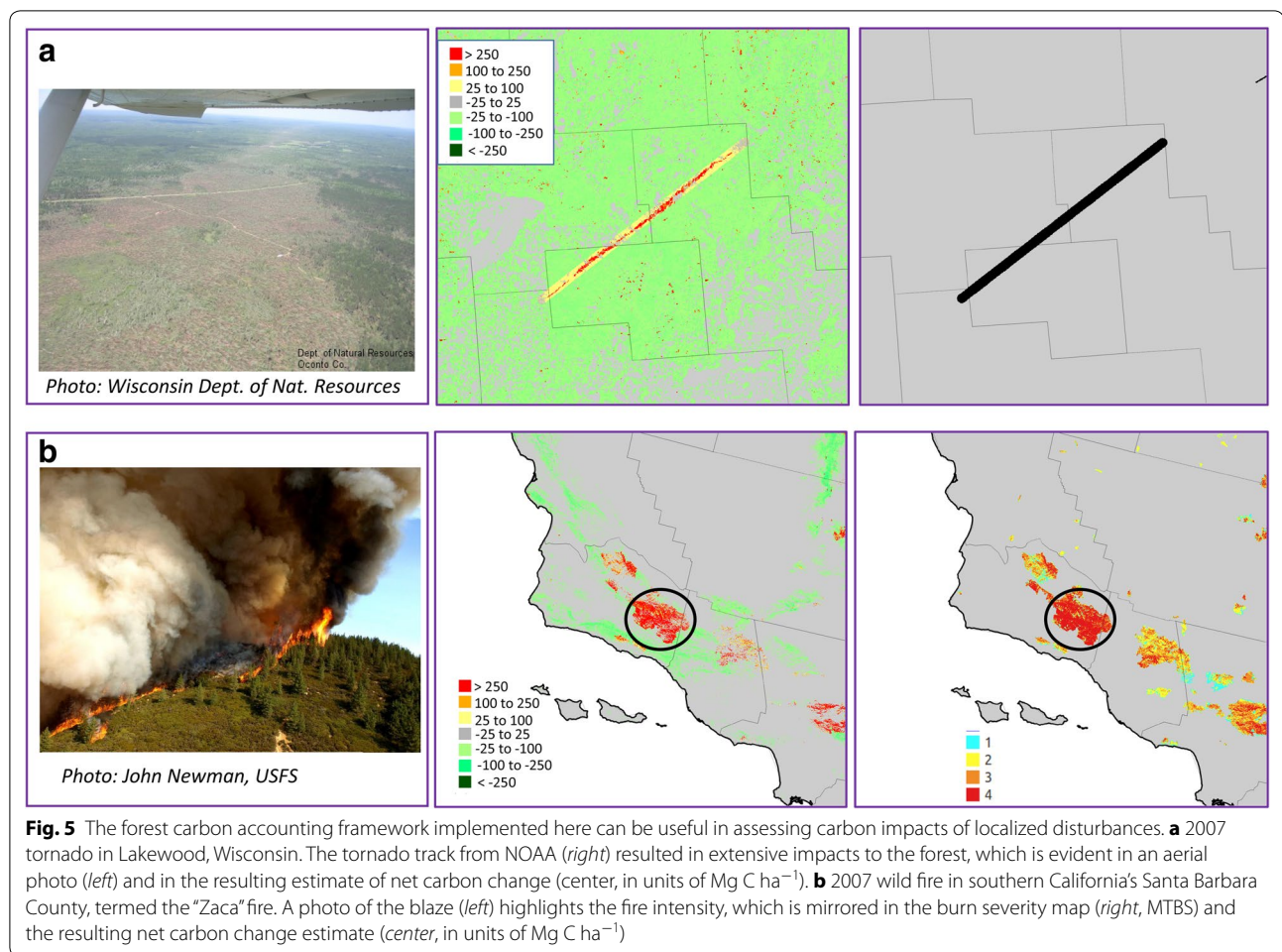


Fig. 4 Average annual net carbon change by disturbance type in **a** the North (79 million ha of forest), South (87 million ha), and West (56 million ha) regions and **b** by FIA region: northeast (NE; 41 million ha), southeast (SE; 35 million ha), southcentral (SC; 52 million ha), northern lake states (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)



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 ($-8 \pm 1 \text{ Tg C year}^{-1}$), forest land to non-forest

land ($6 \pm 1 \text{ Tg C year}^{-1}$), and forest land remaining forest land ($-267 \text{ Tg C year}^{-1}$). 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

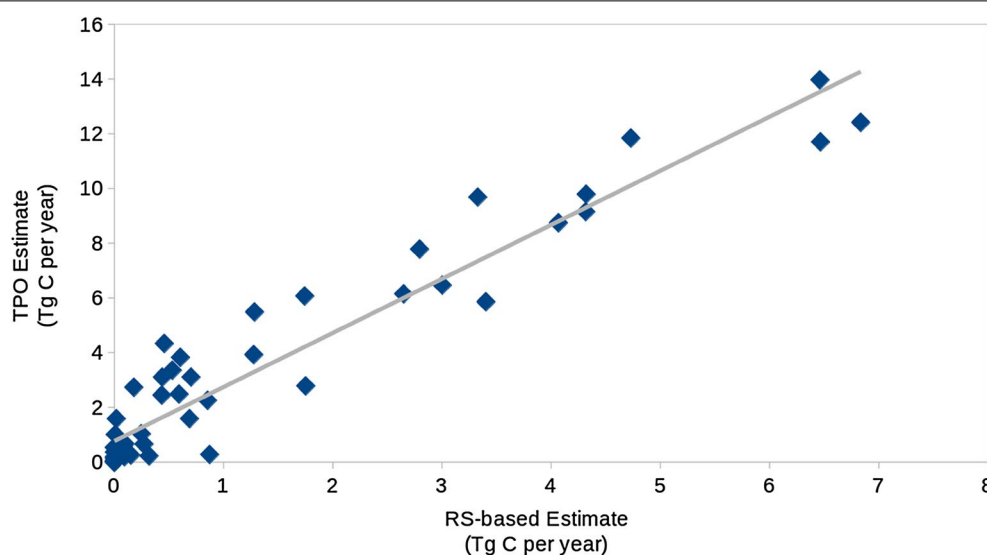


Fig. 7 Relation between C losses from harvest as estimated from timber product output (TPO) data and from an independent remote sensing-based estimate. $TPO = 1.98 \times RS + 767,777$; $R^2 = 0.91$. Data points represent results aggregated to the state-level

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 ($342 \text{ Tg C year}^{-1}$) 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 $-436 \text{ Tg C year}^{-1}$ 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 $-269 \pm 49 \text{ Tg C year}^{-1}$ 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.

Author details

¹ Ecosystem Services Unit, Winrock International, 2121 Crystal Drive Suite 500, Arlington, VA 22202, USA. ² Applied Geosolutions, 55 Main Street Suite 125, Newmarket, NH 03857, USA. ³ NASA Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA 91109, USA. ⁴ USDA Forest Service, Northern Research Station, Saint Paul, MN 55108, USA. ⁵ Present Address: Forests Program, World Resources Institute, 10 G Street NE Suite 800, Washington, DC 20002, USA.

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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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Meeting GHG reduction targets requires accounting for all forest sector emissions

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Tara W Hudiburg^{1,4} , Beverly E Law², William R Moomaw³ , Mark E Harmon² and Jeffrey E Stenzel¹ ¹ Department of Forest, Rangeland and Fire Sciences, 875 Perimeter Dr MS 1133, University of Idaho, Moscow, ID 83844, United States of America² Department of Forest Ecosystems and Society, 321 Richardson Hall, Oregon State University, Corvallis, OR 97333, United States of America³ Center for International Environment and Resource Policy, The Fletcher School, and Global Development and Environment Institute, Tufts University, Medford MA, United States of America⁴ Author to whom any correspondence should be addressed.E-mail: thudiburg@uidaho**Keywords:** carbon, forests, wood products, climate mitigation, GHG mandatesSupplementary 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 CO₂ emissions. For states seeking to reach GHG reduction mandates by 2030, it is important that state CO₂ 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 CO₂. Both reports emphasize the need to increase atmospheric CO₂ 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 CO₂ 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 CO₂ 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 CO₂. 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 CO₂ 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) CO₂e per year ($-857 \text{ g CO}_2\text{e m}^{-2} \text{ yr}^{-1}$) (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 CO₂e per year ($-551 \text{ g CO}_2\text{e m}^{-2} \text{ yr}^{-1}$), 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 CO₂e yr⁻¹ per state) the ranking is due to much lower harvest removals in California (~ 12 MMT CO₂e yr⁻¹) compared to almost double in

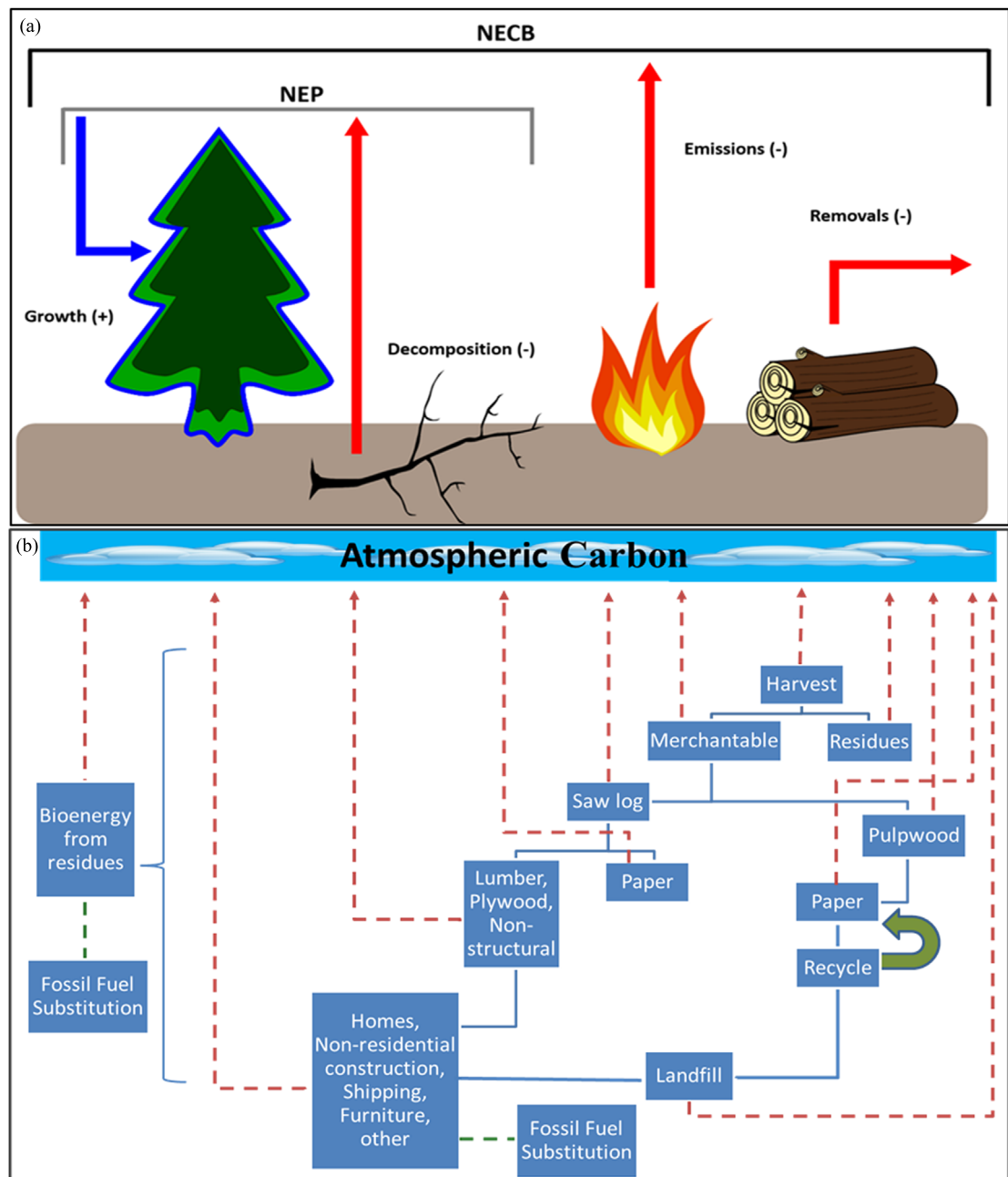


Figure 1. Conceptual diagram of Forest-GHG (a) describes the natural, land-based forest carbon sink where the net of growth and decomposition is net ecosystem production (NEP), and after accounting for removals from fire and harvest, the balance is net ecosystem carbon balance (NECB), (b) describes the cascade of wood products until eventual deposition in landfills or the atmosphere and shows the pathway of emissions.

Washington (~ 20 MMT $\text{CO}_2\text{e yr}^{-1}$) and triple in Oregon (~ 31 MMT $\text{CO}_2\text{e yr}^{-1}$). 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

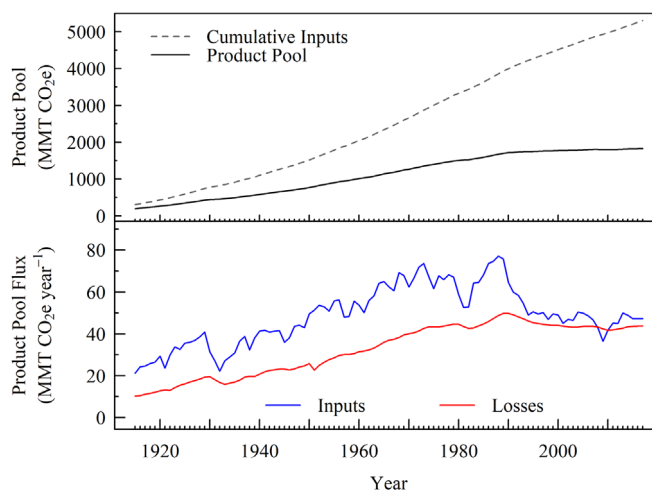


Figure 2. Wood product inputs and outputs from 1900 to 2016 for Washington, Oregon, and California. (A) Cumulative production in MMT CO₂e per year assuming no losses over time (dotted grey line) versus the realized in-use wood product pool over time after accounting for decay (losses). (B) Yearly product 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 CO₂e. Negative numbers indicate a carbon sink (CO₂ 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.

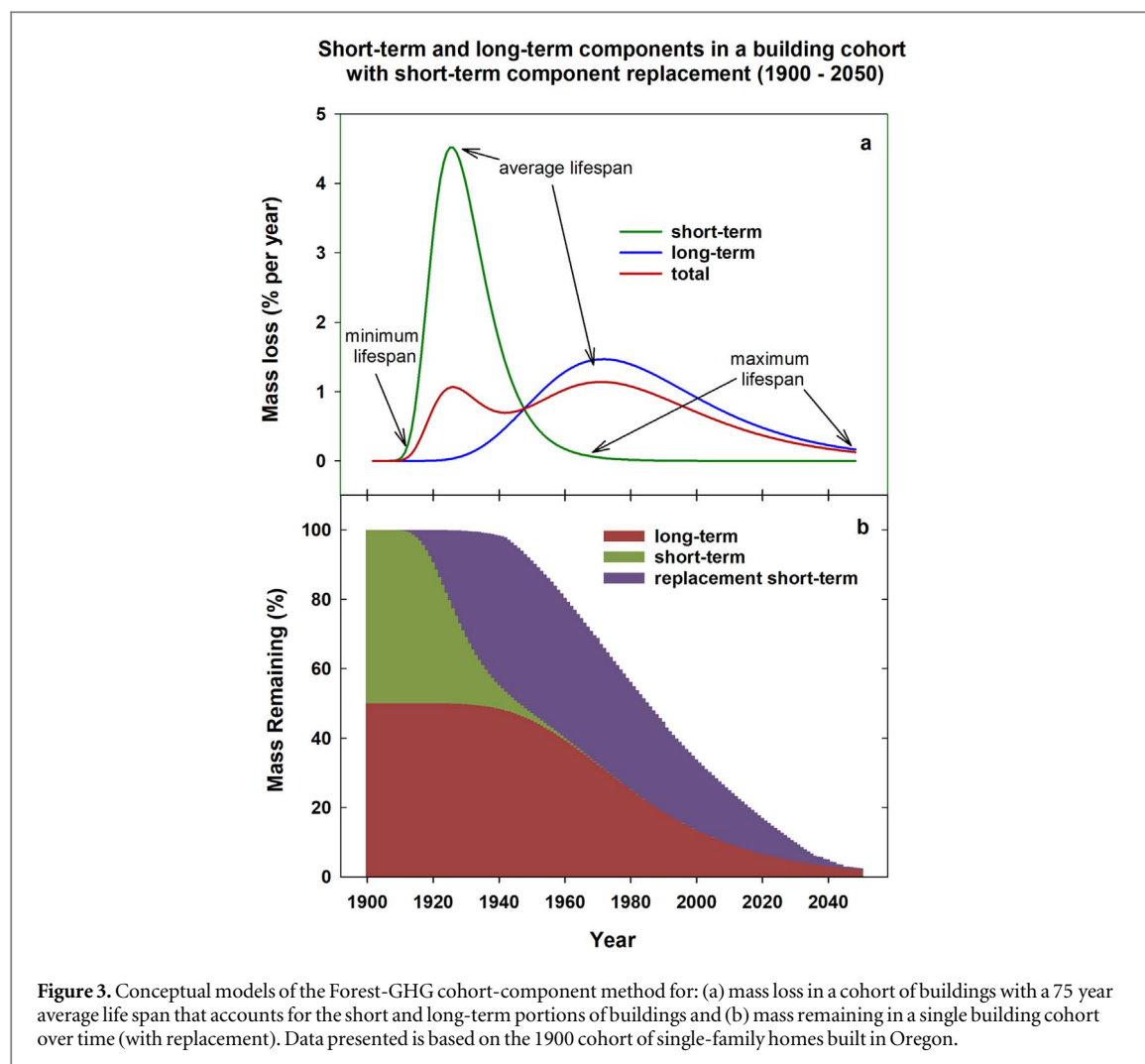
Ecosystem	Washington	Oregon	California	Total
1. Forested area (million hectares)	9.7	12.4	11.9	34.0
2. Net ecosystem production (NEP)	−89.9	−102.0	−99.8	−291.6
3. Fire emissions	5.1	5.3	10.3	20.7
4. Harvest removals	18.5	30.5	11.5	60.5
Net ecosystem carbon balance (NECB) (sum of rows 1 through 4)	−66.4	−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 CO₂e of wood harvested in all three states since 1900 (figure 2), only 2028 MMT CO₂e are currently stored in wood products with half stored in Oregon (1043 MMT CO₂e). 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 CO₂e 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



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 CO₂e annually from the atmosphere and

potentially reducing fossil fuel emissions by up to another 20 MMT CO₂e 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 CO₂ 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 CO₂ emissions of 491 MMT CO₂e 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 time-frame 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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ORCID iDs

Tara W Hudiburg  <https://orcid.org/0000-0003-4422-1510>

William R Moomaw  <https://orcid.org/0000-0003-2690-2339>

Mark E Harmon  <https://orcid.org/0000-0002-4195-8288>

Jeffrey E Stenzel  <https://orcid.org/0000-0001-8881-0566>

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CONSERVATION

A global map of roadless areas and their conservation status

Pierre L. Ibisch,^{1,2*} Monika T. Hoffmann,¹ Stefan Kreft,^{1,2} Guy Pe'er,^{2,3,4} Vassiliki Kati,^{2,5} Lisa Biber-Freudenberger,^{1,6} Dominick A. DellaSala,^{7,8} Mariana M. Vale,^{9,10} Peter R. Hobson,^{1,2,11} Nuria Selva^{12*}

Roads fragment landscapes and trigger human colonization and degradation of ecosystems, to the detriment of biodiversity and ecosystem functions. The planet's remaining large and ecologically important tracts of roadless areas sustain key refugia for biodiversity and provide globally relevant ecosystem services. Applying a 1-kilometer buffer to all roads, we present a global map of roadless areas and an assessment of their status, quality, and extent of coverage by protected areas. About 80% of Earth's terrestrial surface remains roadless, but this area is fragmented into ~600,000 patches, more than half of which are <1 square kilometer and only 7% of which are larger than 100 square kilometers. Global protection of ecologically valuable roadless areas is inadequate. International recognition and protection of roadless areas is urgently needed to halt their continued loss.

The impact of roads on the surrounding landscape extends far beyond the roads themselves. Direct and indirect environmental impacts include deforestation and fragmentation, chemical pollution, noise disturbance, increased wildlife mortality due to car collisions, changes in population gene flow, and facilitation of biological invasions (1–4). In addition, roads facilitate “contagious development,” in that they provide access to previously remote areas, thus opening them up for more roads, land-use changes, associated resource extraction, and human-caused disturbances of biodiversity (3, 4). With the length of roads projected to increase by >60% globally from 2010 to 2050 (5), there is an urgent need for the development of a comprehensive global strategy for road development if continued biodiversity loss is to be abated (6). To help mitigate the detrimental effects of roads, their construction should be concentrated as much as possible in areas of relatively low “environmental values” (7). Likewise, prioritizing the protection of remaining roadless areas that are regarded as important for biodiversity and ecosystem functionality requires an assessment of their extent, distribution, and ecological quality.

Such global assessments have been constrained by deficient spatial data on global road networks. Importantly, recent publicly available and rapidly improving data sets have been generated by crowd-sourcing and citizen science. We demonstrate their potential through OpenStreetMap, a project with an open-access, grassroots approach to mapping and updating free global geographic data, with a focus on roads. The available global road data sets, OpenStreetMap and gROADS, vary in length, location, and type of roads; the former is the data set with the largest length of roads (36 million km in 2013) that is not restricted to specific road types (table S1). OpenStreetMap is more complete than gROADS, which has been used for other global assessments (7), but in certain regions, it contains fewer roads than sub-

global or local road data sets [see the example of Center for International Forestry Research data for Sabah, Malaysia (8); table S1]. Given the pace of road construction and data limitations, our results overestimate the actual extent of global roadless areas.

The spatial extent of road impacts is specific to the impact in question and to each particular road and its traffic volume, as well as to taxa, habitat, landscape, and terrain features. Moreover, for a given road impact, its area of ecological influence is asymmetrical along the road and can vary among seasons, between night and day, according to weather conditions, and over longer time periods. We conducted a comprehensive literature review of 282 publications dealing with “road-effects zones” or including the distance to roads as a covariate, of which 58 assessed the spatial influence of the road (table S2). All investigated road impacts were documented within a distance of

¹Centre for Economics and Ecosystem Management, Eberswalde University for Sustainable Development, Alfred-Moeller-Straße 1, 16225 Eberswalde, Germany. ²Society for Conservation Biology–Europe Section, 1133 15th Street Northwest, Suite 300, Washington, DC 20005, USA.

³Department of Conservation Biology, UFZ–Centre for Environmental Research, Permoserstraße 15, 04318 Leipzig, Germany. ⁴German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany. ⁵Department of Environmental and Natural Resources Management, University of Patras, Seferi 2, 30100 Agrinio, Greece. ⁶Department of Ecology and Natural Resources Management, Center for Development Research, University of Bonn, Walter-Flex-Straße 3, 53113 Bonn, Germany. ⁷Geos Institute, 84 4th Street, Ashland, OR 97520, USA. ⁸Society for Conservation Biology–North America Section, 1133 15th Street Northwest, Suite 300, Washington, DC 20005, USA. ⁹Department of Ecology, Federal University of Rio de Janeiro, Av. Brg. Trompowski s/n, 21044-020 Rio de Janeiro, Brazil. ¹⁰Society for Conservation Biology–Latin America and Caribbean Section, 1133 15th Street Northwest, Suite 300, Washington, DC 20005, USA. ¹¹Writtle College, Lordship Road, Writtle, Chelmsford, Essex CM1 3RR, 01245 42420, UK. ¹²Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland.

*Corresponding author. Email: pierre.ibisch@hnee.de (P.L.I.); nuriselva@gmail.com (N.S.)

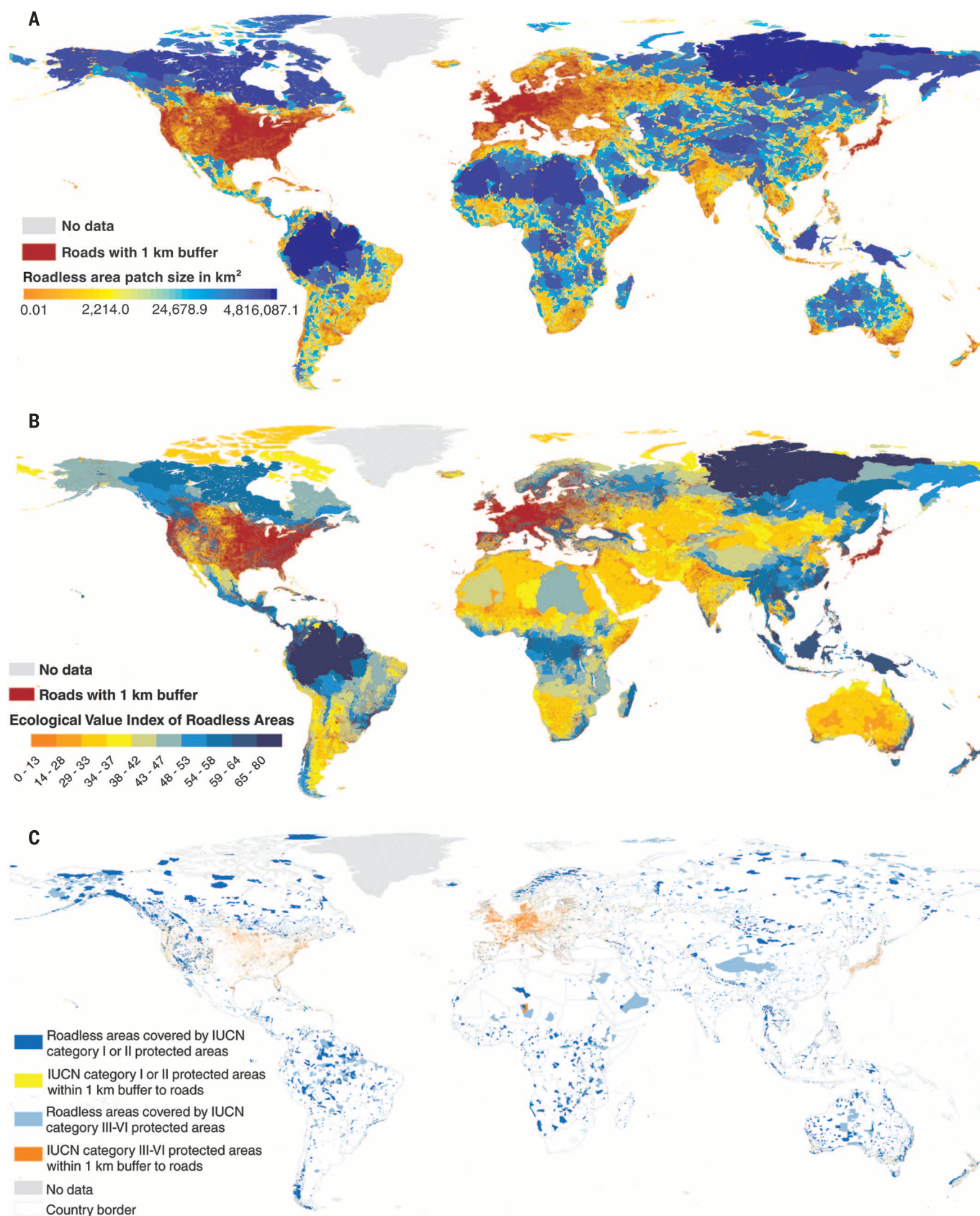


Fig. 1. The global distribution of roadless areas, based on a 1-km buffer around all roads. The distribution is depicted according to (A) size classes, (B) the ecological value index of roadless areas (EVIRA; based on patch size, connectivity, and ecosystem functionality), and (C) representation in protected areas (8).

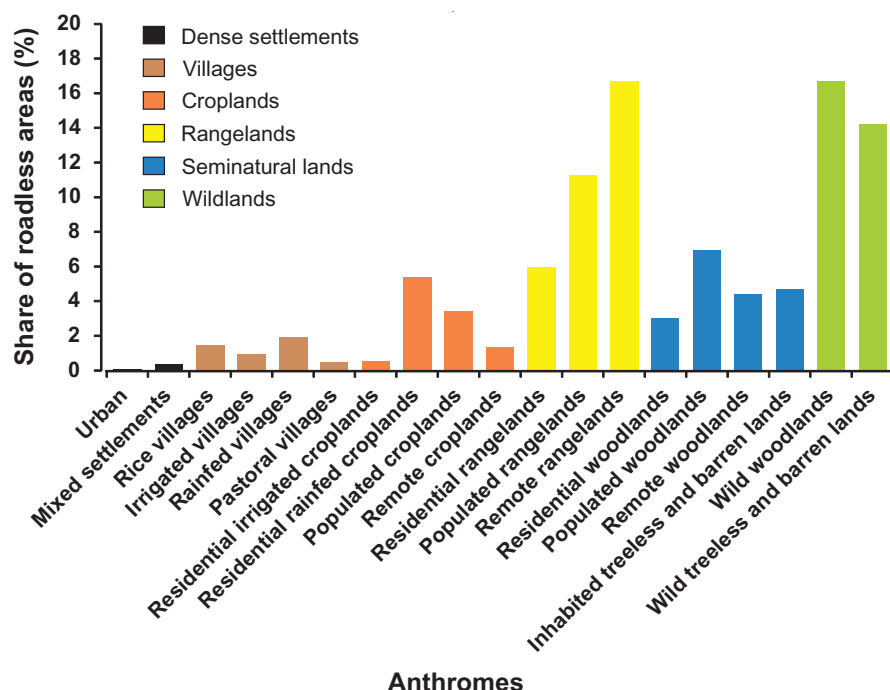


Fig. 2. Extent of roadless areas (1-km buffer) across anthromes. The majority of the world's roadless areas are in remote and unmodified landscapes, but they also occur in anthropogenically modified landscapes. The so-called anthromes were mapped according to (10).

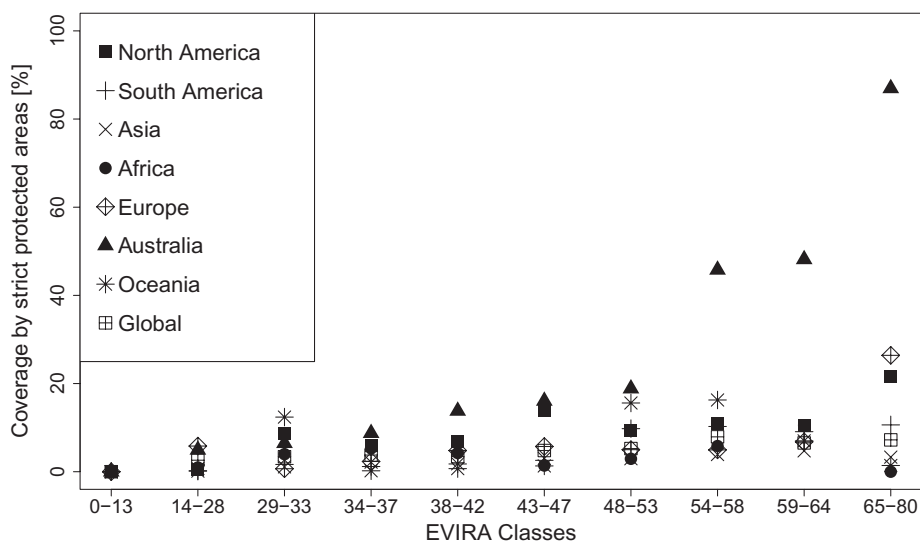


Fig. 3. Coverage of roadless areas by strictly protected areas (IUCN categories I and II) compared with global and continental EVIRA values. If priority were given to protecting roadless areas with high ecological functionality, we should see a positive correlation, with higher coverage associated with higher EVIRA values.

1 km from the road, 39% reached out to 2 km from the road, and only 14% extended out to 5 km from the road (fig. S1). Because the 1-km buffer along each side of the road represents the zone with the highest level and variety of road impacts, we defined roadless areas as those land units that are at least 1 km away from all roads and, therefore, less influenced by road effects. We com-

pared results from using this criterion with the outcomes from using an alternative 5-km buffer (see fig. S2 and table S3). We excluded all large water bodies, as well as Greenland and Antarctica, which are mostly covered by ice, from the analyses.

Roadless areas with a 1-km buffer to the nearest road cover about 80% of Earth's terrestrial surface (~105 million km²). However, these roadless areas

are dissected into almost 600,000 patches. More than half of the patches are <1 km²; 80% are <5 km²; and only 7% are >100 km² (table S4 and fig. S3). If the buffer is extended to 5 km, there is a substantial reduction in roadless areas to about 57% of the world's terrestrial surface (~75 million km²), dissected into 50,000 patches (fig. S2 and table S3). The occurrence, distribution, and size of roadless areas differ considerably among continents (Fig. 1A and fig. S4). For instance, the mean size of roadless patches (1-km buffer) is 48 km² in Europe, compared with >500 km² in Africa. Because of comparatively large gaps in available spatial data on roads in many segments of the tropics, the number and size of roadless areas are overestimated and should be treated with caution (e.g., Borneo; table S1).

All identified roadless areas were assessed for a set of ecological properties that were selected to reflect their relative importance to biodiversity, ecological functions, and ecosystem resilience: patch size, connectivity, and ecosystem functionality (9) (table S5). We normalized these three indicators to between 0 and 100 to calculate an additive and unitless index of the ecological value of each roadless area identified (termed the ecological value index of roadless areas, or EVIRA) [Fig. 1B and fig. S5; the specific rationale and technicalities of the chosen indicators are described in table S5 (8)]. The EVIRA values range from 0 to 80. A sensitivity analysis shows that ecosystem functionality and patch size are the best single indicators for the final index values (table S6 and figs. S6 to S8). Areas with relatively high index values tend to have a lower coefficient of variation (fig. S9).

We used the International Union for Conservation of Nature (IUCN) and UN Environment Programme-World Conservation Monitoring Centre data set of global protected areas to determine the extent of roadless areas that are protected (8) (Fig. 1C). The roadless areas distribution across human-dominated landscapes was determined following the classification of so-called anthromes, defined as biomes shaped by human land use and infrastructure (10) (Fig. 2 and table S7).

When examining the density of roads within different biomes, large discrepancies in distribution are apparent. The tundra and rock and ice-covered biomes are nearly entirely roadless, whereas temperate broadleaf and mixed forests have the lowest share of roadless areas (41%; figs. S9 and S10). Boreal forests of North America and Eurasia still retain large tracts of roadless areas (figs. S10 and S11). In the tropics, large roadless landscapes (>1000 km²) remain in Africa, South America, and Southeast Asia, with the Amazon having the single largest roadless segment. In relation to the anthromes (10), about two-thirds of the world's roadless areas can be described as remote and unmodified landscapes [26% uninhabited or sparsely inhabited treeless and barren lands; 21% natural and remote seminatural woodlands, with 17% wild woodlands therein (8); Fig. 2 and table S7]. The remaining one-third consists of rangelands, indicating that roadless areas can also occur in anthropogenically modified landscapes.

Fig. 4. Synergies and conflicts between conservation of roadless areas and the United Nations' Sustainable Development Goals. Scores <−0.5 (blue bars) indicate that conflicts with the goal prevail; scores between −0.5 and 0.5 (yellow) indicate a mixture of synergies and conflicts with the goal; and scores >0.5 (green) indicate prevailing synergies with the goal [for details, see table S11 (8)]. The scores reflect substantial imminent conflicts between various Sustainable Development Goals and conservation of roadless areas (table S11).



About one-third of the world's roadless areas have low EVIRA values. Patches with relatively low EVIRA values (ranging from 0 to 37; namely, <50% of the maximum value) account for 35% of the overall roadless area distribution, because most are small, fragmented, isolated, or otherwise heavily disturbed by humans. Some large tracts of roadless areas,

such as arid lands in northern Africa or central Asia, occur in areas of sparse vegetation and low biodiversity and, thus, have low index values for ecosystem functionality (9) (Fig. 1B). High EVIRA values occur both in tropical and boreal forests. The relative conservation value of roadless areas is context-dependent. Comparatively small or

moderately disturbed roadless areas have higher conservation importance in heavily roaded environments, such as most of Europe, the conterminous United States, and southern Canada.

Although the world's protected areas cover 14.2% of the terrestrial surface, only 9.3% of the overall expanse of roadless areas is within protected areas (all IUCN categories; Fig. 1C and table S8). There is no major difference in the coverage of roadless areas by strictly protected areas (IUCN categories I and II) versus the coverage of the overall landscape by strictly protected areas (3.8% roadless versus 4.2% overall). Only in North America, Australia, and Oceania are more than 6% of roadless areas under strict protection (table S8). If conservation efforts were to prioritize functional, ecologically important roadless areas, we would find a positive relation between strict protection coverage and EVIRA values of roadless areas. However, with the exception of Australia, this is not the case (Fig. 3 and table S9). Asia and Africa have particularly low protection coverage for roadless areas with high EVIRA values. For instance, we found gaps in the Asian tropical southeast, as well as in boreal biomes.

The recent Global Biodiversity Outlook (11) gives a bleak account of the progress made toward reaching the United Nations' biodiversity agenda as specified in the 20 Aichi Targets of the Convention on Biological Diversity (12). Governments have failed on several accounts to keep their use of natural resources well within safe ecological limits (target 4); to halt or at least halve the rate of habitat loss and substantially reduce the degradation and fragmentation of natural habitats (target 5); and to appropriately protect areas of particular importance for biodiversity and ecosystem services (target 11). To achieve global biodiversity targets, policies must explicitly acknowledge the factors underlying prior failures (13). Despite increasing scientific evidence for the negative impacts of roads on ecosystems, the current global conservation policy framework has largely ignored road impacts and road expansion. Furthermore, key policies on road infrastructure and development, such as the Cohesion Policy of the European Union, fail to take into account biodiversity.

In the much wider context of the United Nations' Sustainable Development Goals, conflicting interests can be seen between goals intended to safeguard biodiversity and those promoting economic development (14). We analyzed how roadless areas relate to the global conservation and sustainability agendas. As a transparent synthesis, we calculated simple scores of conflicts versus synergies of Sustainable Development Goals and Aichi Targets with the conservation of roadless areas (tables S10 and S11). Roads are explicitly mentioned in the Sustainable Development Goals only for their contribution to economic growth (goal 8), promoting further expansion into remote rural areas, and consideration is given neither to the environmental nor the social costs of road development. The resulting scores reflect substantial imminent conflicts (Fig. 4 and table S10); only in five Sustainable Development Goals do synergies with conservation of roadless

areas prevail, and four Sustainable Development Goals are predominantly in conflict with conservation of roadless areas. Maybe even more surprisingly, several of the Aichi Targets are ambivalent with respect to conserving roadless areas, rather than being in synergy entirely [six conflicting versus 11 synergistic targets (8); table S11].

There is an urgent need for a global strategy for the effective conservation, restoration, and monitoring of roadless areas and the ecosystems that they encompass. Governments should be encouraged to incorporate the protection of extensive roadless areas into relevant policies and other legal mechanisms, reexamine where road development conflicts with the protection of roadless areas, and avoid unnecessary and ecologically disastrous roads entirely. In addition, governments should consider road closure where doing so can promote the restoration of wildlife habitats and ecosystem functionality (4). Our global map of roadless areas represents a first step in this direction. During planning and evaluation of road projects, financial institutions, transport agencies, environmental nongovernmental organizations, and the engaged public should consider the identified roadless areas.

The conservation of roadless areas can be a key element in accomplishing the United Nations' Sustainable Development Goals. The extent and protection status of valuable roadless areas can serve as effective indicators to address several Sustainable Development Goals, particularly goal 15 ("Protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss") and goal 9 ("Build resilient infrastructure, promote inclusive and sustainable industrialization and foster innovation"). Enshrined in the protection of roadless areas should be the objective to seek and develop alternative socioeconomic models that do not rely so heavily on road infrastructure. Similarly, governments should consider how roadless areas can support the Aichi Targets (see tables S10 and S11). For instance, the target of expanding protected areas to cover 17% of the world's terrestrial surface could include a representative proportion of roadless areas.

Although we acknowledge that access to transportation is a fundamental element of human well-being, impacts of road infrastructure require a fully integrated environmental and social cost-benefits approach (15). Still, under current conditions and policies, limiting road expansion into roadless areas may prove to be the most cost-effective and straightforward way of achieving strategically important global biodiversity and sustainability goals.

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SUPPLEMENTARY MATERIALS

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PLANT PATHOLOGY

Regulation of sugar transporter activity for antibacterial defense in *Arabidopsis*

Kohji Yamada,^{1,2*} Yusuke Saijo,^{3,4} Hirofumi Nakagami,^{5†} Yoshitaka Takano^{1*}

Microbial pathogens strategically acquire metabolites from their hosts during infection. Here we show that the host can intervene to prevent such metabolite loss to pathogens. Phosphorylation-dependent regulation of sugar transport protein 13 (STP13) is required for antibacterial defense in the plant *Arabidopsis thaliana*. STP13 physically associates with the flagellin receptor flagellin-sensitive 2 (FLS2) and its co-receptor BRASSINOSTEROID INSENSITIVE 1-associated receptor kinase 1 (BAK1). BAK1 phosphorylates STP13 at threonine 485, which enhances its monosaccharide uptake activity to compete with bacteria for extracellular sugars. Limiting the availability of extracellular sugar deprives bacteria of an energy source and restricts virulence factor delivery. Our results reveal that control of sugar uptake, managed by regulation of a host sugar transporter, is a defense strategy deployed against microbial infection. Competition for sugar thus shapes host-pathogen interactions.

Plants assimilate carbon into sugar by photosynthesis, and a broad spectrum of plant-interacting microbes exploit these host sugars (1, 2). In *Arabidopsis*, pathogenic bacterial infection causes the leakage of sugars to the extracellular spaces (the apoplast) (3), a major site of colonization by plant-infecting bacteria.

Although leakage may be a consequence of membrane disintegration during pathogen infection, some bacterial pathogens promote sugar efflux to the apoplast by manipulating host plant sugar transporters (4, 5). Interference with sugar absorption by bacterial and fungal pathogens reduces their virulence, highlighting a general



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Mariana M. Vale, Peter R. Hobson and Nuria Selva (December 15,
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Editor's Summary

Too many roads

Roads have done much to help humanity spread across the planet and maintain global movement and trade. However, roads also damage wild areas and rapidly contribute to habitat degradation and species loss. Ibisch *et al.* cataloged the world's roads. Though most of the world is not covered by roads, it is fragmented by them, with only 7% of land patches created by roads being greater than 100 km². Furthermore, environmental protection of roadless areas is insufficient, which could lead to further degradation of the world's remaining wildernesses.

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The Effects of Postfire Salvage Logging on Aquatic Ecosystems in the American West

JAMES R. KARR, JONATHAN J. RHODES, G. WAYNE MINSHALL, F. RICHARD HAUER, ROBERT L. BESCHTA, CHRISTOPHER A. FRISSELL, AND DAVID A. PERRY

Recent changes in the forest policies, regulations, and laws affecting public lands encourage postfire salvage logging, an activity that all too often delays or prevents recovery. In contrast, the 10 recommendations proposed here can improve the condition of watersheds and aquatic ecosystems.

Keywords: aquatic ecosystems, postfire salvage logging, public land management, salmonids, western forests

Throughout the American West, a century of road building, logging, grazing, and other human activities has degraded stream environments, causing significant losses of aquatic biodiversity and severe contractions in the range and abundance of sensitive aquatic species, including native salmonid fishes (Rieman et al. 2003). Compounding these problems, federal land management has worsened ecological degradation, rather than conserving or restoring forest ecosystems (Leopold 1937, Langston 1995, Hirt 1996). Land managers' focus on commodity extraction—sharpened by recent changes in forest policy, regulations, and laws that encourage salvage logging after fires—perpetuates this trend and its harmful impacts. Here we focus on the effects of such postfire salvage logging on public lands and aquatic ecosystems. To curb ecological damage from postfire salvage logging, we urge the adoption of 10 recommendations based on decades of ecological research.

Although often done in the name of postfire restoration, salvage logging typically delays or prevents natural recovery in several important ways (Beschta et al. 1995, 2004, Lindenmayer et al. 2004). These impacts tend to have a multiplier effect, because fire-affected ecosystems are sensitive to further disturbances.

- Postfire salvage logging generally damages soils by compacting them, by removing vital organic material, and by increasing the amount and duration of topsoil erosion and runoff (Kattleman 1996), which in turn harms aquatic ecosystems. The potential for damage to soil and water resources is especially severe when ground-based machinery is used.
- Postfire salvage logging has numerous ecological ramifications. The removal of burned trees that provide shade may hamper tree regeneration, especially on high-elevation or dry sites (Perry et al. 1989). The loss of future soil organic matter is likely to translate into soils that are less able to

hold moisture (Jenny 1980), with implications for soil biota, plant growth (Rose et al. 2001, Brown et al. 2003), and stream flow (Waring and Schlesinger 1985). Logging and associated roads carry a high risk of spreading nonindigenous, weedy species (CWWR 1996, Beschta et al. 2004).

- Increased runoff and erosion alter river hydrology by increasing the frequency and magnitude of erosive high flows and raising sediment loads. These changes alter the character of river channels and harm aquatic species ranging from invertebrates to fishes (Waters 1995).
- Construction and reconstruction of roads and landings (sites to which trees are brought, stacked, and loaded onto trucks) often accompany postfire salvage logging. These activities damage soils, destroy or alter vegetation, and accelerate the runoff and erosion harmful to aquatic systems (figure 1).
- By altering the character and condition of forest vegetation, salvage logging after a fire changes forest fuels and can increase the severity of subsequent fires (CWWR 1996, Odion et al. 2004).

James R. Karr (e-mail: jrkarr@u.washington.edu) is a professor in the School of Aquatic and Fishery Sciences and the Department of Biology, University of Washington, Seattle, WA 98195. Jonathan J. Rhodes is a senior hydrologist at Planeto Azul Hydrologic Consultants, Portland, OR 97293. G. Wayne Minshall is a professor emeritus in the Department of Biological Sciences, Idaho State University, Pocatello, ID 83209. F. Richard Hauer is a professor at the Flathead Lake Biological Station, Division of Biological Sciences, University of Montana, Polson, MT 59860. Robert L. Beschta is a professor emeritus in the Department of Forest Engineering, and David A. Perry is a professor emeritus in the Department of Forest Science, at Oregon State University, Corvallis, OR 97331 (Perry's current address is PO Box 8, Kapa'au, HI 96755). Christopher A. Frissell is a watershed ecologist and fishery biologist at the Pacific Rivers Council, Polson, MT 59860. © 2004 American Institute of Biological Sciences.



Figure 1. Postfire recovery and salvage logging in the Malheur National Forest, Oregon. After a 1996 fire, vegetation along an old road was recovering naturally in 1998 (top). In 1999, road reconstruction and salvage logging on the same slopes (bottom) reversed this recovery, increasing soil erosion and surface runoff into a tributary that supports steelhead trout (*Oncorhynchus mykiss*), a salmonid listed as threatened at the time under the Endangered Species Act. Such increases in sediment delivery lower the survival rates of steelhead and other aquatic species. Photographs: Jonathan J. Rhodes.

- Postfire salvage logging undermines the effectiveness of other costly postfire rehabilitation efforts, most of which are aimed at reducing soil erosion and runoff (Robichaud et al. 2000).

In short, by adding another stressor to burned watersheds, postfire salvage logging worsens degraded aquatic conditions accumulated from a century of human activity (CWWR 1996, NRC 1996, 2002, McIntosh et al. 2000). The additional damage impedes the recovery and restoration of aquatic systems, lowers water quality, shrinks the distribution and abundance of native aquatic species, and compromises the

flow of economic benefits to human communities that depend on aquatic resources (Beschta et al. 2004).

The impacts of fire, and of salvage logging and its associated activities, vary in severity from site to site, depending on a site's natural conditions and on its history of human use. Fires burn in a mosaic of intensities; most areas burn at moderate to low intensity. High-severity burns place the most stress on watersheds and aquatic systems. By themselves, the effects of fire create few problems for aquatic populations that have access to high-quality stream environments (Gresswell 1999); fire even provides benefits, such as pulsed additions of spawning gravel and wood. But where a history of environmental degradation and fragmentation of aquatic populations already exists, fire can threaten certain species, and salvage logging adds another layer of stress.

The effects of postfire salvage logging are especially significant on steep slopes, in erosion-prone soils, on severely burned sites (where the impacts listed above can be particularly pronounced), and in riparian and roadless areas. Riparian areas affect aquatic environments more than remoter uplands do; they influence water quality, physical habitat, and the abundance of aquatic species (Gregory et al. 1991, Naiman et al. 1998). Logging, landings, and roads in riparian zones degrade aquatic environments by lessening the amount of large wood in streams, elevating water temperature, altering near-stream hydrology, and increasing sedimentation. Roadless areas comprise some of the least disturbed living systems and are therefore especially important to the restoration of watersheds and freshwater systems. Consequently, logging activities in these

areas undermine the conservation and restoration of aquatic ecosystems (FEMAT 1993, Henjum et al. 1994) even as they increase the risk of extirpation for already imperiled, fragmented, and sensitive populations.

Avoiding damage from salvage logging: Ten recommendations

Continued postfire salvage logging ignores many threats to aquatic resources, virtually guaranteeing trajectories toward unsustainable ecosystems. Halting this deterioration should be a policy priority. To protect streams, wetlands, and associated watersheds and to foster their restoration, we offer the following 10 policy recommendations.

Allow natural recovery to occur on its own, or intervene only in ways that promote natural recovery. Many interventions in postfire landscapes delay or prevent recovery by adding to fires' short-term effects. Allowing unimpeded natural recovery of burned landscapes is typically more cost-effective and often results in more rapid recovery than postfire salvage logging (Kauffman et al. 1997). Natural recovery is particularly important on public lands, which, despite widespread degradation, are still in better condition than many private

lands. Today public lands represent the best starting point for restoring aquatic systems. In Oregon, for example, 14 of 25 at-risk fish species or subspecies live in watersheds within the boundaries or immediately downstream of national forests (Henjum et al. 1994).

Any intervention should aim to reduce the effects of past and present human disturbances, rather than focus solely on fire impacts: Postfire treatments can and should be compatible with aquatic restoration. A crucial component of aquatic restoration is to maintain and reestablish more-natural process rates (e.g., hydrology, sediment transport, nutrient cycling, and species demographics); obliterating existing roads, for example, would help restore hydrologic and erosion regimes. Recovery is also aided by reestablishing the connectivity of aquatic populations, establishing more-natural flow patterns in regulated or diverted rivers, reducing the extent and consequences of road networks, and diminishing the negative effects of livestock grazing. Lost or damaged parts of ecosystems, such as native species that are imperiled or otherwise important, should be restored along with ecological processes.

Retain old or large trees. Dead or alive, burned or unburned, large trees are vital for postfire recovery; they provide habitat for many species, reduce soil erosion, aid soil formation, and nourish streams as their leaves fall or their trunks decay (Henjum et al. 1994). Whether large dead trees present a fire risk for the future is a matter of debate. Although they typically do not increase fire severity or the rate of fire spread at a fire front when down (Brown et al. 2003), standing dead trees can send flaming debris ahead of a fire front and ignite spot fires. In contrast, there is no debate about the key role that large trees play in aquatic systems and many ecological processes (Rose et al. 2001). Because of the trees' market value, however, postfire logging typically targets large and even live trees.

Protect soils. Fire-affected soils are especially vulnerable to additional disturbance (e.g., compaction or increased erosion). Soils deserve special care because soils and soil productivity are irreplaceable within human time scales and are crucial to forest recovery, stream conditions, and hydrologic processes. Particular care should be taken to protect shallow, severely burned, erosion-prone, and otherwise fragile soils. Although it is best to prevent postfire salvage logging, in some circumstances doing so may not be possible. In such rare circumstances, higher-risk practices, such as logging with ground-based equipment, should not be used, and sensitive areas should be avoided to limit aquatic impacts. No logging should be done on moderately and severely burned areas and on other sites prone to soil damage and excessive sedimentation. Helicopters and full-suspension cable yarding systems that use existing roads and landings damage soils the least, although they may still delay or prevent recovery of vulnerable areas.

Protect ecologically sensitive areas. Riparian and roadless areas, regions with steep slopes, and watersheds with sensitive or imperiled aquatic species should not be salvage logged. Impacts in riparian and roadless areas influence areas with the highest regional biodiversity, including rare and endangered species; they also have wide repercussions that spread across landscapes, including downstream.

Avoid creating new roads and landings in the burned landscape. Roads and landings cause enduring damage to soils and streams, help spread noxious weeds, and hinder revegetation. Roads are a primary cause of reduced water quality and of contractions in the distribution and number of native salmonids on public lands. Reducing road mileage in national forests should be a primary postfire response. A decade ago, for example, the road densities of three national forests in the US Northwest averaged 2.5 miles per square mile (western Colville National Forest; 1 mile = 1.61 kilometers), 3.5 miles per square mile (Winema National Forest), and 3.7 miles per square mile (Ochoco National Forest) and attained 11.9 miles per square mile in some watersheds (Henjum et al. 1994). On a regional scale, the national forests of California's Sierra Nevada have a mean road density of about 1.7 miles per square mile, despite the relatively high proportion of wilderness and roadless areas within these forests.

Limit reseeding and replanting. Seeding with nonnative species can impede native plant regeneration (Amaranthus et al. 1993, Beyers 2004) and often spreads invasive species in vulnerable fire-affected soils. Native seed sources or colonists are almost always sufficient for early natural reestablishment of native species, so planting should be considered only when natural regeneration is unlikely; such planting should use only regional stocks of native species. When seed sources of particular species have been lost, replanting should supplement those natives that have become reestablished, not overwhelm them. Replanting dense stands of fast-growing conifers—a common postfire management practice—truncates the biologically rich early stages of ecological succession and can increase the severity of future fires (Odion et al. 2004). Other treatments should be carefully scrutinized for their potential to spread noxious weeds. For instance, straw mulch applied extensively to reduce erosion after the 2002 Hayman Fire in Colorado was contaminated with cheatgrass (Robichaud et al. 2003), an invasive grass difficult to control or eradicate once established. Upslope degradation will ultimately influence aquatic ecosystems.

Do not place structures in streams. In-stream structures (e.g., sediment traps, riprap, check dams, or artificially placed large wood) rarely provide ecological benefits that outweigh the physical damage or expense of installing and maintaining them (Beschta et al. 1994). Although events after a fire may appear catastrophic, periodic fire actually provides the pulsed inputs of sediment and wood that are crucial to maintain the complexity of aquatic habitat (Hauer et al. 1999). Sediment

Forum

abatement should focus on reducing or eliminating human sources of sediment (e.g., culverts and roads) because they tend to be chronic. In contrast, protecting and maintaining natural sediment-processing mechanisms should be a priority in burned landscapes.

Protect and restore watersheds before fires occur. Because it is difficult to reverse a fire's effects rapidly after the fact, prefire conservation and restoration are more likely than postfire rehabilitation measures to protect soils, hydrologic patterns, and aquatic resources (Dunham et al. 2003). Actions taken before fires occur—such as removing unnatural migration barriers to reconnect fragmented fish populations and curtailing activities that increase runoff and erosion or degrade water quality and physical habitats—can increase the resiliency of soils, aquatic habitats, fish, and other organisms to the effects of fires. Thus, fire management policies should strive to reestablish the dynamics of 19th-century and earlier fire regimes; natural and prescribed fires may help meet this objective.

Continue research, monitoring, and assessment. Carefully planned research, monitoring, and assessment should be routine components of programs on the effects of postfire forest treatment. Uncertainties about the effects of salvage logging remain; rigorous retrospective evaluation of forest treatments' effects on fire, forests, and aquatic systems are needed before continuing the present practice of aggressive salvage logging. Despite efforts to fund evaluations (i.e., monitoring and assessment) of the effectiveness of thinning and other so-called restoration practices, no such provisions made it into the Healthy Forests Restoration Act of 2003 (Service 2003). Research is needed, for example, to shed light on the long-term responses to fire in low-elevation forests where salvage logging has not taken place and on how aquatic systems are changed by these responses. Improved understanding of these issues should be a priority in the few suitable areas remaining on federal lands. Such areas can serve as experimental controls for research on the effects of fire on wildland watersheds and associated aquatic systems. Long-term, landscape-scale experimental studies should take priority over logging in these areas. Establishing controls—large, untreated areas in a variety of settings—is vital to long-term environmental research.

Educate the public. Citizen awareness is key to informed management of public lands. Although forest fires are often portrayed as “disasters” or “natural catastrophes,” fires are crucial to the maintenance of healthy forests (Gresswell 1999, Pyne 2001) and associated aquatic ecosystems (Beschta et al. 1995, 2004, Lindenmayer et al. 2004). Despite common misconceptions, forest and aquatic ecosystems evolved with, and depend on, natural fire cycles; it is important to recognize this dependence and incorporate it into natural resource decisions. Policymakers and the public need to recognize that not all forests are the same: Some forest types in the

western United States are at risk from fires that are abnormally severe and destructive, but in other forest types, severe fires are the norm (Veblen 2003). Throughout much of the West, the climate is sufficiently wet to grow trees, and conditions periodically become dry enough for forests to burn.

Conclusions

Contrary to these recommendations, changes in regulations, policies, and laws in the past few years seek to expedite post-fire salvage logging at the same time that they diminish the role of science in decisionmaking and raise barriers to citizen participation (Service 2003). Many areas burned during the last two years have been partially logged or are proposed for logging. In Arizona, for example, the USDA Forest Service (2004) is proposing to log, using ground-based machinery, more than 40,000 acres (16,196 hectares) that were moderately to severely burned in the 2002 Rodeo-Chediski Fire. The agency's proposal for salvage logging within the area burned by the 2002 Biscuit Fire in Oregon includes more than 8000 acres (3293 hectares) of roadless area in a region noted for its rich biological diversity, including imperiled salmonids. According to Jack Williams, former forest supervisor for the Rogue River and Siskiyou National Forests, the agency's plan risks long-term ecological damage and guarantees controversy that will generate delays, litigation, and protests (Williams 2004). The July 2004 proposal to roll back protection of roadless areas from postfire salvage and other logging may be the single largest rollback of protection of public lands in the nation's history (Pope 2004).

In addition, the Forest Service's requirements for public involvement have been relaxed, making public input into agency decisionmaking more difficult. Some categories of postfire salvage logging are now categorically excluded from requirements for detailed analysis and public disclosure of environmental impacts. The Forest Service is now allowed to use “emergency” exemptions to proceed rapidly with post-fire logging on the basis of the burned trees' economic value as timber; ecological losses—economic and noneconomic—can be ignored in seeking such exemptions. These policies and procedures do not, for example, require consideration of watershed protection measures (e.g., retention of large trees, protection of roadless and riparian areas, and protection of local and downstream aquatic resources). They do increase the likelihood of additional harm to aquatic and terrestrial systems, while authorizing the Forest Service to ignore citizen input and scientific information.

Managing public lands for the benefit of present and future generations is a challenge—a process most likely to succeed in an open atmosphere that actively uses existing scientific and technical information and expertise. Our recommendations can serve as core guidelines for averting further harm to aquatic systems already stressed after fires. Success will depend on vision and leadership at the highest levels of government and in land management agencies, as well as on the relevant expertise, authority, and commitment of local public land managers. A commitment to these changes

at the national and local levels will help to protect the public interest and to conserve our natural heritage in the aquatic environments on and downstream of public lands.

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LETTER

Ecological integrity is both real and valuable

James R. Karr¹  | Eric R. Larson²  | Ellen W. Chu³¹University of Washington, Sequim, Washington, USA²Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana, Illinois, USA³Ecologist and Editor, Port Townsend, Washington, USA**Correspondence**

James R. Karr, University of Washington,
102 Galaxy View Court, Sequim, WA
98382, USA.
Email: jrkarr@uw.edu

Abstract

Ecological integrity has been criticized as a “bad fit as a value” for conservation biology and restoration ecology. But work over the past four decades centered on ecological integrity—especially biological integrity—has given rise to effective methods for biological monitoring and assessment to better understand the disintegration of living systems, including under scenarios of rapid climate change. Revealing when and where living systems have been altered by human activity, such methods have been adapted and applied most comprehensively in streams and rivers, but also in other ecosystems, ranging from tropical forests to marine coral reefs and on all continents except Antarctica. Equally important, restoration and maintenance of biological integrity is already a fundamental goal in law and offers an inspiring framework for communication and engagement—among scientists, resource managers, law- and policymakers, and the public. This essay builds the case that ecological integrity has proved both real and valuable as a conservation paradigm.

KEYWORDS

beneficial use, biological integrity, Clean Water Act, ecological integrity, freshwater, index of biological integrity (IBI), multimetric index (MMI), reference condition, river, stream

Rohwer and Marris (2021) (hereafter R&M) have critiqued ecosystem integrity, calling it “a bad fit as a value for conservation biology and restoration ecology.” The authors discuss several definitions of the word *integrity*, find problems with them, and conclude that the word and concept therefore have no utility for conservation. We are sympathetic to some concerns these authors raise—including challenges in defining ecosystems and the potential for management agencies to misapply concepts in ecosystem integrity—but we completely disagree with their conclusion.

For better and worse, humans have been transforming this planet for tens of thousands of years—from mass mammalian extinctions some 10,000–50,000 years ago; to the advent of agriculture about 10,000 years ago, which shows hints of altering the climate even then; to the dense human civilizations agriculture made possible; to the global transformations of air, land, water, and living systems that we see today (ArchaeoGLOBE Project, 2019; IPCC, 2021; Ruddiman et al., 2015). Now, however, after more than a half century of scientific advances, the concept of biological integrity has given

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rise to effective methods for biological monitoring and assessment to deploy against the accelerating disintegration of living systems—multimetric indexes that share familiar properties with measures of economic and human health and, most important, directly measure the status of the biota. In this rejoinder to R&M, we wish to build a case for a counterproposition—that ecological integrity, particularly biological integrity, has proved to be both real and valuable as a conservation paradigm.

The evolution of our ideas was inspired by a convergence between the words of Aldo Leopold and those of the US Clean Water Act (CWA). As Leopold (1949) wrote in one deeply personal and highly philosophical essay (also quoted by R&M), “A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise.” Similarly, the act’s first objective is “to restore and maintain the physical, chemical and biological integrity of the nation’s waters” (Pub. L. No. 92-500, § 2, 86 Stat. 816, codified as amended at 33 U.S.C. §§ 1251–1387 [2013]). Both of these declarations emphasize the centrality of what is alive. It is not about protecting the Earth but about protecting Earth’s living systems. The concept of biological integrity, and the multimetric biological indexes founded on that concept, initially led to many real-world accomplishments in river and water resource protection and later, to assessing and conserving diverse environments (freshwater, marine, wetland, and terrestrial). Starting with fish, indexes of biological integrity (IBI) have incorporated varied biological assemblages as indicators (bacteria, plants, invertebrates, vertebrates, and more; Table 1); such indexes have been demonstrably valuable in conservation biology, restoration ecology, and water resource management.

We disagree with a number of premises in R&M’s article, including their statement that ecosystem integrity and ecological integrity are equivalents and that “the general practice in the field” is to use the ideas interchangeably. In fact, neither the terms nor the concepts are interchangeable. While ecosystems may be difficult to define, ecology—the scientific study of living systems—is not. Ecology, the science, explores biological phenomena across multiple levels of organization: individual health, population demography, community organization, energy flow and nutrient cycling in ecosystems, and the mosaic nature of landscapes. We agree with MacArthur (1972) that “[t]he question is not whether such [levels] exist but whether they exhibit interesting patterns about which we can make generalizations.” A view of biological organization comprising this full spectrum—rather than an ecosystem-by-ecosystem view—is essential to defining biological integrity and to judging when living systems are altered by anthropogenic factors. For

example, the effects of toxic pollutants may reveal themselves as observed changes in the health of individual organisms (lesions in fish, extra legs in amphibians). Similarly, altered physical habitat or changes in a river’s flow regime may show up as shifts in trophic organization and in species losses (disappearance of long-lived predators, proliferation of filamentous cyanobacteria).

We further disagree with R&M’s contention that the concept of ecological integrity cannot explain losses of conservation value as ecosystems change. They note that ecosystems are always changing, that not all changes are bad, that ecosystems cannot therefore possess integrity, and that “‘ecosystem integrity’ cannot be valuable.” The implication is that any notion of ecological integrity inherently lacks value and can therefore not be used to explain any loss in value. Yet surely we can agree that value is lost if a stream community harboring multiple species of mayflies, stoneflies, and caddisflies is replaced—for example, downstream of a waste treatment plant—by a community dominated by sewage sludge worms. Or when a river is dammed, replacing miles of free-flowing water with a slow-moving reservoir, wiping out an entire spawning population of 100-pound chinook salmon and thereby removing the marine-derived nutrients the fish had brought to the watershed every year for millennia.

It is a pioneering accomplishment of ecological assessments based on the concept of ecological integrity, which incorporate direct measures of biological condition, that such assessments are able to document and quantify losses in value, particularly, losses due to human impact. Grantham et al. (2020), for example, have developed a globally consistent, continuous index of forest condition in relation to degree of human modification—the forest landscape integrity index, or FLII—which has shown that only 40.5% of global forest has “high landscape-level integrity,” clearly a loss in conservation values. Indeed, many changes in ecosystems represent a severe loss of the supporting, provisioning, regulating, and cultural services critical to (and therefore valuable for) human survival (Millennium Ecosystem Assessment, 2005).

R&M further assert that “integrity has a hard time explaining common judgments about loss of ecological value” and that “other such goals, such as biodiversity and complexity, seem to do a better job of accounting for common judgments about the loss of value.” Again, we disagree. R&M never define “common judgments.” If common judgment sees timber production as the highest and best use of forests on Washington State’s Olympic Peninsula, should that judgment dictate conservation practices there? If common judgment says, in contrast, that only old-growth forests have value, should logging never be permitted? Well before a recent boom in functional trait-based ecology

TABLE 1 Multimetric measurement of biological condition after passage of the CWA continues as an active area of research and application. A Google Scholar keyword search (February 28, 2017) on *IBI* and *biological integrity* produced 12,200 hits, which had increased to 18,300 hits 4 years later (November 11, 2021). The breadth of habitats (e.g., rivers, lakes, reservoirs, wetlands, coral reefs, estuaries, forest, shrubland, grassland, caves); taxonomic groups (e.g., fish, macroinvertebrates, vascular plants, algae, diatoms, birds, amphibians, microbes, nematodes); and geographical areas span the world (at least 100 countries on all continents but Antarctica). Selected examples appear here.

Reference	Taxa, location, habitat	Results and applicability
Ruaro et al. (2020)	Reviews past work across taxa and habitats globally	Recommendations for best practices and standardization in developing and using multimetric indexes (MMI); context for successful programs and cautions about pitfalls and unresolved issues
Feio et al. (2021)	Global-scale review of river assessment, study design, sampling methods, taxa, etc.	Comprehensive exploration of the reasons for biological assessment and the need to apply such assessments to improve restoration; identifies major gaps and describes characteristics of successful programs; calls for coordination for global river conservation and restoration
Hilderbrand et al. (2020)	Microbes in Maryland, USA, headwater streams	Stream microbe samples used to document relationships between microbial biotic index, environmental attributes, and invertebrate and fish IBIs; creates new microbial biotic index to apply to river restoration
França et al. (2019)	Macroinvertebrates in Brazilian urban streams	Urban water body assessments revealing degradation of physical habitat, water quality, or biology in 91% of sampled urban stream sites; local example of participatory scientific monitoring, education, and community science
Liu et al. (2020)	Algae in US lakes	Addition of blue-green algal metric in diatom multimetric index improves detection of anthropogenic disturbances to lakes, especially in medium- and highly disturbed lakes
Schrandt et al. (2021)	Nekton index for urbanized Tampa Bay estuary, Florida, USA	Development of nekton biological index (macroinvertebrate and fish) for estuary monitoring; index sensitive to prolonged red tides
Hallett et al. (2019)	Fish community in urbanized southwestern Australia estuary	Fish community index: success from collaborative partnership, index testing and validation, robust monitoring regime, sustained resources from managers; platform for assessing and reporting bioregional estuarine condition
Carter et al. (2019)	Shrublands of Nevada, USA	Tracks plant community metrics to assess shrubland communities influenced by and in relation to diverse human uses; quantifies natural reference and socially desirable conditions
Spyreas (2019)	Wetland plants in Illinois, USA	Floristic quality assessments to evaluate habitat conservation value, ecological integrity, and naturalness, including systematic discussion of successes and failures
Wang et al. (2021)	Fish in global freshwater and marine environments	Molecular surveillance approaches like eDNA; promising new opportunities to guide conservation actions
Birk et al. (2013)	Europe's aquatic ecosystems: rivers, lakes, coastal waters	Success in protecting aquatic ecosystems across state boundaries and administrative barriers
USEPA (2016)	Many taxa across US freshwater habitats	Development and application of a biological condition gradient to measure biological integrity across freshwater habitats
Evans et al. (2020)	Global links between ecological integrity and human health	Links ecological degradation, infectious disease, and other aspects of human health

Note: A search on related keywords (November 11, 2021) showed the breadth and depth of scholarly work on relevant topics: *ecological integrity of streams* 202,000 hits, *ecological integrity and human health* (427,000 hits), *ecosystem integrity* (864,000 hits).

Abbreviations: CWA, Clean Water Act; eDNA, environmental DNA; IBI, index of biological integrity; MMI, multimetric index.

(Malatterre et al., 2019; McGill et al., 2006), ecological integrity was specifically conceptualized to incorporate a wider set of metrics (Angermeier & Karr, 1994)—metrics including, but not limited to, biodiversity and not dependent on ill-defined “common judgment.” As widely practiced today, indexes founded on ecological integrity improve our understanding of when and where living systems have been altered by human activity. This understanding in turn provides a foundation for societal decisions and policymaking about whether ecosystem services—and therefore ecological values—have been gained or lost.

The objectives of the CWA enjoin compliance and enforcement activities that protect the quality of water resources and the health of ecosystems, as well as that of human communities dependent on those resources (Hitt & Hendryx, 2010). The concept of biological integrity is particularly useful in this regard. After multimetric measures of biological integrity were first implemented in the 1980s, they became widespread over the next 40 years, informing restoration, conservation, and regulation under the act (Kuehne et al., 2017). Previously, nearly a century of enforcement under the Water Pollution Control Act had relied on water quality criteria centered on chemical pollutants and toxicology. Two exceptions—studies of diatoms (Patrick, 1949) and of benthic macroinvertebrates (Hilsenhoff, 1977)—used a single biological metric to indicate organic enrichment in streams. Then, Karr et al. (Fausch et al., 1984; Karr, 1981; Karr, 2006; Karr et al., 1986) proposed the first multimetric biological index, the IBI, and operational criteria for biological integrity that could be applied under the CWA.

IBI speaks directly to the act's broadly conceived “beneficial use” mandate; it has long documented and emphasized that impairment cannot be reversed solely by curbing point-source chemical pollutants (Karr & Dudley, 1981). Metrics incorporated into the first IBI included several measures of taxonomic diversity (akin to R&M's preferred biodiversity criterion), in combination with relative abundances of fishes that were tolerant or intolerant of pollutants or sediment, relative abundance of species at different trophic levels, and others. Under the umbrella of conserving or restoring beneficial uses to humans, the CWA called for the explicitly biological conditions of “fishable and swimmable” waters. For people, landscapes that lack safe drinking water (Westling et al., 2020), places to swim (Fesenmyer et al., 2021), or fish to eat (Gibson-Reinemer et al., 2017) are less valuable than landscapes supplying these benefits. What more logical way to measure and restore very real biological benefits than by applying biological standards?

The multimetric framework of IBI has equally real analogs in other complex systems and shares core

conceptual components with those analogs—specifically, a framework to diagnose ecological (specifically biological) condition, validated metrics used for diagnosis, and reference benchmarks. Familiar multimetric indexes include the consumer price index or Dow Jones Industrial Average and the Apgar test for assessing a newborn's condition right after birth. Indicators like these for economic and human health are assessed against normative reference conditions defined by, for example, body temperature, urine chemistry, or cholesterol levels prevailing in healthy individuals. Applying lessons learned from public health and medicine, measures of biological condition are first calibrated against a gradient of human influence, then chosen and validated as metrics that indicate changes in key biological attributes, the way a fever indicates illness in people. Validated metrics are then assessed against regional reference benchmarks (see Karr & Rossano, 2001 and Elozegi et al., 2017 for more discussion of medical and public health templates). The idealized reference condition—ecological integrity—is defined as an ecological system able to support and maintain an adaptive biological system comprising the full range of parts and processes expected for that region, a system whose evolutionary legacy remains intact (Karr, 2009; Karr & Chu, 1999).

In reality, however, as R&M note, we cannot know or measure such an idealized condition anywhere: historical data are absent, and humans have already changed living systems globally (ArchaeoGLOBE Project, 2019; Ruddiman et al., 2015). R&M contend that conservationists have regarded pre-European reference conditions in North America as essential to ecological integrity. Not so; bioassessment, particularly of rivers and streams, has long used benchmarks independent of historical baselines. Moreover, as IBI-like tools were implemented worldwide over the past half century, practical and effective definitions of reference condition have been established in diverse ways according to available data, including in areas experiencing thousands of years of intensive human use (e.g., Fausch et al., 1984 and Stoddard et al., 2006 for North America; Pont et al., 2006 and Poikane et al., 2017 for Europe; and Liu et al., 2017 for China).

Unlike R&M's complicated discussion of the meaning of *integrity*, we define biological integrity as one endpoint on a gradient of biological conditions, ranging from relatively free of human disturbance to nothing left alive. In practice, however, defining biological reference conditions does not mean that all places can, or even should, be managed with a goal of achieving biological integrity. For example, it might be reasonable to set a conservation goal for a stream in Mount Rainier National Park at or near biological integrity, but such a goal would be unreasonable for a stream

running through Seattle. For lands under intensive human use—farms, cities, or timberlands—a more reasonable goal would be ecological health. Maintaining ecological health on such lands means managing them to prevent degradation of the land for future use, as well as to prevent degradation of areas beyond the site (Karr, 1996). Soils, for example, should not be eroded or depleted to preclude future productivity, and atmospheric contamination from a factory should not poison downwind regions. No land uses that have such deleterious effects are sustainable.

Key to the utility of bioassessment tools founded on integrity, such as IBI, is the ability to assess biological condition; to diagnose human and nonhuman causes of ecological degradation; and, on the basis of these results, to prevent more degradation or propose remedies. In water bodies, such as Jordan Creek in Illinois, for example (Figure 1), human transformations go far beyond adding pollutants. They can and have altered water quality, habitat structure, flow regime, energy sources, and biotic interactions, with cascading consequences for river life (Karr, 1991; Karr et al., 1986). Both the index and component metrics can be examined to identify human actions likely to be responsible for declining biological condition in rivers, leading to numerous real-world successes. To date, multimetric biological assessments have been completed in the United States for over a million stream and river miles nationwide (United States Environmental Protection Agency [USEPA], 2020). A special reservoir fish assessment index has even been developed to track the biological condition of fish communities living in entirely artificial environments, such as reservoirs managed by the Tennessee Valley Authority (Jennings et al., 1995). Such assessments have transformed water resource management on a global scale (Ruaro et al., 2020; Feio et al., 2021; see the selected examples in Table 1).

Consider the progress in Ohio's rivers, for example, thanks to 40 years of leadership by Ohio EPA. Multimetric biological indexes helped the state's water resource managers bring the biological condition of the Scioto River into compliance with biological criteria newly established under CWA water quality standards and, in so doing, enhance fishing, hunting, canoeing, and other outdoor recreation (Karr et al., 2020; see Figure 2). With similar work in the Auglaize River watershed, the percentage of cultivated acres under soil-conserving tillage practices rose from less than 5% to more than 90%. Soil erosion and nonpoint pollution from sediment- and nutrient-containing runoff decreased, in turn reducing stream sedimentation and blooms of organic matter; less soil erosion will also sustain the watershed's long-term agricultural productivity. And the Auglaize's fish community, assessed using Ohio's fish IBI, came into compliance



FIGURE 1 Post–World War II agricultural intensification (David & Gentry, 2000) caused many streams of the midwestern United States to fail to meet the beneficial-use standards and the physical, chemical, and biological integrity objectives of the 1972 Clean Water Act (CWA) (Thornbrugh et al., 2018). Jordan Creek in Vermilion County, Illinois (40.0409 N, –87.8467 W), experienced declines in physical habitat integrity as a consequence of channelization and dredging (Karr & Schlosser, 1978); declines in chemical integrity as a consequence of massively increased nutrient loads without any historical precedent (David & Gentry, 2000); and declines in biological integrity through alteration of its fish fauna caused by changes in flow regime and energy sources after riparian destruction (Larimore et al., 1952; Larimore & Bayley, 1996; Schlosser, 1982). Biodiversity and complexity alone would be inappropriate benchmarks for any restoration of Jordan Creek. This creek could never have as much biodiversity or habitat complexity as a larger downstream river (Xenopoulos & Lodge, 2006). Neither is complexity an appropriate goal for chemical integrity under the CWA (Kaushal et al., 2018). Rather, ecological integrity explicitly sets benchmarks for physical, chemical, and biological integrity (inclusive of biodiversity) in reference to habitat constraints (e.g., size) and geographic place (i.e., ecoregion). Image courtesy of Eric Larson

with the state's biological criteria for warm-water and excellent warm-water habitat.

This systematic work had five lessons to teach: (1) standardized monitoring enables connecting the dots

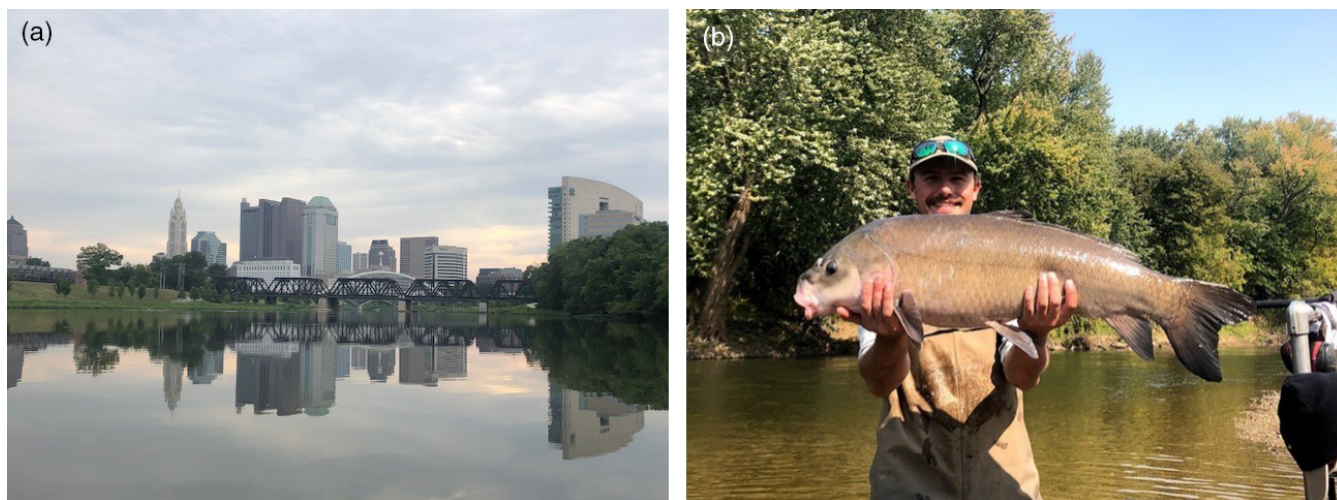


FIGURE 2 Despite massive expenditures in the 1960s and 1970s to improve wastewater treatment technologies, the lack of comprehensive biological criteria left no mechanism to effectively protect the biota of rivers (Barbour et al., 2000) until index of biological integrity (IBI) was developed in the 1970s (Karr, 1981). Biological monitoring and assessment played a key role in improving the biological condition and water quality, as mandated by the Clean Water Act (CWA), of the Scioto River in Central Ohio (a) (Karr & Yoder, 2004). The river's biological condition was below biological standards when the first fish samples were collected, in 1979–1981. By 2005, nearly all sampled sites on the river attained or exceeded the minimum threshold for “warm-water habitat,” and by 2009 most sampled sites qualified as “exceptional warm-water habitat.” By 2017, as many as 70 species of fish, many absent for more than a century, could again be found in the 40-mile reach of the mainstem Scioto River in and downstream of Columbus (Yoder et al., 2019). Intolerant and moderately intolerant species returned, including larger individuals of long-lived species like the black buffalo *Ictalurus nebulosus* (b). Images courtesy of Matt Sarver

among stressors, exposures, and responses; (2) biological data represent the gold standard for monitoring any living system, even in artificial environments, powerfully complementing physical and chemical data; (3) biological benefits from improved agricultural practices are fast and easy to see; (4) more biological data mean less need for chemical data to show progress toward attaining designated uses under the CWA; and, arguably most important, (5) better land management leads to dramatic improvements in the biological condition of rivers (Karr & Yoder, 2004). All this and more illustrate precisely the clear, specific values and reasons motivating protections and interventions that R&M say are desirable.

Multimetric biological assessment has demonstrated its effectiveness in diagnosing and understanding human and natural causes of ecological changes across time and space for nearly half a century, and it can and will continue to do so. Biological responses to human-fueled global change are well studied in birds and plants, and global change researchers are starting to pay attention to these bioindicator patterns (Menzel, 2002). In the Northern Hemisphere, some bird species, for example, migrate earlier in spring or shift their breeding areas farther north; some species whose phenology does not shift have suffered population declines (Moller et al., 2008). Advances or delays in plant and insect phenology and in

species' distributions have produced mismatches between birds and insect food sources and between plants and pollinators (Hughes, 2000). Such complex coevolutionary mutualisms—relationships R&M dismiss as too fleeting or otherwise out of step with integrity—are critical for maintaining global ecosystem services. The full gamut of these bioindicators will be important for understanding climate change and making societal decisions in the future.

Even so, because species and ecosystems have adapted to natural and human-catalyzed climate change throughout geological time, R&M conclude that ecological integrity has no utility with regard to conservation under the accelerating and ever more obvious consequences of human-induced climate change. Quite the contrary: the biological signals that multimetric biological assessments are designed to track are precisely what conservationists need to know as this latest massive human transformation of our own habitat unfolds. The ability of assessments founded on ecological integrity to measure rapid changes on land and in water can tell us which restoration or adaptation actions are working in response to climate change and which are not. Such assessments can and will help us understand which of multiple human causes of degradation most acutely alter living systems in particular places as the climate changes. Beavers moving north and climate refugees from rapidly altering habitats (both invoked by

R&M) teach us a great deal about which ecosystem services and values we may or may not be losing, as well as the lessons we need to control the human activities that drive climate change. Projects have already been undertaken in degrading trout streams, for example, to understand the role played by climate-induced changes in flow regimes (which IBI-style indexes have long been used to assess) (Williams et al., 2015); biological monitoring following beaver reintroductions (Dittbrenner et al., 2018) can tell us whether or not a given watershed is recovering. Such deep looks at the whole biology of places—not only at one species or another—are the most valuable means to understand what we are doing to, and what we can do to protect, the places we live.

In sum, nearly everyone can agree that healthy living systems are central to the future of human society. Our direct experience and the evidence proffered in this essay have shown that the concept of ecological integrity—particularly, biological integrity—can be and has been translated into measurable, practicable criteria for protecting living ecosystems and the services they provide. Multimetric indexes based on these principles have proved effective for assessing the health of living systems, from water resources to tropical bird communities and on all continents but Antarctica (Ruaro et al., 2020). Multiple metrics, each calibrated along a gradient of human influence, do a better job than unidimensional benchmarks, including biodiversity, of gauging success toward meeting specific biological criteria and of capturing overall ecological health. As R&M note, biodiversity as a sole benchmark leads to the “bizarre” logic that diverse tropical ecosystems are inherently more valuable than less-diverse boreal or high-latitude ecosystems.

In contrast, multidimensional assessments founded on integrity and calibrated for unique living systems show great past and future promise. Moreover, the words *integrity* and *health* evoke important human values, thereby opening the door to wide-ranging societal conversations and collaborations among scientists, resource managers, law- and policymakers, and especially the general public (Karr 1993). They offer an inviting framework for constructive debate about conservation strategies, especially in this era of rapid climate change (Wurtzebach & Schultz, 2016). To integrate ethics, science, and law, Bridgewater et al. (2015) propose a “scientific and legal construct for ecological integrity” that would become part of the rule of law—“a global environmental constitutional norm,” no less, for “maintaining the integrity of Earth’s ecological systems.” We need every strategy we can muster to realize the vision articulated by Leopold and the CWA: to restore and maintain the integrity of the living world.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Eric R. Larson and James R. Karr conceptualized the work. James R. Karr, Eric R. Larson, and Ellen W. Chu wrote, reviewed, edited, and revised the manuscript.

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ETHICS STATEMENT

No human or animal subjects were used in the preparation of this paper.

ORCID

James R. Karr  <https://orcid.org/0000-0001-5973-1121>

Eric R. Larson  <https://orcid.org/0000-0002-9232-5907>

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High-Biomass Forests of the Pacific Northwest: Who Manages Them and How Much is Protected?

Olga N. Krankina · Dominick A. DellaSala ·
Jessica Leonard · Mikhail Yatskov

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Abstract To examine ownership and protection status of forests with high-biomass stores (>200 Mg/ha) in the Pacific Northwest (PNW) region of the United States, we used the latest versions of publicly available datasets. Overlay, aggregation, and GIS-based computation of forest area in broad biomass classes in the PNW showed that the National Forests contained the largest area of high-biomass forests (48.4 % of regional total), but the area of high-biomass forest on private lands was important as well (22.8 %). Between 2000 and 2008, the loss of high-biomass forests to fire on the National Forests was 7.6 % (236,000 ha), while the loss of high-biomass forest to logging on private lands (364,000 ha) exceeded the losses to fire across all ownerships. Many remaining high-biomass forest stands are vulnerable to future harvest as only 20 % are strictly protected from logging, while 26 % are not protected at all. The level of protection for high-biomass forests varies by state, for example, 31 % of all high-biomass federal forests in Washington are in high-protection status compared to only 9 % in Oregon. Across the conterminous US, high-biomass forest covers <3 % of all forest land and the PNW region holds 56.8 % of this area or 5.87 million ha. Forests with high-biomass stores are important to document and monitor as they are scarce,

often threatened by harvest and development, and their disturbance including timber harvest results in net C losses to the atmosphere that can take a new generation of trees many decades or centuries to offset.

Keywords Forest biomass · Forest management · Forest conservation · Carbon · Pacific Northwest

Introduction

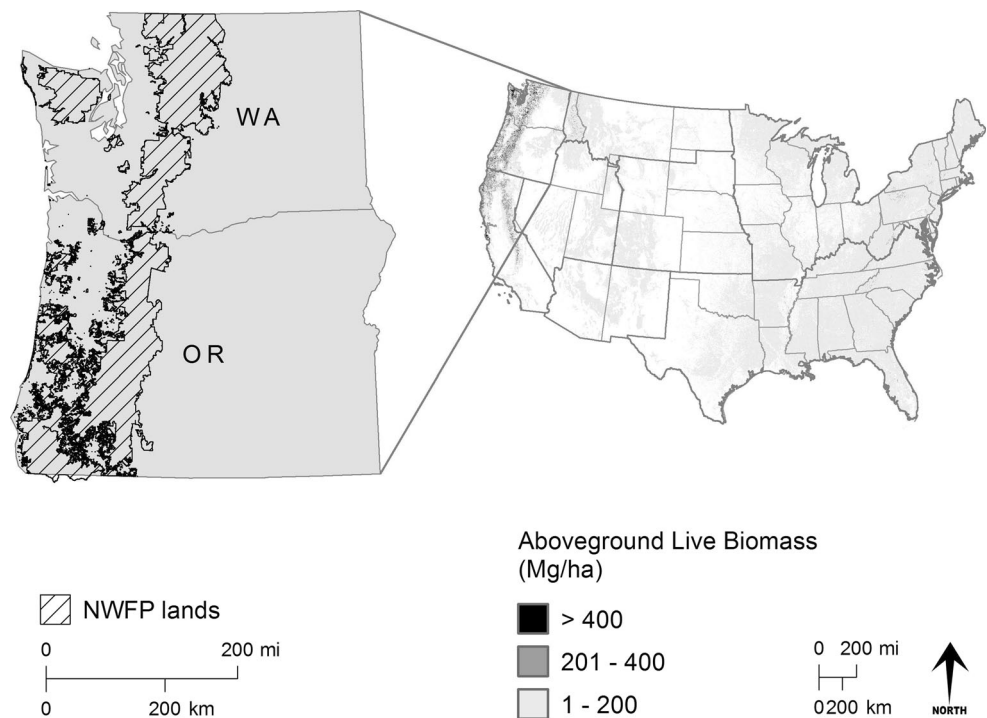
Forests are a critical part of the global biological carbon (C) cycle and can contribute to climate stabilization through uptake and storage of atmospheric C in live and dead trees and in soils (Nabuurs et al. 2007; Ryan et al. 2010). With increasing interest in incorporating forest C stores in forest management and climate change mitigation strategies, there is a growing need for improved understanding of spatial distribution of forest biomass across continents, regions, and landscapes. This is because biomass density (the quantity of biomass per unit area, or Mg dry weight per hectare) indicates the amount of C removed from the atmosphere and retained by vegetation and determines the amount of C that is emitted to the atmosphere (as CO₂, CO, and CH₄ through burning and decay) when ecosystems are disturbed (Houghton et al. 2009). The advances in forest monitoring using satellite imagery have been substantial over the past few decades and this technology is moving toward operational readiness for monitoring, reporting, and verification of forest cover, associated C stock, and their change over time (Goetz and Dubayah 2011). Mapping forest biomass has evolved into a major research priority and multiple methods have been proposed (e.g., Gonzalez et al. 2010; Lefsky 2010; Le Toan et al. 2011; Cartus et al. 2012). Biomass maps derived from

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O. N. Krankina (✉) · M. Yatskov
College of Forestry, Oregon State University, Corvallis,
OR 97331-5704, USA
e-mail: olga.krankina@oregonstate.edu

D. A. DellaSala · J. Leonard
Geos Institute, 84-4th St, Ashland, OR 97520, USA

Fig. 1 Forest biomass classes across the conterminous United States as derived from the aggregated version of NBCD2000 dataset with location of study area in the Pacific Northwest and lands managed under Northwest Forest Plan



a combination of remote sensing and in situ data not only deliver transparent and current estimates of C stocks but also capture spatial variability necessary for prioritizing areas for conservation and other aspects of policy development and analysis. New remote sensing instruments aim to improve estimates of forest biomass across the globe at sufficient spatial resolution to inform climate change policies and to reduce uncertainty in regional to global scale C budgets (Goetz and Dubayah 2011). Yet, the bulk of policy analysis continues to rely on established forest inventories that deliver non-spatial estimates of forest biomass (e.g., Heath et al. 2011). Improved awareness of strengths and limitations of newly developed biomass maps is needed for effective use of these resources to inform policy development, implementation, and public scrutiny.

The impact of forest management practices on C exchange between forests and the atmosphere tends to increase in proportion to the amount of biomass C on site: while net losses of forest C to the atmosphere occur following any major forest disturbance, these losses are proportionally greater in high-biomass forests. Exceptional levels of C are stored in late-successional forests of the Pacific Northwest (PNW; Smithwick et al. 2002) and southeast Alaska (Leighty et al. 2006), and these forests are among the most C dense ecosystems in the world (Keith et al. 2009). The PNW forests contain substantial remnants of productive, high-biomass old-growth forests (Smithwick et al. 2002; Spies 2004; DellaSala 2011), whereas in other temperate regions these forests have been eliminated for

centuries. Protecting biodiversity of late-successional forests was among the primary goals of the Northwest Forest Plan (NWFP) that shifted forest management on ~10 million ha of federal lands in the PNW from predominately timber extraction to ecosystem management and biodiversity conservation (Fig. 1; NWFP 2002; Mouer et al. 2005; DellaSala and Williams 2006). This change in management resulted in a considerable increase in C stores on federal forest lands within the first decade of plan implementation and this trend can be expected to continue into the future if the limits on timber harvest set under the NWFP are maintained (Krankina et al. 2012).

In the U.S., the national forest planning rule and national road map for responding to climate change require the Forest Service to conduct baseline C inventories so that C can be managed as a “multiple use” across the ~80 million ha national forest system (USDA Forest Service 2010; 2012). Monitoring forest C stores is also integral to the development of an emerging C market for private forest lands (e.g., Alig et al. 2010; California Climate Action Registry www.climateregistry.org/ accessed December 17, 2007). The largest national ground-based dataset was developed by the USDA Forest Inventory and Analysis (FIA) Program and used extensively in studies of forest biomass at national, regional, and state levels (Smith 2002; Heath et al. 2011). Summaries of plot data are available at county level (Van Deusen and Heath 2010), but the sampling method is designed to produce averages for large areas rather than characterizing spatial distribution at fine

Table 1 Area estimates of forest biomass classes and disturbances by land ownership class in Oregon and Washington States combined (thousand ha)

Ownership class	Forest area in biomass classes ^a	Forest area disturbed from 2000 to 2008			High-biomass ^b forest area disturbed from 2000 to 2008		Total forest area ^c	Total land area
		Fire		Other disturbance				
		Low (1–200 Mg/ha)	High (201–400 Mg/ha)	Very high (>400 Mg/ha)	Fire	Other disturbance		
USFS	3,784		2,121	716	236	35	7,495	10,003
NPS	131		265	156	4	1	560	865
BLM	288		343	152	8	48	902	6,511
Other Public	1,149		597	179	7	69	2,125	5,101
Private	3,108		1,174	163	6	364	5,061	19,936
Total	8,459		4,499	1,366	261	518	16,142	42,416

^a Excluding 2000–2008 disturbance^b >200 Mg/ha^c In year 2000

resolutions needed for local management decisions. The FIA dataset was used in combination with remotely sensed data to map forest biomass across the conterminous USA at 240 m resolution (Blackard et al. 2008) and at 30-m resolution (National Biomass and Carbon Dataset for the year 2000 (NBCD2000); <http://www.whrc.org/mapping/nbcd/index.html>, accessed November 21, 2012; Kellndorfer et al. 2006, 2013). Both datasets are freely available to the public.

Our objective was to develop and demonstrate a simple method for using the NBCD2000 dataset to map forests with high-biomass stores in the PNW, examine their ownership and protection status, and assess the area of different types of disturbance affecting high-biomass forests between 2000 and 2008. The overall purpose was to provide an example of using newly available spatial datasets to answer some common questions of forest conservation.

Study Area and Methods

The study area encompasses 42.4 million ha in two states, Oregon (OR) and Washington (WA), that together form the Forest Service's Pacific Northwest Region (Fig. 1; Table 1). Within this region, we examined the area covered by the NWFP and its land-use allocations in greater detail. The overall approach relies on using the latest versions of publicly available spatial datasets for overlay, aggregation, and GIS-based computation of forest area in broad biomass classes across a range of categories that characterize ownership, land-use allocations, disturbance, and protection status of forest lands.

The primary source of data for mapping forest biomass classes was the NBCD2000 dataset (Kellndorfer et al. 2006, 2013). The dataset represents live aboveground biomass of trees with >5 in (12.7 cm) diameter at breast height (DBH) in 30 m pixels. Biomass values in NBCD2000 dataset were predicted using statistical fusion of several data sources, including high-resolution InSAR data acquired from the 2000 Shuttle Radar Topography Mission (SRTM); optical remote sensing data from the Landsat ETM+ sensor (three seasons); USGS National Land Cover Dataset 2001 (NLCD 2001); LANDFIRE (existing vegetation type; USGS 2011); USGS National Elevation Dataset; and USDA FIA data (Kellndorfer et al. 2006; 2013). The biomass values were estimated for each pixel and then averaged at a "stand" patch level (~2 ha average). The standard error of biomass values based on bootstrap validation with USDA FIA plot data is ± 139 Mg/ha.

We used the values from NBCD2000 dataset within the PNW study region to assign the 30-m pixels to four biomass classes: <1 Mg/ha (labeled non-forest), 1–200 Mg/ha

(Low Biomass), 201–400 Mg/ha (High Biomass), and >400 Mg/ha (very high biomass). We chose these broad biomass classes because of the high-estimated standard error of the source biomass dataset. Classification breaks were chosen to separate the total forest area into comparable parts with all biomass classes represented within each ownership class. Furthermore, 200 Mg/ha in aboveground live tree biomass approximates the biomass store common for harvest-age productive Douglas-fir (*Pseudotsuga menziesii*) stands (Krankina et al. 2012), the regional average of inventory plots on USDA FS forestlands (Heath et al. 2011), and the lower range of biomass in old-growth forests, while 400 Mg/ha approximates the mid-range for old-growth stands (Smithwick et al. 2002; Keith et al. 2009). In addition to the primary 30-m resolution NBCD2000 dataset, we also used an aggregated version of this dataset at 240-m resolution (<http://www.whrc.org/mapping/nbcd/index.html>; accessed November 21, 2012) to characterize the share of PNW high-biomass forest area in the nationwide total (Fig. 1; Online Resource 2).

Because NBCD2000 reflects the distribution of biomass circa year 2000, we updated our biomass class map by removing all pixels identified as disturbed in LANDFIRE 2008 dataset (<http://landfire.cr.usgs.gov/viewer/>; accessed August 31, 2012; and obtained on DVD from Heather Kreilick hkreilick@usgs.gov). The Vegetation Disturbance layer for 1999–2008 provides spatial information on vegetation transitions at 30-m resolution, including disturbance year, type, and severity of disturbance derived mainly from Landsat TM/ETM and MODIS data (Vogelmann et al. 2011; USGS 2012). To characterize the impact of disturbance on high-biomass forests, we computed the disturbed area by biomass class with separation of “fire” from other disturbance types that were examined in aggregate (Table 1). This update of our biomass class map accounts for losses of high-biomass forest to various kinds of disturbance but does not reflect recruitment of high-biomass forests with tree growth over time. We acknowledge this bias but could not eliminate it as the required spatial data are not readily available.

USDA FIA plot-level biomass data were used to assess the accuracy of our updated biomass class map, i.e., the agreement of field-based estimates of forest biomass from FIA plots with assignment of corresponding map pixels to biomass classes. The FIA plot data are publically available (<http://www.fia.fs.fed.us/tools-data/>, accessed December 5, 2013) with the exception of precise plot location coordinates. FIA staff has unrestricted access to the plot location coordinates and the co-author who is a FIA staff member (Mikhail Yatskov) used plot coordinates to identify mapped biomass class for each FIA plot. This was the only step that relied on data not publicly available.

Forest inventory plots are distributed across all ownerships on a hexagonal grid with one plot being roughly

representative of 2,400 ha of land area (Bechtold and Patterson 2005). Plots are re-measured on 10-year cycles to track the land-use change over time as well as changes in biomass, plant species composition, parameters associated with disturbances, and other factors represented by more than 300 collected variables (Smith 2002). Our FIA dataset included 11,887 plots measured during a 10-year cycle that started in 2001. For the reference dataset, we selected a subset of 3,339 plots that were not disturbed since last inventory cycle and were measured between 2008 and 2010. The latter criterion was added to make sure that plot measurements used in our accuracy assessment were not among those used to develop the NBCD2000 dataset (Kellndorfer et al. 2006; 2013) and to minimize the time difference between FIA plot measurements in the field and the biomass class map which was updated to year 2008. We then removed from our reference dataset the plots that were not measured in the field and plots where the proportion of forest cover was <90 % to eliminate plot observations with ambiguous attribution to a specific biomass class. The resulting dataset included 2,898 plots; in each of them live aboveground biomass (Mg/ha) for trees >12.7 cm DBH was estimated from field measurements using regional biomass equations (Zhou and Hemstrom 2010). These estimates were assigned to circles with a radius of 56.4 m (1 ha area) that were overlaid with our updated biomass class map using ArcGIS 10.1. For each circle, we calculated the area that belonged to different classes on our biomass map. The circles where the majority biomass class occupied <90 % of the total area were dropped from the set and the remaining 2,226 plots were used to evaluate the performance of the biomass class map. We constructed a confusion matrix and calculated accuracy metrics, including the error of omission (exclusion) and commission (inclusion) for each class, the overall agreement, and chance-corrected agreement (Kappa, Cohen 1960; See Online Resource 1 for details).

To characterize the current protection status and ownership of high-biomass forests, we used the Protected Areas Database of the United States (PADUS), version 1.2. (US Geological Survey, Gap Analysis Program (GAP), <http://gapanalysis.usgs.gov/padus/download/>, accessed November 21, 2012). PAD-US is an inventory of marine and terrestrial protected areas that are defined as being dedicated to the preservation of biological diversity and to other natural, recreation, and cultural uses, managed for these purposes through legal or other effective means (National Gap Analysis Program 2011). For our analysis, we examined two sets of variables: GAP Status Code (values range from 1 to 4 in decreasing levels of protection) and Ownership class that included National Park Service (NPS), US Forest Service (USFS), Bureau of Land Management (BLM), and Other Public (including other federal, state, country, and Native

Table 2 Forest area and biomass classes on Northwest Forest Plan land allocations within Oregon and Washington (thousand ha)

State	NWFP Land-use allocation ^a	Total land area	Forest area (≥1 Mg/ha)	High-biomass forest area ^b		
				Total	IRA ^c	GAP 1 and 2 status
Oregon	AW/CR	854.2	704.5	361.6	39.3	256.3
	LSR	1,383.8	1,123.8	740.1	103.4	34.7
	Matrix	1,675.3	1,343.9	817.1	34.3	2.0
	State total	3,913.4	3,172.2	1,918.8	177.0	293.1
Washington	AW/CR	1,880.6	1,219.9	828.0	39.7	760.5
	LSR	976.5	802.5	566.4	220.9	22.2
	Matrix	720.1	516.5	295.4	58.5	6.5
	State total	3,577.4	2,538.9	1,689.8	319.0	789.2
Grand total		7,490.8	5,711.1	3,608.6	496.1	1,082.2

^a Administratively Withdrawn/ Congressionally Reserved (AW/CR); late-successional reserves (LSR); after Mouer et al. (2005)

^b >200 Mg/ha; high biomass and very high biomass classes combined

^c Inventoried roadless areas

American lands). We assumed that lands not classified into these four categories were Private. In addition, we examined overlap between high-biomass forests and Inventoried Roadless Areas (IRA; http://sagemap.wr.usgs.gov/ftp/unitedstates/USFS/ira_us_dd.htm, accessed November 21, 2012) to determine how well this administrative category can contribute to protection of high-biomass forests in our study area. The intent of the 2001 roadless area conservation rule is to provide lasting protection for these roadless areas in the context of multiple-use management, primarily for the purpose of “watershed and ecosystem health” (USDA Forest Service 2000). Most of these areas are concentrated in the western United States and Alaska. Finally, we examined the extent of high-biomass forests within the NWFP land-use allocations (<http://www.reo.gov/gis/data/gisdata/index.htm>, accessed June 13, 2012). The NWFP record of decision divided federal land into seven land-use allocations of varying levels of protection; Mouer et al. (2005) combined or further split some allocations and we used these generalized land-use categories for our study area (Table 2).

To characterize the current protection status of high-biomass forests, we used polygon data on ownership, disturbance (between 2000 and 2008), land management allocations, and protection status as masks in the Spatial Analyst Toolbox within ArcGIS 10.1 to extract the biomass class map for each land category of interest. We then computed the area of biomass classes using Zonal Statistics tool in the Spatial Analyst Toolbox.

Results

The assessment of accuracy of our biomass class map with ground measurements on FIA plots indicated that 85.8 % of plots in our sample were mapped correctly with a Kappa value of 65.9 % (Online Resource 1). A large portion of FIA plots with biomass values close to the lower limit of

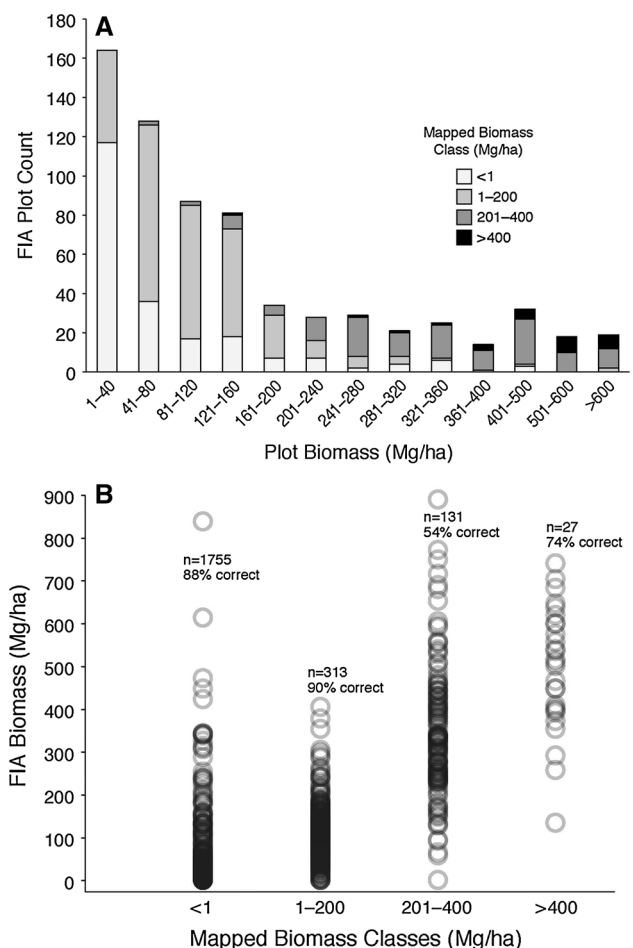


Fig. 2 Agreement between NBCD2000 dataset and biomass estimates for FIA plots in the Pacific Northwest study area: **a** FIA plot counts by mapped biomass classes and **b** distribution of forest biomass values in FIA plots across mapped biomass classes in NBCD2000 dataset

Low-Biomass Class were mapped as non-forest (assigned biomass values <1 Mg/ha in NBCD2000 dataset): among plots with field-based biomass estimates of 1–40 Mg/ha, 77 % were incorrectly assigned to <1 Mg/ha class, while

among the plots with biomass ranging from 80 to 200 Mg/ha <25 % were similarly misclassified (Fig. 2a). For the high-biomass class (201–400 Mg/ha), omission and commission errors were well balanced, but in the very high-biomass Class (>400 Mg/ha), the error of omission (71 %) was greater than that of commission (25.9 %, Online Resource 1); in other words—the Very High-Biomass Class (>400 Mg/ha) was under-reported in our biomass class map. The distribution of plot-level biomass values by mapped biomass class demonstrates the degree of biomass class separation and confusion (Fig. 2b). Because of significant confusion between the two high-biomass classes, we opted to report most results for the combined high-biomass class (>200 Mg/ha). Within the combined high-biomass class, 88.6 % of FIA plots were classified correctly and the overall accuracy of three-class biomass map was higher—88.0 %, Kappa 71.0 % (Online Resource 1). Where the results for the very high-biomass class are reported, they likely reflect under-estimation of the area for this class and may have lower overall accuracy.

The total area of mapped forest cover in our PNW study area is 16.1 million ha (Table 1, Online Resource 3) which is generally consistent but lower than the forest area estimate for OR and WA reported by Smith et al. (2001): 51,612,000 acres or 20.9 million ha. The definition of forest cover used in this study (≥ 1 Mg/ha aboveground live tree biomass) is different from definition adopted in the FIA program (Smith et al. 2001); therefore, these area estimates are not directly comparable. The map-based estimate of forest cover excluded forest area disturbed from 2000 to 2008; this combined with the inclusion of lands without tree cover within FIA definition of forest likely accounts for most of the difference in estimates.

High-Biomass Forests Distribution and Losses—Total forest area that was disturbed from 2000 to 2008 was 1.82 million ha or 1.25 % per year on average. With disturbed forest area excluded, high-biomass (>200 Mg/ha) forest area was 5.87 million ha or 41 % of the total forest area, while very high-biomass forests occupied 1.37 million ha or 10 % (Table 1). These high-biomass forests represent a large proportion of all high-biomass forests nation wide (Fig. 1; Online Resource 2). The aggregated version of NBCD2000 used at the national scale suggests that within the conterminous United States, the PNW region holds 56.8 % of forest area with biomass >200 Mg/ha and as much as 77.2 % of forest area with biomass >400 Mg/ha. The coarser resolution of the national dataset (240 m) may have resulted in omission of high-biomass forests where they occur in dispersed small patches and this hampers comparison of high-biomass forest areas in different parts of the country. However, the scarcity of high-biomass forests and their extreme overall concentration in western United States is evident: high-biomass forest occupies

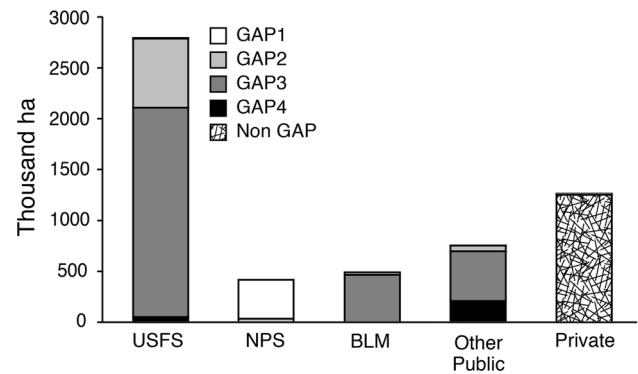


Fig. 3 High-biomass (>200 Mg/ha) forest area distribution by ownership and GAP status for the Pacific Northwest study area

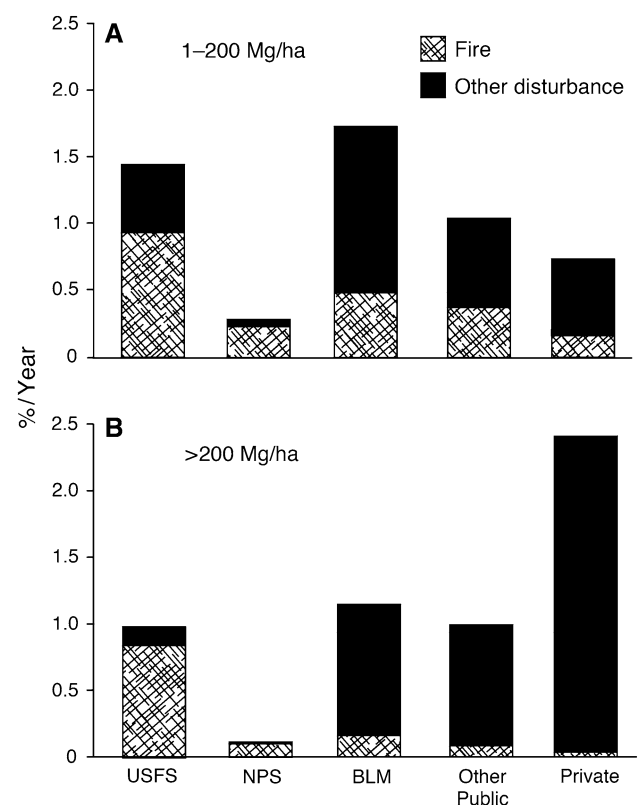


Fig. 4 Average annual disturbance rates for forests in the Pacific Northwest study area between 2000 and 2008: **a** low-biomass forests; **b** high-biomass forests

<3 % of all forest land in conterminous US, and the PNW and Pacific Southwest regions combined hold 89 % of those forests (Fig. 1; Online Resource 2).

Among ownership types in the PNW, USFS lands (primarily National Forests) contained the largest area of high-biomass forests (48.4 % of regional total), but private lands contained a significant portion of high-biomass forest as well (22.8 %; Table 1; Fig. 3). More than half of very

high-biomass area was on USFS lands, while the share of other four ownership classes was 11–13 % in each. As a fraction of total forest area in an ownership class, the proportion of high-biomass forest area was the largest on NPS and BLM lands (76.6 and 68.1 %, respectively), while on private lands, the proportion of high-biomass forest was relatively low (38.6 %) with only 3.7 % in >400 Mg/ha class (Table 1; Fig. 3).

On NPS land, the proportion of forest area disturbed by all factors between 2000 and 2008 was only 0.16 % per year on average, other ownership classes had much higher disturbance rates (Fig. 4). On USFS lands, fire was the dominant disturbance factor, while other types of disturbance played a much greater role in all other ownerships. The loss of high-biomass forest stands to disturbance both in terms of total area (Table 1) and as a proportion of area in 2000 (Fig. 4) was smaller than the loss of low-biomass forest area with one important exception: on private lands, the loss of high-biomass forest was four times greater than low-biomass forests. The loss of private high-biomass forests between 2000 and 2008 was 21.3 % (364,000 ha) and was mostly associated with non-fire disturbance (primarily logging). The loss of high-biomass forests to fire on USFS lands was 7.6 % of their area in year 2000 (236,000 ha). Overall, the area of high-biomass forest logged on private lands exceeded the total area burned across all ownerships (Table 1). Among public ownerships, the rate of forest loss was greatest on BLM lands (1.25 % per year in high-biomass forest; Fig. 4), mostly to non-fire disturbance (logging). Across all ownerships, the average annual rate of disturbance of high-biomass forest was 1.32 % with fire responsible for about one-third of this loss.

Protection Status of High-Biomass Forests in the PNW—NWFP lands in OR and WA contained 3.6 million ha of high-biomass forest or 61.5 % of the regional total (Table 2). This area was somewhat greater in OR than in WA, but high-biomass area within IRAs and in high-protection GAP status (Gap 1 and 2) was much greater in WA. For example, 31 % of all high-biomass forest lands in WA were in high-protection GAP status compared to only 9 % in OR. Fire was the primary disturbance factor within NWFP lands and fire losses of high-biomass forest between 2000 and 2008 totaled 217,000 ha, while all other factors combined accounted for 74,000 ha loss. However, the average rate of high-biomass forest loss to disturbance on NWFP lands was 0.83 % per year—lower than 2.37 % per year on private lands or 1.32 % per year regional average rate (Fig. 4).

IRAs contained 496,000 ha or 17.5 % of all high-biomass forest lands in USFS ownership in our study area (Table 2) and 132,000 ha or 18.4 % of very high-biomass forests. GAP status information was available only for public lands and primarily reflected the ownership status of

high-biomass forests (Fig. 3). High-biomass forest lands with GAP1 status were concentrated on NPS lands, while GAP2 and three occurred mainly on USFS forest lands (with GAP3 prevailing). On other public ownerships, high-biomass forests were in GAP3 and four status (Fig. 3). Across all ownerships, only 20 % of high-biomass forest had strict protection from logging under GAP 1 or 2 status, while 26 % were in GAP4 or no-GAP status receiving little to no protection.

Discussion

The mapping of forest biomass has improved greatly in past decades with increasing use of satellite and aircraft remote sensing. NBCD2000 dataset appears to represent the full range of biomass values better than the Blackard et al. (2008) dataset, where over-estimation of low biomass values and under-estimation of high biomass were reported. Conversely, NBCD2000 assigned biomass values <1 Mg/ha to majority of pixels that coincide with FIA plots with biomass ranging from 1 to 40 Mg/ha; thus under-reporting the area of forest with low-biomass (Fig. 2). For stands with very high-biomass, NBCD2000 tends to under-estimate biomass (Online Resource 1; Fig. 2).

The accuracy metrics in our analysis indicate a moderate level of agreement between the updated biomass class map (Online Resource 3) and the reference data (85.6 % overall agreement for 4-class biomass map, 88.0 % with High Biomass and very high biomass classes combined; Online Resource 3). This suggests that the aggregation of pixel-level biomass values into broad classes served to mitigate the problem of high error in the source NBCD2000 dataset and the map can be considered robust. Yet, at the pixel or stand level, the accuracy of large-area datasets remains inadequate for effective operational monitoring of C stocks (Houghton et al. 2009; Goetz and Dubayah 2011). In the future, the combined use of passive optical remote sensing with light detection and ranging (LiDAR) instruments and the new generation of radar sensors is widely expected to improve the accuracy of biomass maps and meet the needs of forest C monitoring (Gonzalez et al. 2010; Lefsky 2010; Le Toan et al. 2011; Goetz and Dubayah 2011). Nevertheless, currently available biomass maps can provide useful information on patterns of spatial distribution and abundance or scarcity of high-biomass forests over large areas and their losses due to disturbance (Fig. 1; Online Resource 2, 3). Combined with data on land-use designations and protection status of forest lands, the available biomass maps can help assess the ownership status and the extent to which high-biomass forests are protected versus those vulnerable to future harvests.

Our results are broadly consistent with earlier studies that used remote sensing methods to assess the area of mature, old-growth, and large-diameter forests (LDF) in the PNW and their loss to disturbance (Strittholt et al. 2006; Healey et al. 2008). However, the focus on biomass rather than stand age (Strittholt et al. 2006) or stand structure (Healey et al. 2008) makes our results more relevant to planning C management in forest ecosystems as part of climate change mitigation policies (USDA Forest Service 2010, 2012). It is also a likely reason for differences in results. For example, Strittholt et al. (2006) report that 26 % of old-growth forest were strictly protected (GAP1 and GAP2), whereas only 20 % of high-biomass forest were similarly protected (Tables 1, 2; Fig. 3). Furthermore, the loss of LDF across all ownerships during the period following implementation of the NWFP was reported by Healey et al. (2008) at 0.73 % annually, whereas our estimate of high-biomass forest loss to disturbance was nearly twice as high (1.32 % per year), primarily because of logging on private lands. Thinning has become a major type of logging on NWFP lands, and thinned stands were presumed to retain their LDF status (Healey et al. 2008) but thinning significantly reduces forest biomass store. Clearly, the NWFP offers less protection for high-biomass forests compared to LDF or old growth, especially for the most productive stands that can reach 200 Mg/ha biomass level when they are relatively young (~40 years old). Protecting high-biomass forest may be a greater challenge as it presents a more direct conflict with economic gains from timber harvest than protection of old growth, especially old growth with relatively low biomass stores.

While the biomass maps used in this analysis have been available to the public for some time, to our knowledge they have not been used for a quantitative assessment of the area of high-biomass forests and their protection status. The development of approaches and methods for spatial data analysis, like the one presented here, is needed so that forest managers and interest groups can extract pertinent information from available biomass maps. The established FIA sampling methods and analysis tools target broad-scale averages (Van Deusen and Heath 2010; Heath et al. 2011) and cannot deliver adequate characterization of the spatial distribution of forests across the range of biomass values. Forests with high-biomass stores are important to document as they are scarce (Fig. 1, Online Resource 2) and often threatened by harvest and development. The disturbance of high-biomass forests especially timber harvest results in net C losses to the atmosphere that can take a new generation of trees many decades or centuries to offset (e.g., Houghton et al. 2009; Krankina et al. 2012). Yet, protection of high-biomass forests and their C stocks is not among options for managing C on forest lands proposed by

the national road map for responding to climate change (USDA Forest Service 2010), the Pacific Coast Action Plan on Climate and Energy (<http://www.pacificcoastcollaborative.org/Documents/Pacific%20Coast%20Climate%20Action%20Plan.pdf>, accessed December 9, 2013), or The President's Climate Action Plan (<http://www.whitehouse.gov/sites/default/files/image/president27sclimateactionplan.pdf>, accessed December 9, 2013). Our biomass class map (Online Resource 3) can help identify critical gaps in protection of high-biomass forests in the PNW, better target future conservation programs related to C stores and climate change mitigation efforts, and support the inclusion of high-biomass forest protection in the set of climate change mitigation options on forest lands.

Availability of data on spatial distribution of high-biomass forests could have improved the effectiveness of forest conservation under the NWFP. The NWFP was an important step forward in protecting late-successional habitat for threatened species (e.g., Mouer et al. 2005; DellaSala and Williams 2006) and, as a side benefit, resulted in active C sequestration on federal forest lands (Turner et al. 2011; Krankina et al. 2012). However, there is a surprising discrepancy in protection level of high-biomass forests in OR and WA and overall limited protection from harvest (GAP3, GAP4 or no-GAP) for ~70 % of high-biomass forests managed under NWFP (Table 2). Among publicly owned forest lands, BLM has the highest concentration of high-biomass forests (Fig. 3), which were harvested at a higher rate compared to other public ownerships in 2000–2008 (Fig. 4). Many of the remaining high-biomass forests on BLM lands are designated for logging under recent proposals for expanded timber harvest on NWFP lands (e.g., DeFazio et al. 2012; Wyden 2013).

The vulnerability of old-growth forest to wildland fire on USFS lands has dominated the debate on future conservation strategies in the PNW (Spies et al. 2006; DellaSala and Williams 2006; Healey et al. 2008). This debate largely overlooked the impact of ongoing logging on public lands, yet logging accounts for a greater loss of high-biomass forest than fire on BLM lands and in the other public lands category that includes state and tribal forests (Table 1; Fig. 4). While not all harvested high-biomass forests are old growth, this continued harvest on public lands depletes the cohort of stands where old-growth characteristics can develop over time. In addition, fire and other natural disturbances in high-biomass forests transfer C from live biomass into dead biomass pool, but the total C store on site remains high, while logging moves C off-site leaving a greatly reduced total C store on forest land (Krankina and Harmon 2006).

Significant portions of high-biomass forests in the PNW that are vulnerable to additional losses are privately owned (Fig. 3). The biomass class map can help identify areas

where privately owned high-biomass forests are concentrated and where targeted conservation incentives for private owners may be effective in protecting the diverse ecosystem services provided by high-biomass forests, especially long-term C storage (Foley et al. 2009). Studies of the effect of C price on private forest owner behavior in Western OR showed that even at a low C price some extension of harvest rotation can be expected (Im et al. 2007; Alig et al. 2010). In addition to slowing the losses of high-biomass forests and reducing associated C emissions, significant net sequestration of C can be expected from postponing harvest of relatively young and productive high-biomass forests on private lands (Krankina and Harmon 2006; Foley et al. 2009; Ryan et al. 2010). The incentives to postpone harvest can also help inform stakeholder's importance of protecting high-carbon forests for purposes of climate change mitigation.

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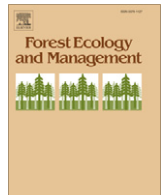
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Carbon balance on federal forest lands of Western Oregon and Washington: The impact of the Northwest Forest Plan

Olga N. Krankina^{*}, Mark E. Harmon, Frank Schnekenburger, Carlos A. Sierra¹

Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

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ABSTRACT

The management of federal forest lands in the Pacific Northwest (PNW) region changed in early 1990s when the Northwest Forest Plan (NWFP) was adopted with the primary goal to protect old-growth forest and associated species. A major decline in timber harvest followed, extending an earlier downward trend. The historic and projected future change in carbon (C) stores and balance on federally managed forest lands in Western Oregon (OR) and Western Washington (WA) was examined using the LANDCARB 3.0 simulation model. The projections include C stores on-site, in harvested wood products and disposal and reflect a set of contrasting visions of future forest management in the region formulated as five alternative management scenarios that extend to year 2100. A significant and long-lasting net increase in total C stores on federal forest lands relative to early 1990s level was projected for both OR and WA under all examined management scenarios except the *Industry Scenario* which envisioned a return to historic high levels of timber harvest. In comparison with the *Industry Scenario*, the low levels of timber harvest under the NWFP between 1993 and 2010 were estimated to increase total C stores by 86.0 TgC (5.1 TgC year⁻¹ or 2.16 MgC ha⁻¹ year⁻¹) in OR; in WA the respective values were 45.2 TgC (2.66 TgC year⁻¹ or 1.33 MgC ha⁻¹ year⁻¹). The projected annual rate of C accumulation, reached a maximum between 2005 and 2020 approaching 4 TgC year⁻¹ in OR and 2.3 TgC year⁻¹ in WA, then gradually declined towards the end of projection period in 2100. Although not the original intent, the NWFP has led to a considerable increase in C stores on federal forest lands within the first decade of plan implementation and this trend can be expected to continue for several decades into the future if the limits on timber harvest set under the NWFP are maintained. The primary goal of the NWFP to protect and restore old-growth forest may take several decades to achieve in WA whereas in OR the area protected from clearcut harvest may be insufficient to meet this goal before the end of projection period in 2100.

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1. Introduction

Forests are a critical part of the global biological carbon (C) cycle and their management may contribute to stabilizing the concentration of the greenhouse gas C dioxide in the atmosphere (Pacala and Socolow, 2004). The potential of forest ecosystems to store C is well established (e.g., Post et al., 1990; Nabuurs et al., 2007; Keith et al., 2009), but the degree to which this potential is being met under different management systems is uncertain. The conversion of older forests to younger forests has generally been shown to release C to the atmosphere (Cooper, 1983; Harmon et al., 1990; Dewar, 1991; Harmon and Marks, 2002; Trofymow et al., 2008) and management decisions regarding remaining older forest

stands is an important factor in determining how the C balance of forest landscapes changes over time. This is especially important in the Pacific Northwest (PNW) where forests have some of the highest biological potential to store C (Harmon et al., 1990; Smithwick et al., 2002; Birdsey et al., 2007). The PNW is also the region where substantial remnants of productive, high-biomass old-growth forests have survived (DellaSala, 2010) whereas in other temperate forest regions they have been eliminated for centuries. Carbon inventories in the productive high-biomass old-growth forests of the PNW provide a robust measure of the upper limit of C storage (Smithwick et al., 2002) which is rarely available to assess the full potential of C sequestration associated with restoring late-successional forests.

The PNW region has recently experienced major changes in forest management. The adoption of the Northwest Forest Plan (NWFP) in 1994 resulted in a significant decline in timber harvest on federal forest lands extending an earlier downward trend (e.g., Alig et al., 2006). For example, in Oregon (OR) during the peak harvests in the 1970s and 1980s, over five billion board feet (BBF,

^{*} Corresponding author. Tel.: +1 541 737 1780.

E-mail addresses: krankinao@fs.lorst.edu (O.N. Krankina), csierra@bgc-jena.mpg.de (C.A. Sierra).

¹ Present address: Max-Planck-Institut für Biogeochemie, Hans-Knöll-Straße 10, 07745 Jena, Germany.

Scribner scale)² per year were removed from federal forest lands; in the early 1990s timber removals were about half that amount and in early 2000s the harvest fell below 0.5 BBF (Warren, 2008). This recent period of low timber harvests can be expected to cause significant changes in forest C stores at present and for many decades into the future if the provisions of the NWFP are maintained.

The NWFP assumed that forests in 0.7% of the Plan area would be lost to stand-replacing wildfire per decade, and that 1% of the entire Plan area (or 3% of total late-successional forest area) would be harvested per decade (i.e., a 0.17% year⁻¹ combined annual rate of disturbance). Monitoring results, albeit short-term, suggest that during the first 10 years of the Plan estimated gains of older forest far outpaced losses, resulting in a net increase of between 1.25 and 1.5 million acres (500–600 thousand ha) of older forest on federally managed land. This rate of gain was about twice the first decadal gain expected under the Plan (Mouer et al., 2005).

Several regional studies used different methods to examine recent changes in the C balance of PNW forests. Following peak timber harvest of the 1980s, forests of the PNW were losing C (Cohen et al., 1996; Song and Woodcock, 2003) with losses of coarse woody debris representing a significant permanent loss not compensated by regrowth (Harmon et al., 1990). A net uptake of 13.8 TgC year⁻¹ (1.68 MgC ha⁻¹ year⁻¹) was estimated using Biome-BGC model for forests of western OR in 1995–2000; after accounting for harvest removals and fire emissions the regional net biome production (NBP) was reported at 8.2 TgC year⁻¹ (1.00 MgC ha⁻¹ year⁻¹, Law et al., 2004). An expanded state-wide assessment by Turner et al. (2007) estimated NBP in 1996–2000 at 6.1 ± 10.2 TgC year⁻¹ with climate fluctuations responsible for significant interannual variation. Most of the reported C sink was associated with public forest lands in western OR. Net C uptake in OR forests in 2000–2005 estimated from Biome-BGC simulations (1.10 MgC ha⁻¹ year⁻¹) was consistent with the estimate derived from forest inventory data (1.33 ± 0.29 MgC ha⁻¹ year⁻¹; Turner et al., 2011). While there is a general consensus that the forests managed under the NWFP have been net sinks of C in recent years and that declining timber harvests contributed to this sink, there is little agreement on expected future changes in the C balance of these forests and the role of management decisions in historic and future C dynamics. Furthermore, it is unclear how long into the future the provisions of the NWFP will be maintained as alternative approaches to the management of federal forest lands are being proposed, including a return to higher timber harvest levels (e.g., BLM, 2008).

Climate change is generally expected to reduce C uptake and increase losses to the atmosphere in PNW forests through decline in forest productivity and increased intensity and frequency of wildfires (e.g., Law et al. 2004; Lenihan et al., 2008; Crookston et al., 2010). Other studies project regional C sinks for decades into the future even with timber harvests exceeding the planned NWFP levels (Smith and Heath, 2004; Alig et al., 2006; Im et al., 2010). The contradictory conclusions regarding the impact of management decisions on C balance of PNW forests (e.g., Mitchell et al., 2012; Trofymow et al., 2008; Perez-Garcia et al., 2005; Harmon and Marks, 2002) have contributed to confusion among stakeholders and decision-makers and stifled the development of effective climate change mitigation measures in the forest sector (Maness, 2009).

The main objective of this study was to analyze the effect on forest sector C stores of varying levels of timber harvest in federally managed forest lands within the NWFP area of OR and Washington

(WA). The LANDCARB Model (Mitchell et al., 2012) was used to simulate historic change in C stores on federal forest lands since the onset of wide-spread clear-cut logging in the 1950s up to the present time and to project future change for a set of forest management scenarios representing a broad range of alternatives that are under consideration. The analysis of results focused on assessment of change in forest sector C balance as a result of the NWFP and alternative management scenarios.

2. Methods

2.1. Study area

The study area includes federally managed lands in the NWFP area of western OR (Coast Range, Willamette Valley, and Western Cascades) and western WA (Olympic Peninsula, Western Lowlands and Western Cascades; Fig. 1) where federal forest lands represent 39% and 33% of the total forest area, respectively (Mouer et al., 2005). The total study area is 4.3 million ha or 44% of the entire land area covered by the Plan (9.9 million ha total in OR, WA and Northern California). According to Mouer et al. (2005), at the start of the Plan older forest occupied between 30% and 34% (depending on the definition) of forest-capable public lands managed by the Forest Service, Bureau of Land Management, and National Park Service that were in the range of the northern spotted owl. Forests meeting the most strict definition of old-growth – “Large, multistoried older forest” – occupied about 12% of forest-capable public land. Conservation of these older forests was among the primary goals of the NWFP.

The NWFP record of decision divided federal land into seven land-use allocations; Mouer et al. (2005) combined or further split some allocations. Specifically, three categories of late-successional reserves were grouped together; lands with overlapping late-successional reserve and adaptive management area designations were treated as late-successional reserves (LSRs). Administratively withdrawn and congressionally reserved lands were grouped together (AW/CR). Matrix and adaptive management areas were the land allocations where scheduled timber harvest activities may take place; these were grouped together as well as riparian reserves, which were never mapped separately from Matrix lands at the scale of the entire Northwest Forest Plan. We used these generalized land-use categories and associated area estimates for our study area in western OR and WA (Table 1).

The distribution of stands by age groups within each state and land allocation in the early 1990s (Table 1) was approximated by the proportion of different stand categories reported in Mouer et al. (2005). This report combined “Potentially forested but presently nonstocked” (PF) and “Seedling and sapling” (SS) categories into “very young” forest category (<10 in. diameter at breast height (DBH) and <20 years old); the small-sized trees (10–20 in. DBH) were labeled “young” and assigned stand age 21–60 years old; the old-growth area estimate was based on zone-indexed definition (and assigned age >150 years old) and the balance of area was presumed to be in the mature category (61–150 years old). Note that the range of stand ages included in each of these four age groups varies from about 20 years in the “Very Young” group to >300 years in the “Old-Growth” age group.

2.2. LANDCARB model

The simulation model used for this analysis was LANDCARB 3.0, which builds on earlier modeling work (e.g., Harmon and Marks, 2002) and simulates the accumulation and loss of C over time in a landscape where forest stands are represented by a set of grid cells (Mitchell et al., 2012,

² Approximately 24 million m³. The conversion factor from thousand board feet (MBF, Scribner long-log scale) to cubic meters increased from approximately 4–4.5 in the 1970s to greater than 7 by 1998 (Spelter 2002). In early 2000s 0.5 BBF was approximately 3.6 million m³.



Fig. 1. Study area in Western Oregon and Western Washington with boundaries of counties. FIA data from shaded counties were used to calibrate the LANDCARB model.

Table 1

Area of aggregated land use allocations and age groups of forest stands on federally managed lands in the Northwest Forest Plan area in early 1990s (after Mouer et al., 2005; thousand ha).

Land use allocations ^a	Age groups				Total (%)
	Very Young	Young	Mature	Old-Growth	
<i>Western Oregon</i>					
AW/CR	74.6	166.7	32.1	164.7	438.1 (18.7)
LSR	280.8	173.3	141.4	337.2	932.7 (39.8)
Matrix	346.6	229.2	131.8	267.1	974.7 (41.5)
Total (%)	702.0 (29.9)	569.2 (24.3)	305.3 (13.0)	769.0 (32.8)	2345.5 (100)
<i>Western Washington</i>					
AW/CR	334.9	173.0	173.3	377.9	1059.0 (53.0)
LSR	188.4	137.7	97.0	197.6	620.7 (31.1)
Matrix	129.9	82.9	43.5	62.7	318.9 (15.9)
Total (%)	653.2 (32.7)	393.6 (19.7)	313.8 (15.7)	638.2 (31.9)	1998.6 (100)

^a Administratively Withdrawn/Congressionally Reserved (AW/CR); Late-Successional Reserves (LSR).

<http://landcarb.forestry.oregonstate.edu/tutorial-modules.aspx>, last visited March 24, 2012). Model simulations were run for a grid of 20 by 20 cells (400 cells total), with a cell size of 100 × 100 m (1 ha). In this analysis we assumed that all forested cells were initiated by either a stand-replacing wildfire or a clearcut harvest. In each year of the simulation, disturbance was assigned to a sub-set of cells and for all other cells the successional change of C stores was projected. The count of age of tree stands (cells) begins from zero in the year of disturbance and continues until the cell is disturbed again. The proportion of cells thus assigned to different stand ages approximates the age-class structure of a forest landscape. The number of grid cells in model runs was selected to be sufficient to prevent the output fluctuations from randomly prescribed natural disturbance events (fire) from obscuring the trends in C stock change over time without excessive computation time to run the model.

The proportion of landscape disturbed annually by wildfire and clearcut harvest was defined based on fire return interval and harvest rotation, respectively. The proportion of stands (cells) disturbed annually by fire is the inverse of fire return interval: e.g., 200-year fire return interval means that on average 1/200% or

0.5% of the total forest area or an average of two random grid cells out of 400 is disturbed per year in LANDCARB simulations. The proportion of the landscape affected annually by timber harvest relates to the harvest rotation length in a similar fashion. To approximate the variability of the area disturbed annually we modeled the probability of disturbance using the Poisson distribution. This probability distribution is used when the process being represented is discrete in time and/or space. The mean and variance of this distribution are represented by the parameter λ , which is the average number of occurrences of a certain event per unit of time. Since we are assuming that in model simulations cells would be disturbed each year based on rotation length and fire return interval, $\lambda = (1/\text{rotation length})$ or $\lambda = (1/\text{fire return interval})$, for timber harvest and fire, respectively. The model was run for 1200 years, but only the last 250-year period between 1850 and 2100 was used in the analysis and reported.

Each stand grid cell contained four layers of vegetation (upper trees, lower trees, shrubs, and herbs), each having up to seven live biomass components (C pools), eight dead pools, three stable (soil) pools representing highly decomposed material, and two pools representing charcoal. The live parts included: (1) foliage, (2) fine

roots, (3) branches, (4) sapwood, (5) heartwood, (6) coarse roots, and (7) heart-rot. Each of the live parts of each layer contributed material to a corresponding dead pool. Thus foliage added material to the dead foliage, etc. All of the dead pools added material to one of three stable pools (stable foliage, stable wood, and stable soil) and fires created surface charcoal from live parts or dead pools. Sub-surface charcoal was formed from surface charcoal incorporated into the mineral soil and became protected from future fires, whereas surface charcoal was lost during subsequent fires.

The part of the LANDCARB model tracking forest products is patterned after the FORPROD model (Harmon et al., 1996). Harvested wood is processed into products that are either in-use or disposed. C stores in wood products and disposal vary according to their inputs and losses on an annual basis. In a manufacturing step, harvested wood C produces inputs for the different product C stores such as long-term structures (life-span >30 years), short-term structures (life-span <30 years), paper, and mulch. Once the new product inputs as well as losses due to combustion, decomposition, and disposal have been computed, product stores are updated each year. Disposed products can be either sent to open dumps (high combustion and decomposition rates), landfills (no combustion and very low decomposition rates), incinerated (instantaneous loss) or recycled into the original product. Stores in disposal are also updated annually after inputs and losses from decomposition and combustion are computed. The parameters used in manufacturing, product use, and disposal can vary over time to reflect changes in efficiency, uses, and disposal practices. These and other LANDCARB 3.0 model parameters are in Appendix; module structure and calculation procedures are at <http://landcarb.forestry.oregonstate.edu/tutorial-modules.aspx> last visited March 24, 2012.

The model outputs used in this analysis included landscape-level average C stores (total and by component: live biomass, dead, stable, products, and disposal) in each simulation year, annual net change in C stores (C balance; positive for net increases, negative for net losses), and the proportion of cells in different age groups. Five repeated runs of each management treatment were performed to allow for calculation of model output averages and standard errors.

2.3. Model calibration

The LANDCARB model was parameterized to represent the successional change in C stores for the environmental conditions representative of western OR and WA. The model used constant monthly climate inputs that represent historic averages for selected counties in OR and WA (separately; Fig. 1). To approximate average forest growth patterns we calibrated the model projections of live tree biomass over stand age to be consistent with the average values of forest biomass by stand age derived from USDA Forest Inventory and Analysis plots (FIA data). We generated the reference data set using the Carbon Online Estimator (COLE, Van Deusen and Heath, 2010, <http://www.ncasi2.org/COLE/index.html>) for a set of counties within the NWFP area of western OR (current as of August 28, 2009) and western WA (current as of October 23, 2009; Fig. 1).

We used COLE results for the Douglas-fir (*Pseudotsuga menziesii*) forest type which is dominant in our study region and is better represented in FIA dataset than other forest types. Within the study area this type is dominated by Douglas-fir and western hemlock (*Tsuga heterophylla*) and these two species were included in LANDCARB simulations (Appendix Table A1). Other tree species were not simulated as they account for <3% of total live tree C in Douglas-fir forest type within the study area (<http://www.ncasi2.org/COLE/index.html>; last visited February 29, 2012). The COLE report provided estimates for a full set of forest C pools but we used only live tree C

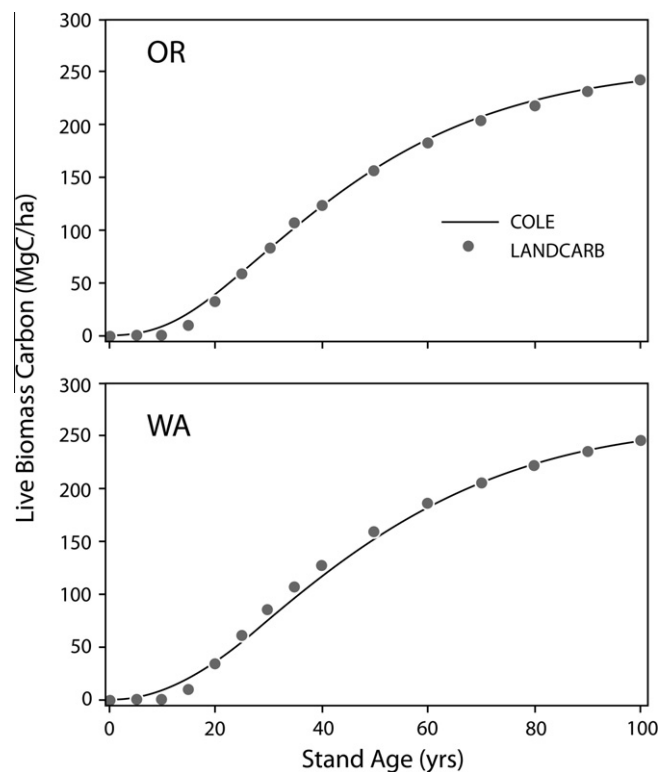


Fig. 2. Results of LANDCARB model calibration with FIA data for Western Oregon (OR) and Western Washington (WA): live biomass change with age of forest stands.

because it is expected to be more robust than other reported estimates. The calibration of LANDCARB focused on younger age classes (<100 years old) because older forests are poorly represented in the FIA dataset with too few stands to provide robust averages. The calibration resulted in a very close alignment of live tree biomass predictions by LANDCARB and the averages of FIA plot measurements in both states (Fig. 2).

2.4. Simulation of initial conditions ca. 1993

The regional fire history was represented in two different intervals:

- (1) prior to year 1910 a natural wildfire regime was simulated with a return interval of 200 years,
- (2) to represent the effects of fire suppression from 1910 onward the wildfire return interval was doubled on 50% of the cells.

This historic fire regime was simulated by LANDCARB for all three land-use allocations under the NWFP (AW/CR, LSR, and Matrix); in addition, historic timber harvest was simulated for each land-use allocation separately. The simulated distribution of cells by age classes in 1993 was compared to observed area distributions in the early 1990s (Table 1) and adjustments were made to historic logging assumptions (described below) to approximate the observations more closely.

For AW/CR lands no logging was assumed initially but simulations of the historic fire regime alone resulted in a low proportion of cells in younger age classes in 1993 as compared to observations: 19.0% of the cells were projected to be younger than 60 years by LANDCARB, while the observed proportion of stands in this age group on AW/CR lands was 55.1% in OR and 47.9% in WA (combined “very young” and “young” from Table 1). With harvests

Table 2

Management scenarios for federal forest lands in the Northwest Forest Plan area (see descriptions in text for details).

#	Land use allocation	Treatments		Management scenarios				
		Harvest	Fire suppression	1. Industry	2. NWFP-plan	3. NWFP-implemented	4. Conservation with fire suppression	5. Conservation with fire restoration
1	AW/CR	NO	YES	X	X	X	X	
2		NO	NO					X
3	LSR	60-year rotation	YES	X				
4		NO	YES		X	X	X	
5		NO	NO					X
6	Matrix	60-year rotation	YES	X				
7		120-year rotation	YES		X			
8		200-year rotation	YES			X		
9		Thinning only	YES				X	
10		Thinning only	NO					X

placed in 40% of grid cells in OR and 31% in WA between 1934 and 1993, the simulated proportion of younger forests was brought closer to that observed in AW/CR lands: 55.3% in OR and 47.9% in WA.

For LSR and Matrix lands the logging history was represented in three different periods:

- (1) from 1950 to 1960 logging was simulated assuming an average harvest rotation of 120 years and timber removal of 85% of stem wood to account for the fact that during this period harvests were limited by road access and utilization standards of harvest were generally low;
- (2) an intensification of logging was modeled from 1960 to 1965 using a 60-year rotation and timber removal of 90% of stem wood;
- (3) from 1966 to 1993 rotation ages varied from 50 to 100 years to approximate the reported pattern of change in harvest on federal lands (Warren, 2008) and the observed stand distribution by age groups in early 1990s (Table 1). Timber removal was assumed to be 90% of stem wood.

The final simulated proportions of land area in various age groups in 1993 matched closely the observed values across all three land-use allocations in the two states (Table 1) with deviations <0.6% in all cases.

2.5. Post-1993 scenarios

Five post-1993 management scenarios were developed to represent contrasting visions of future forest management in the region in a generalized form, similar to the story-line scenarios used by the Intergovernmental Panel on Climate Change to project future fossil fuel emissions (IPCC, 2000). These scenarios reflected a broad spectrum of management alternatives proposed for the federal lands by different interest groups, ranging from maximizing timber harvest with clearcutting to eliminating clearcutting completely and restricting timber harvest to thinning of young stands. Each scenario included a set of simple treatments for the three land-use allocations on federally managed lands in the NWFP area (Table 2). Scenarios 1–4 assumed that the fire suppression regime described above was extended to 2100 on all federal forest lands and Scenario 5 assumed no fire suppression so that the pre-1910 fire regime was restored (Table 2). In all scenarios no timber harvest was projected for AW/CR lands; for LSR and Matrix lands harvest was projected as follows:

2.5.1. Industrial harvest scenario (Industry)³

Logging was modeled assuming a harvest rotation length of 60 years until 2100 on both LSR and Matrix lands.

2.5.2. NWFP-planned scenario (NWFP-p)

Logging on Matrix lands was modeled assuming a 120-year harvest rotation length until 2100, in line with the expected level of timber harvest under the NWFP (Mouer et al., 2005). The LSR lands had no timber harvest.

2.5.3. NWFP-implemented scenario (NWFP-i)

Logging was modeled assuming a 200-year rotation length until 2100 on Matrix lands in line with the harvest level from 1994 to 2004 which was below that initially planned under the NWFP (Warren 2008). The LSR lands had no harvest.

2.5.4. Conservation with suppression of fire scenario (Cons – fire)

Logging was modeled in the Matrix lands assuming 50% of the stands were thinned at ages 20 and 40 years old. At each thinning 40% of the stem volume was cut; of the trees cut, 90% of the stem wood was harvested and moved off-site. This thinning plan resulted in 35% of all cells thinned (many of them twice) between 1994 and 2100. LSR lands had no timber harvest.

2.5.5. Conservation with fire restoration scenario (Cons + fire)

The logging regime in this scenario is the same as in the Cons – fire Scenario above but the fire regime was projected to return to the pre-suppression level (200-year fire return interval) starting in 1994. This scenario was designed to assess the impact of restoring the natural/pre-settlement fire regime as part of conservation-oriented forest management.

These five management scenarios involved ten different disturbance treatments across three land-use allocations (Table 2). Fire restoration was included in all three treatments of the Cons – fire Scenario, whereas fire suppression was applied in all other treatments. Therefore in further narrative different treatments were generally identified by harvest prescriptions only, with fire suppression mentioned as needed for clarity. For each treatment, the LANDCARB model output represented average per-ha C stores in all simulated C pools in each year of simulation between 1850 and 2100 in a landscape composed of 400 individual stands (cells) where historic disturbance and appropriate future fire and harvest treatments were applied (Table 2, Figs. 3, 4 and 6). Landscape-level net C balance was calculated as the change in total C store between two consecutive years of the simulation (Fig. 5). The landscape-level average values of C store and net C balance were multiplied by land area in respective land-use allocations in OR and WA (Table 1) and summed across all allocations to calculate state-level and regional (OR + WA) totals of C stores and annual net C balance for each scenario (Figs. 7–9, Table 3). The state and regional-level averages (Fig. 10 and in text) are the LANDCARB simulation results weighted by the areas of relevant land-use allocations in OR and WA (Table 1). All C totals and averages include C in wood products and in disposal (landfills) unless a sub-set of C pools is specified.

³ Abbreviated name of scenario in parenthesis

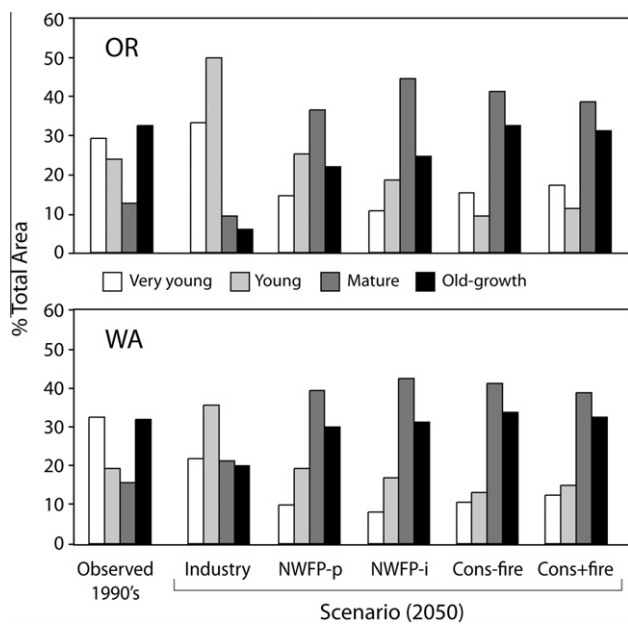


Fig. 3. Proportions of federal forest area in different age groups: at the start of NWFP (early 1990s; observed) and projected to 2050 under different management scenarios for Western Oregon (OR) and Western Washington (WA).

3. Results

Future dynamics of *landscape-level average C stores on different land use allocations* varied by treatment (Table 2, Fig. 4). On AW/CR lands, C stores increased over time and fire suppression led to higher average C stores than fire restoration (Fig. 4). The

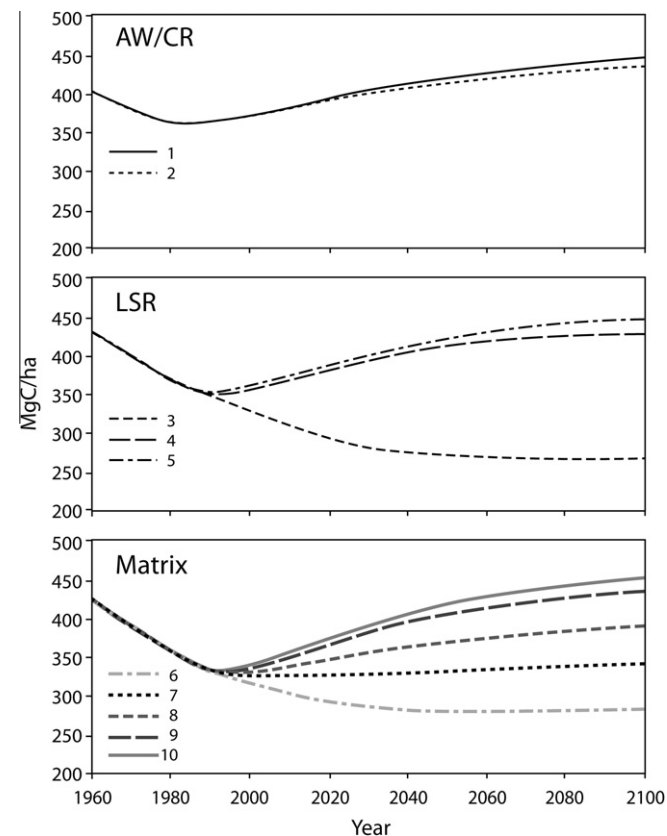


Fig. 4. Historic and projected future carbon stores under different management treatments on NWFP land use allocations in Western Oregon: AW/CR, LSR, and Matrix (see treatment specifications in Table 2 and Methods text).

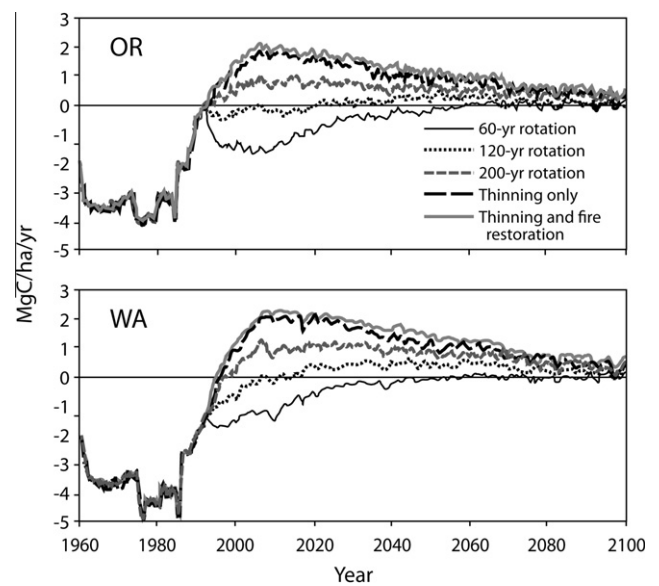


Fig. 5. Historic and projected future annual net carbon balance on Matrix lands under different management treatments in Western Oregon and Western Washington (positive values represent net gains; negative values represent net losses of carbon to the atmosphere).

difference between the two treatments was small, but it increased over time and in 2100 reached 14.0 and 14.6 MgC ha^{-1} in OR and WA, respectively. On LSR lands the no-harvest treatment with and without fire suppression resulted in a similar pattern of increase in C stores over time, whereas the 60-year rotation treatment caused the average C stores to decline by 84 MgC ha^{-1}

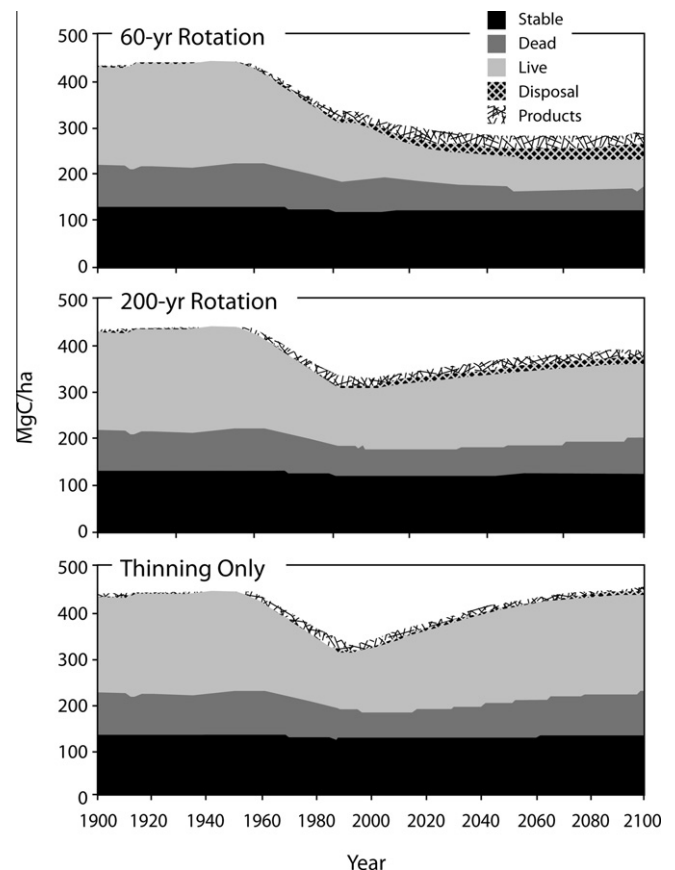


Fig. 6. Composition of carbon stores on Matrix lands in Western Oregon under three management treatments.

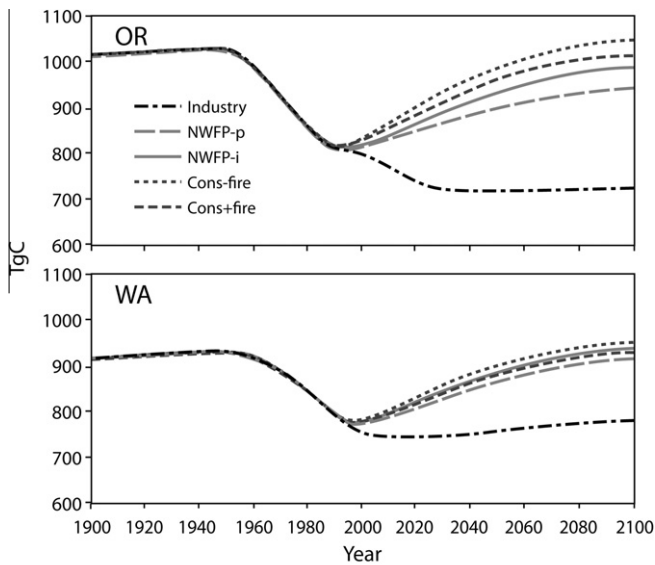


Fig. 7. Historic and projected future change in C stores under alternative management scenarios – totals for all land-use allocations combined in Western Oregon (OR) and Washington (WA).

between 1993 and 2100 (Fig. 4). Most of the loss under the 60-year rotation treatment occurred early in the projection period; after 2060 in OR and after 2040 in WA C stores became relatively stable. The difference in average C stores on LSR lands between the 60-year rotation treatment and the no-harvest treatment became stable by year 2100 at 175 MgC ha⁻¹ in OR and 185 MgC ha⁻¹ in WA.

On Matrix lands (Fig. 4), combined fire suppression and thinning treatments resulted in greater increase of the average C store by year 2100 than all other treatments: from 323 to 451 MgC ha⁻¹ in OR and from 339 to 481 MgC ha⁻¹ in WA. Harvest on a 200-year

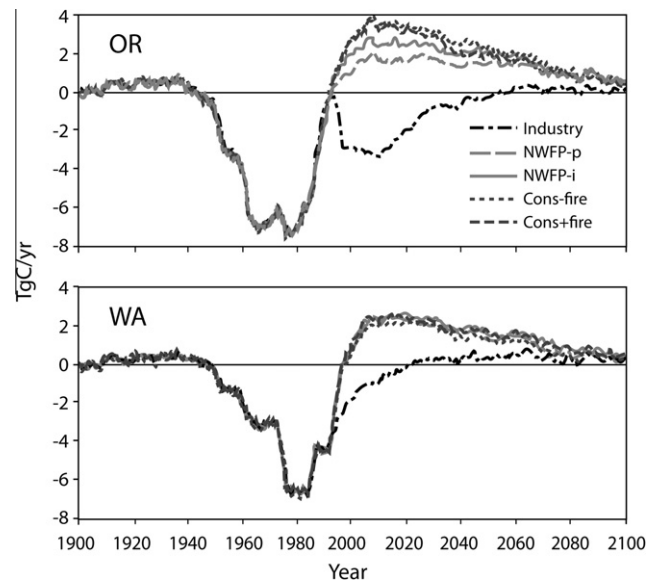


Fig. 8. Annual net carbon balance on federal forest lands between 1900 and 2100 under different management scenarios in Western Oregon and Western Washington (positive values represent net gains; negative values represent net losses of carbon to the atmosphere).

rotation with fire suppression produced a smaller increase in C stores (from 323 to 391 MgC ha⁻¹ in OR and from 339 to 417 MgC ha⁻¹ in WA by 2100) while the 120-year rotation increased C stores on Matrix lands only slightly (from 323 to 340 MgC ha⁻¹ in OR and from 339 to 362 MgC ha⁻¹ in WA) after a small initial decline. Of the 5 treatments considered for Matrix lands (Table 2), harvest on a 60-year rotation led to the lowest C stores on Matrix lands (284 MgC ha⁻¹ in OR and 302 MgC ha⁻¹ in WA by 2100). Thus, Matrix lands were a net sink of C over the

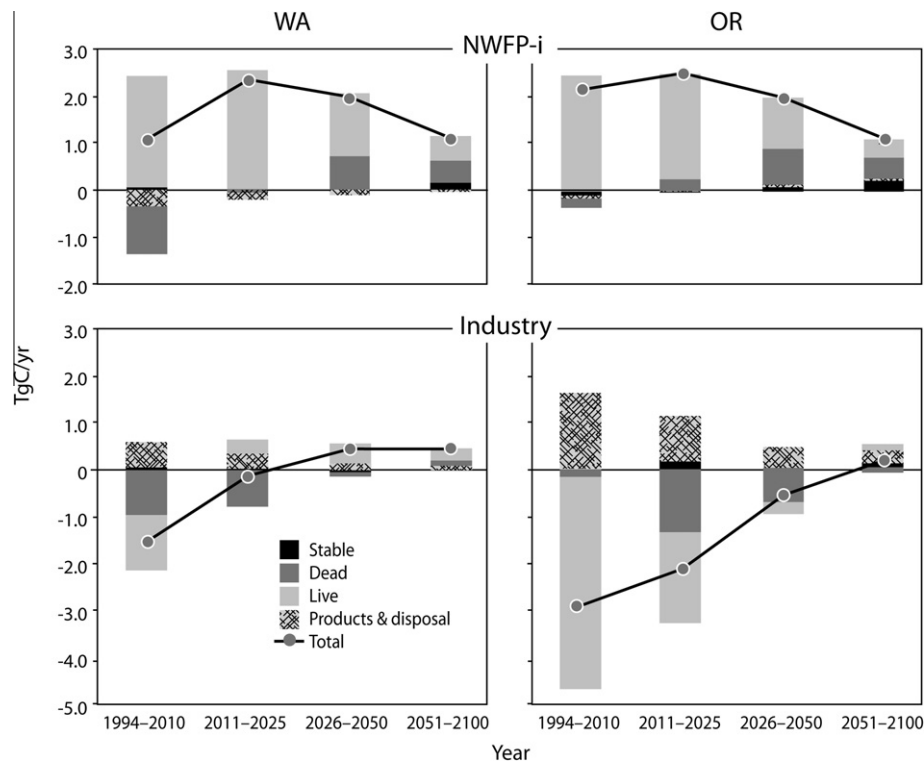


Fig. 9. Average periodic rate of total C stock change (line) and change in different C pools (vertical bars) under NWFP-i Scenario and Industry Scenario in Western Oregon and Western Washington. Positive values represent net gains; negative values represent net losses.

Table 3

Selected metrics of projected impact of management scenarios on C stores and area of old-growth forest.

Scenario	Change in total C store ^a since 1993 (TgC)				Average annual rate in 1994–2010 (MgC ha ^{−1} year ^{−1})	Wood harvested in 1994–2100, (TgC)	Change between 1993–2100 (TgC)			% Old-growth area in 2100
	2010	2025	2050	2100			On-site	Products in use	Disposal	
<i>Western Oregon</i>										
Industry	−49.7	−82.2	−96.3	−87.0	−1.25	307.5	−155.2	21.7	46.4	7.6
NWFP-p	22.5	46.8	84.5	129.3	0.56	121.9	113.0	−3.2	19.4	21.7
NWFP-i	36.3	73.5	123.3	179.0	0.91	74.7	176.4	−10.1	12.6	22.1
Cons-fire	49.8	101.9	169.4	237.6	1.25	6.8	256.1	−21.6	3.0	33.3
Cons + fire	46.1	94.6	152.4	205.8	1.16	7.3	224.2	−21.5	3.1	30.2
<i>Western Washington</i>										
Industry	−26.9	−28.8	−18.0	5.4	−0.79	154.0	−17.4	−2.0	24.8	21.6
NWFP-p	13.4	44.6	89.5	139.0	0.39	41.8	148.4	−17.9	8.5	31.5
NWFP-i	18.3	53.5	102.4	156.7	0.54	26.3	170.6	−20.2	6.3	31.7
Cons-fire	22.8	63.3	118.1	176.8	0.67	5.7	197.1	−23.7	3.4	35.1
Cons + fire	19.3	56.6	103.0	148.0	0.57	5.9	168.3	−23.7	3.4	31.9

^a Total store includes C on-site, in wood products and disposal.

entire projection period under treatments that included thinning (with and without fire suppression) or harvest at 200-year rotation with fire suppression. If the harvest were conducted on a 120-year rotation then the net C balance on Matrix lands would remain close to zero and under a 60-year rotation Matrix lands were projected to be a net source of C for several decades, then approach zero net C balance around year 2060 (Fig. 5).

The composition of C stores differed substantially among treatments with differences increasing over the projection time. The greatest differences were on Matrix lands (Fig. 6): by year 2100 under the 200-year rotation treatment live tree biomass on Matrix lands averaged 156 MgC ha⁻¹ in OR and 162 MgC ha⁻¹ in WA (38–39% of the total C store) whereas under the 60-year rotation treatment live biomass averaged ~67 MgC ha⁻¹ (both in OR and WA; 22–24% of total C store). The highest C store in wood products and disposal (53 and 54 MgC ha⁻¹ in OR and WA, respectively) resulted from the 60-year harvest rotation on Matrix lands (Fig. 6). This was a significant proportion of total C store associated with each hectare of Matrix lands (about 18% in 2100), while other scenarios resulted in much lower C store in wood products and disposal. C accumulation in wood products and disposal pools under 60-year rotation treatment on Matrix lands made up for only a small fraction of C lost from live and dead biomass pools resulting in a lower total C store by 2100 than under other treatments (Fig. 6).

Changes in state-level total C stores in western OR and WA under different management scenarios (Fig. 7) reflected the combined effect of changes in per-ha average C stores described above and the forest land area in each land-use allocation (AW/CR, LSR and Matrix) within the states (Table 1). The total C store was higher in OR in part because the total forest area included was 18% (437 thousand ha) greater than in WA (Table 1). The differences among scenarios were also greater in OR because future timber harvest prescriptions applied only to LSR and Matrix lands which together accounted for 81% of federal forest land area in OR but only 47% in WA. The federal forest lands transitioned from a net source to a net sink of C in the early 1990s in OR and in the late 1990s in WA and remained a net sink in both states through 2100 for all examined scenarios except the *Industry Scenario* (Fig. 8). The *Industry Scenario* was projected to extend the duration of the historic C source until nearly 2060 in OR and 2020 in WA.

The role of different C pools in the overall state-level net C balance changed over time and the differences among scenarios were substantial (Fig. 9). The live biomass pool was initially responsible for most of the C sink under the *NWFP* and *Conservation* scenarios, while there were small net losses in dead mass and products/disposal pools. For example, in the *NWFP-i Scenario* (Fig. 9), the role

of live biomass declined over time while the role of dead, stable, and products/disposal pools increased. This demonstrates the importance of adequate accounting for all these C pools, not just live biomass. Towards the end of the projection period, the net gains in live biomass represent less than half of the estimated total C sink. The pattern of net C gains and losses was very different in the *Industry Scenario* where net gains in products/disposal pools declined over time and net losses were initially associated mainly with live biomass, but dead C store eventually declined as well (Fig. 9).

Implementation of the *NWFP* was projected to result in a significant and long-lasting net increase in total C stores on federal forest lands relative to the 1993 level (Table 3). This increase was projected for all land-use allocations but it was relatively small on AW/CR lands where management prescriptions were not changed by the plan, and was much greater on LSR and Matrix lands (Fig. 4). If the low initial levels of timber harvest on lands under the *NWFP* were extended into the future (*NWFP-i Scenario*), a significant net increase in C stores is projected for both OR and WA (Table 3). If intensive timber harvest continued as projected under the *Industry Scenario*, the total C stores on federal forest lands would have remained lower than in 1993 throughout the projection period in OR whereas in WA C stores would have returned to the initial (1993) level towards the end of the projection period in 2100 (Table 3, Fig. 7). Between 1993 and 2100 the net changes in C stores in wood products and disposal were generally smaller than changes on-site (Table 3). The net increase in wood products C was projected only for the *Industry Scenario* in OR while in all other scenarios C stores in disposal (landfills) increased between 1993 and 2100. In all scenarios except the *Industry Scenario* the annual rate of C accumulation increased in the beginning of the projection period, reached maximum between 2005 and 2020 approaching 4 TgC year⁻¹ in OR and 2.3 TgC year⁻¹ in WA, then gradually declined (Fig. 8).

If the *Industry Scenario* (rather than initial C store in 1993) was used as a baseline for evaluating forest management alternatives, then the effect of the *NWFP* and *Conservation* scenarios was greater, especially in the beginning of the projection period (Figs. 7–9). In comparison with the *Industry Scenario*, the impact of the *NWFP-i Scenario* on total C stores between 1993 and 2010 was 86.0 TgC (5.1 TgC year⁻¹ or 2.16 MgC ha⁻¹ year⁻¹) in OR; in WA the respective values are 45.2 TgC (2.66 TgC year⁻¹ or 1.33 MgC ha⁻¹ year⁻¹; from Table 3).

Scenario selection had a large impact on C removal with timber harvest: *Conservation* scenarios generated 2–4% and *NWFP* scenarios 17–40% of the timber removals under the *Industry Scenario* over the entire projection period (Table 3). The differences in these and

other state-level impacts of alternative management scenarios were moderated in WA by a relatively large proportion of forest lands in AW/CR land use allocation (Table 1).

The area of old-growth forest in OR is projected to decline under the NWFP from nearly 32% in the early 1990s to 22–25% by 2050 and remain fairly stable in the subsequent 50 years (Tables 1 and 3; Fig. 3). The *Industry Scenario* reduced old-growth area in OR even further (to 7.6%) and only *Conservation scenarios* were projected to maintain the 1990s area of old-growth in OR. In WA however, the NWFP (both as implemented and as planned) and the *Cons + fire Scenario* maintained the initial proportion of old-growth, while the *Cons - fire Scenario* moderately increased old-growth area by 2100 (Table 3). Interestingly, the proportion of old-growth on federal forest lands maintained by the *Industry Scenario* in WA was similar to that achieved by the NWFP in OR.

4. Discussion

The scenarios examined represent, in a generalized form, different visions of future management of forests in the PNW. These scenarios allow one to gauge the range of possible outcomes associated with a set of diverse management paradigms. The five scenarios applied to two states with very similar forest types, broadly comparable land use histories and small but significant differences in allocation of federal forest lands to different land-use categories produced distinct patterns of change in C stores and net C balance with clear differences among scenarios (Figs. 7–9). The NWFP represented a major shift in management of federal forest lands and over time it appears to have increased C stores dramatically in comparison to 1993 and even more so relative to a baseline of reverting to higher timber harvests of the 1980s (Table 3, Figs. 7–9). The reduced levels of timber harvest on federal forest lands in the early 1990s ended the period of net losses of C from federal forests that was estimated to last over 50 years. At the start of the NWFP these forests were close to a point of balance in C exchange between forests and the atmosphere in OR whereas in WA the point of balance was reached a few years later (Fig. 8). In WA, the relatively large proportion of lands in the AW/CR category (Table 1) where the management prescriptions of the NWFP did not apply diminished the differences in state-level impacts among alternative management scenarios (Figs. 7–9). In both states the difference between the *Industry Scenario* and the four other scenarios was far greater than the differences among the remaining four scenarios (two NWFP and two *Conservation scenarios*) that restricted timber harvest to varying degrees.

Comparison with other published estimates of C pools and flux in OR and WA is difficult because of differences in land base and C pools considered. For 8.2 million ha of forest land in western OR, Law et al. (2004) estimated a net C sink of 8.2 TgC year⁻¹ or 1.0 MgC ha⁻¹ year⁻¹ in 1995–2000 with C accumulation in forest products responsible for 17% of this sink. The state-wide estimate by Turner et al. (2011) for 2000–2005 is 1.10 MgC ha⁻¹ year⁻¹ and includes only on-site C (no forest products or disposal). Our estimate of an average annual rate for OR of 0.91 MgC ha⁻¹ year⁻¹ in 1994–2010 (Table 3) is generally in line with the above estimates but our simulations indicate that during this period forest products were losing (Fig. 9) rather than accumulating C as reported by Law et al. (2004). By accounting only for the fate of C harvested during 1995–2000, the Law et al. (2004) study ignores losses from the wood products pool that was in large part generated by peak harvests in earlier years. The LANDCARB model used in this study tracks the legacies of past forest disturbance including C in products and disposal. This likely explains the difference in the assessment of the role of forest product pools.

To better align the scope of C estimates based on Biome-BGC modeling (Law et al., 2004; Turner et al., 2007, 2011) and our results we compared our estimate for net change in C pools on-site (excluding products/disposal) during 1996–2000 with a sub-set of NBP estimates used in Turner et al. (2007) for the same land base and time interval (D. Turner, pers. comm., Fig. 10): the average LANDCARB estimate is 0.74 MgC ha⁻¹ year⁻¹ vs. 1.24 MgC ha⁻¹ year⁻¹ estimated by Biome-BGC. Interestingly, in the LANDCARB estimation the net increase in live forest biomass C of 1.01 MgC ha⁻¹ year⁻¹ is partially offset by 0.25 MgC ha⁻¹ year⁻¹ losses from dead plant material and soil C. The disagreement between the two models likely stems from difference in model treatment of C in dead and soil pools: Biome-BGC outputs suggest that those components are changing in proportion to live biomass (e.g., Turner et al., 2007) whereas in LANDCARB live and dead biomass pools are not synchronized – they are linked functionally and often change out of phase with each other reflecting the legacies of past disturbances (Fig. 9). Furthermore, the two models represent different aspects of C dynamics on forest lands – Biome-BGC outputs clearly reflect year-to-year fluctuations in C flux driven by weather variations while LANDCARB outputs reflect change in C stores over years and decades in response to changing management and natural disturbance regimes (Fig. 10).

Conservation and restoration of old-growth forest and associated species in the PNW was the primary objective of the NWFP and initial analysis of its effects concluded that the goals set for the plan were met or exceeded (Mouer et al., 2005; Rapp, 2008), even though there was evidence of net decline in old-growth forest area (Davis et al., 2011; Ohmann et al., 2012). Our analysis examined longer-term trends and therefore is not directly comparable but it suggests that over the long term the protections under the NWFP are sufficient to maintain and in part restore old-growth forest in WA but not in OR (Table 3). Several factors contribute to differences in the impact of NWFP scenarios on old-growth area in OR and WA and the high proportion of Matrix lands in OR is a major factor—they occupy 41.5% of federal forest lands, a proportion 2.6 times greater than in WA. The planned harvest approximated by rotation of 120 years (*NWFP-p Scenario*) can over time virtually eliminate the old-growth on Matrix lands in both OR and WA. The projected losses are especially great in OR where Matrix lands contained a large area of old-growth forest at the start of the NWFP (267.1 thousand ha or 27.4% of all old-growth in OR; Table 1). The forest land area protected from clearcut harvest under the NWFP (AW/CR plus LSR) is too small

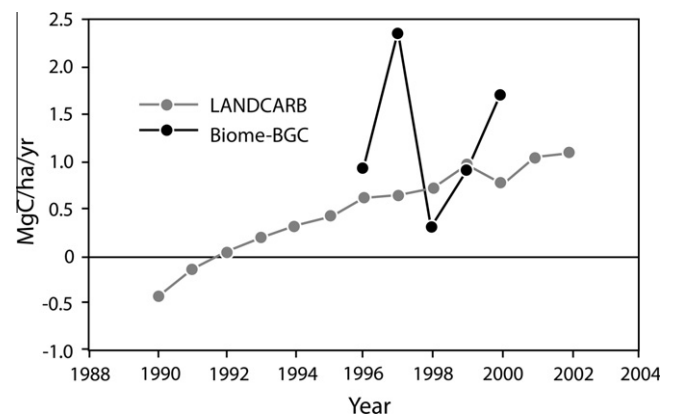


Fig. 10. Comparison of annual C balance estimates for federal forest lands in Western Oregon by two models: LANDCARB and Biome-BGC. LANDCARB estimates are net annual changes in total C store on site; Biome-BGC estimates are Net Biome Production (simulated NEP adjusted for wildfire emissions and timber harvest; Turner et al., 2007; data subset – Turner, pers. Comm.).

in OR to maintain the early 1990s area of old-growth in this state but in WA the protected area is large enough (84.1%, Table 1) to compensate for the loss of old-growth on Matrix lands. In addition, the area of forest in the Mature age group is very small on AW/CR and LSR lands in OR (Table 1) and this limits the recruitment of old-growth forest during most of the ~100 year projection period.

The management of federal forest lands under the NWFP was not intended to increase C stores, yet this outcome was achieved very quickly and effectively (Fig. 7). Other publications also conclude that the potential of forests in the PNW to store additional C is exceptionally high (e.g., Harmon et al., 2004; Foley et al., 2009; Pan et al., 2011). Longer harvest rotations on Matrix lands combined with no harvest on other land-use allocations can be expected to maintain high rates of C sequestration on federal forest lands for many decades (Table 3, Figs. 8 and 9). In comparison to the two NWFP scenarios the additional C sequestration under *Conservation scenarios* is either moderate in OR or small to non-existent in WA (Figs. 7 and 8). However, clearcut harvest even at the low rate allowed under the NWFP can essentially eliminate old-growth from forest lands allocated to rotation-based management (e.g., Thompson et al., 2006). To offset this loss and maintain old-growth at the state level a very large set-aside area is required (e.g., 84% in WA). Thus, forest management for timber production with long harvest rotations appears to be generally compatible with the goal of C sequestration on forest lands, but old-growth conservation may not be possible on the same land base.

Conservation scenarios for both states, with and without fire restoration, are projected to maintain and slightly increase the area of old-growth by approximately 2050 (Fig. 3, Table 3). The management aimed at old-growth restoration represented by the *Conservation scenarios* is fully compatible with the goal of C sequestration at the time-scale of decades examined in this study, but there is a major difference in time needed for achieve these goals. Old-growth restoration takes much longer: in our simulations for the *Conservation scenarios* the peak increases in C stores occurred within a few years after the change in management while the area increase of old-growth age class only began in the 2050–2100 time period (Figs. 7–9).

The potential role of forest management in state-level climate change mitigation efforts is greater in the PNW than in most other regions. Considering that the annual fossil fuel emissions in OR are about 15 TgC year⁻¹ (http://oregon.gov/energy/GBLWRM/Pages/Oregon_Gross_GhG_Inventory_1990–2008.aspx, last visited April 27, 2012), the average estimated net increase in total C stores on federal forest lands between 2010 and 2025 under NWFP-*i Scenario* (2.49 TgC year⁻¹, Fig. 9) is equivalent to 16.6% of state fossil fuel emissions. The average estimated net losses of C from forest lands under the *Industry Scenario* during this time interval are equivalent to adding 2.17 TgC year⁻¹ or 14.5% to state-level fossil fuel emissions. Current state-level accounting of C emissions does not include forests and other ecosystems even though forest management policies in OR control a substantial portion of state-level C emissions. Greater timber production under *Industry Scenario* (Table 3) is unlikely to substitute alternative energy-intensive materials because the ability (or willingness) of consumers to substitute softwood lumber in response to restricted supply proved to be very limited (Adams et al., 1992). However, increased timber production elsewhere is likely (Alig et al., 2006; Wear and Murray 2004) and this “leakage” needs to be addressed in designing climate change mitigation policies (Nabuurs et al., 2007).

Over time the annual net C balance values converge at zero for all management scenarios (Fig. 8) as can be expected if management remains constant (Krankina and Harmon 2006). However, this does not indicate a similarity of outcomes for atmospheric C:

state-level C stores are much lower under the *Industry Scenario* than under both NWFP scenarios (Fig. 7, Table 3) and this difference reflects the amount of C that has been removed from the atmosphere and remains sequestered on land as a result of change in forest management under the NWFP.

5. Uncertainties and limitations

This study exploits the strength of LANDCARB in assessing change in forest C stores given past disturbance regime and future management scenarios. The impact of product substitution or the use of wood for bioenergy on C balance was not simulated and was not included in scenario comparisons. Many of the currently available and commonly used methods for calculating the substitution effect cause overestimates (O'Hare et al., 2009, Law and Harmon 2011; Mitchell et al., 2012). Recent research improved methods of estimating the effect of wood-based bioenergy on atmospheric C and showed the need to re-assess the earlier estimates that did not fully account for C emissions associated with biofuels and therefore were overly optimistic (e.g., O'Hare et al., 2009, Hudiburg et al., 2011). The effect of product substitution is commonly estimated by applying a “displacement factor” to the amount of C transferred to wood products when they are used in place of other more energy-intensive materials (e.g., Hennigar et al., 2008). However, the use of displacement factors as a measure of C emission reduction resulting from each and every piece of wood used is potentially a misrepresentation of substitution effect (Sathre and O'Connor, 2010). The extent of wood substitution for other materials in response to future changes in timber harvest on federal forest lands in the NWFP area is likely low because during similar past reductions in timber supply and associated price increases the consumers were unwilling to substitute softwood lumber (the main wood product in the region) for other products (Adams et al., 1992). Thus, including product substitution is unlikely to influence our overall assessment of differences among management scenarios. The impact on forest management in other land ownerships in the PNW region and other timber-producing regions is likely (e.g., Alig et al., 2006; Wear and Murray, 2004) but was not examined in this study.

The LANDCARB model projections represent average values of C stores in forest stands of different ages within the NWFP area in two states and do not reflect ecological complexities and variability within the study area or possible adaptation of management practices to diverse site conditions. No socio-economic drivers or climate change impacts are considered either and therefore the results are to be interpreted as a comparative assessment of changes in C stores in response to different forest management paradigms rather than likely future dynamics. More realistic quantitative projections of future C balance that reflect the diverse impacts of climate change on forest ecosystems and socio-economic factors that shape the land-use policies in the region require a new research effort to integrate the available forest models.

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Appendix A. Key parameters of LANDCARB model

See Tables A1–A4.

Table A1

Parameter values for tree establishment, growth, mortality and decomposition.

Parameters (units)	Douglas-fir	Western Hemlock
<i>Tree Establishment</i>		
Light _{Max} (fraction of full sunlight)	1.00	0.90
Light _{Min} (fraction of full sunlight)	0.90	0.02
Soil water _{Max} (Mpa)	−0.1	−0.05
Soil water _{Min} (Mpa)	−2.0	−1.7
<i>Growth</i>		
Light compensation point (%)	5	2
Light extinction coefficient (ha·Mg ^{−1})	0.15	0.20
Foliage increase rate _{Max} (dimensionless)	1.00	0.60
Fine root/foliage ratio (dimensionless)	0.33	0.33
Branch/bole ratio (dimensionless)	0.50	0.50
Coarse root/bole ratio (dimensionless)	0.496	0.52
Wood respiration rate _{Max} (year ^{−1}) ^a	0.017	0.017
Rate of heartwood formation (year ^{−1})	0.05	0.02
Height _{Max} (m)	90	85
<i>Mortality</i>		
Tree mortality _{Max} (year ^{−1})	0.015	0.015
Branch prune _{Max} (year ^{−1})	0.020	0.020
Coarse root prune _{Max} (year ^{−1})	0.005	0.005
Tree age _{Max} (year ^{−1})	800	700
Foliage turnover rate (year ^{−1})	0.20	0.25
Fine root turnover rate _{Max} (year ^{−1})	0.50	0.50
<i>Decay Rates^b</i>		
Foliage (year ^{−1})	0.20	0.17
Fine root (year ^{−1})	0.15	0.15
Branch (year ^{−1})	0.07	0.08
Coarse root (year ^{−1})	0.07	0.10
Sapwood (year ^{−1})	0.05	0.05
Heartwood (year ^{−1})	0.02	0.05
<i>Transfer rates to stable pools (both species)^c</i>		
Dead foliage (year ^{−1})	0.0490	
Dead fine root (year ^{−1})	0.0731	
Dead branch (year ^{−1})	0.0099	
Dead coarse root (year ^{−1})	0.0342	
Snag sapwood (year ^{−1})	0.0430	
Snag heartwood (year ^{−1})	0.0240	
Log sapwood (year ^{−1})	0.0277	
Log heartwood (year ^{−1})	0.0148	

^a Optimum respiration temperature is 45 °C; Q₁₀ is 2.0 (dimensionless).

^b Base rates at 10 °C; Q₁₀ is 2.0 (dimensionless).

^c Decay rates for stable foliage, wood, soil, and buried charcoal are 0.100, 0.250, 0.007, 0.002 (year^{−1}), respectively.

Table A3

Fire impact on live mass: percent of live mass that is killed by fire (%Killed); percent of the %Killed that is burned off (lost to the atmosphere; %Burned); percent of the %Killed that is converted to charcoal (%Charcoal). Above refers to above ground mass, Below refers to below ground mass. LTree is lower tree; UTree is upper tree. Note: all wildfires were assumed to be hot (high severity).

Layer	%Killed		%Burned		%Charcoal	
	Above	Below	Above	Below	Above	Below
Herb	100	100	99.5	50	0.5	1.0
Shrub	100	100	99	10	1.0	1.0
LTree	100	100	10	5	2.0	1.0
UTree	100	100	5	2	4.0	1.0

Table A4

Fire impact on dead mass. Note: all wildfires were assumed to be hot (high severity); the severity of prescribed burning of dead material left after clearcut harvest varied.

Detrital Pool	Fire Severity	
	Medium	Hot
<i>gzPercent of dead mass remaining after fire</i>		
Dead foliage	75.0	50.0
Dead fine roots	100.0	75.0
Snag sapwood	100.0	85.0
Log sapwood	95.0	75.0
Snag heartwood	100.0	95.0
Log heartwood	100.0	90.0
Dead branches	75.0	50.0
Dead coarse roots	100.0	90.0
Stable soil	100.0	100.0
Stable foliage	100.0	50.0
Stable wood	100.0	50.0
Charcoal	10.0	5.0
<i>Percent of dead mass converted to charcoal by fire</i>		
Dead foliage	2.0	3.0
Dead fine roots	1.0	2.0
Snag sapwood	1.0	1.7
Log sapwood	2.0	3.5
Snag heartwood	0.0	0.0
Log heartwood	0.0	0.4
Dead branches	5.0	10.0
Dead coarse roots	0.5	1.0
Stable soil	0.0	0.0
Stable foliage	2.0	3.0
Stable wood	2.0	3.0

Table A2

Forest product parameter values (range in values reflects changes in parameter values over time).

Parameters (units)				
<i>Manufacturing</i>		<i>Structural Wood</i>	<i>External Bioenergy</i>	<i>Pulp Wood</i>
Log allocation (%)		93–99	0–2	1–5
<i>Product Use</i>		<i>Disposal (year^{−1})</i>	<i>Decomposition (year^{−1})</i>	<i>Recycling (%)</i>
Long term structure	Allocation (%)	0.010–0.015	0.010–0.015	1–10
Short term structure	75	0.10–0.20	0.10	0–10
Paper	25	0.30–0.40	0.30	0–30
Mulch	n/a	n/a	0.10	n/a
<i>Disposal</i>		<i>Allocation (%)</i>	<i>Combustion (year^{−1})</i>	<i>Decomposition (year^{−1})</i>
Open dump		1–100	0.3	0.30
Landfill		0–89	0.0	0.005
Incineration without energy recovery		0–10	1.0	n/a
Incineration for energy recovery		0–5	1.0	n/a

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Land use strategies to mitigate climate change in carbon dense temperate forests

Beverly E. Law^{a,1}, Tara W. Hudiburg^b, Logan T. Berner^c, Jeffrey J. Kent^b, Polly C. Buotte^a, and Mark E. Harmon^a

^aDepartment of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331; ^bDepartment of Forest, Rangeland, and Fire Sciences, University of Idaho, Moscow, ID 83844; and ^cEcoSpatial Services L.L.C., Flagstaff, AZ 86004

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Strategies to mitigate carbon dioxide emissions through forestry activities have been proposed, but ecosystem process-based integration of climate change, enhanced CO₂, 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 m³·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 CO₂ 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, CO₂, 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/>).

¹To whom correspondence should be addressed. Email: bev.law@oregonstate.edu.

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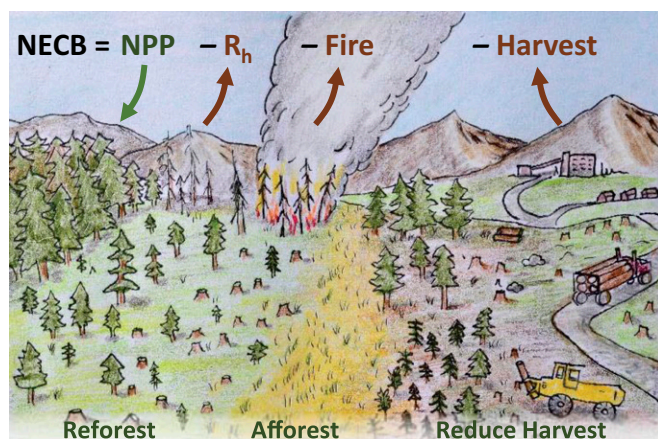


Fig. 1. Approach to assessing effects of mitigation strategies on forest carbon and forest sector emissions. NECB is productivity (NPP) minus R_h and losses from fire and harvest (red arrows). Harvest emissions include those associated with wood products and bioenergy.

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 (R_h)] averaged 28 teragrams carbon per year (Tg C y^{-1}) over all three periods. Fire emissions were unusually high at 8.69 million metric tons carbon dioxide equivalent ($tCO_2e\ y^{-1}$, i.e., $2.37\ Tg\ C\ y^{-1}$) in 2001–2005 due to the historic Biscuit Fire, but decreased to 3.56 million $tCO_2e\ y^{-1}$ ($0.97\ Tg\ C\ y^{-1}$) in 2011–2015 (Table S4). Note that 1 million tCO_2e equals 3.667 Tg C.

Our LCA showed that in 2001–2005, Oregon's net wood product emissions were 32.61 million tCO_2e (Table S3), and 3.7-fold wildfire emissions in the period that included the record fire year (15) (Fig. 2). In 2011–2015, net wood product emissions were 34.45 million tCO_2e and almost 10-fold fire emissions, mostly due to lower fire emissions. The net wood product emissions are higher than fire emissions despite carbon benefits of storage in wood products and substitution for more fossil fuel-intensive products. Hence, combining fire and net wood product emissions, the forest sector emissions averaged 40 million $tCO_2e\ y^{-1}$ and accounted for about 39% of total emissions across all sectors (Fig. 2 and Table S4). NECB was calculated from NEP minus losses from fire emissions and harvest (Fig. 1). State NECB was equivalent to 60% and 70% of total emissions for 2001–2005 and 2011–2015, respectively (Fig. 2, Table 1, and Table S4). Fire emissions were only between 4% and 8% of total emissions from

all sources (2011–2015 and 2001–2004, respectively). Oregon's forests play a larger role in meeting its GHG targets than US forests have in meeting the nation's targets (16, 17).

Historical disturbance regimes were simulated using stand age and disturbance history from remote sensing products. Comparisons of Community Land Model (CLM4.5) output with Forest Inventory and Analysis (FIA) aboveground tree biomass (>6,000 plots) were within 1 SD of the ecoregion means (Fig. S2). CLM4.5 estimates of cumulative burn area and emissions from 1990 to 2014 were 14% and 25% less than observed, respectively. The discrepancy was mostly due to the model missing an anomalously large fire in 2002 (Fig. S3A). When excluded, modeled versus observed fire emissions were in good agreement ($r^2 = 0.62$; Fig. S3B). 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 non-food/nonforage grass crops, hereafter referred to as “grass crops,” had to meet minimum conditions for tree growth, and crop grid cells had to be partially forested (SI Methods and Table S6). These crops are not grazed or used for animal feed. Competing land uses may decrease the actual amount of area that can be afforested. We calculated the amount of irrigated grass crops (127,000 ha) that could be converted to forest, assuming success of carbon offset programs (19). By 2100, afforestation increased stocks by

Table 1. Forest carbon budget components used to compute NECB

Flux, Tg C·y ⁻¹	2001–2005		2006–2010		2011–2015		2001–2015
NPP	73.64	7.59	73.57	7.58	73.57	7.58	73.60
Rh	45.67	5.11	45.38	5.07	45.19	5.05	45.41
NEP	27.97	9.15	28.19	9.12	28.39	9.11	28.18
Harvest removals	8.58	0.60	7.77	0.54	8.61	0.6	8.32
Fire emissions	2.37	0.27	1.79	0.2	0.97	0.11	1.71
NECB	17.02	9.17	18.63	9.14	18.81	9.13	18.15

Average annual values for each period, including uncertainty (95% confidence interval) in Tg C y^{-1} (multiply by 3.667 to get million tCO_2e).

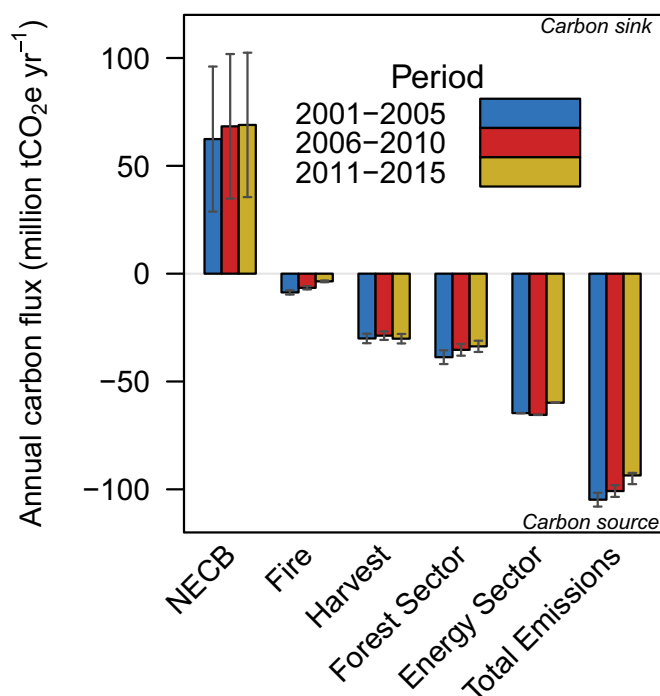


Fig. 2. Oregon's forest carbon sink and emissions from forest and energy sectors. Harvest emissions are computed by LCA. Fire and harvest emissions sum to forest sector emissions. Energy sector emissions are from the Oregon Global Warming Commission (14), minus forest-related emissions. Error bars are 95% confidence intervals (Monte Carlo analysis).

94 Tg C and cumulative NECB by 14 Tg C, and afforestation reduced forest sector GHG emissions by 1.3–1.4% in 2025, 2050, and 2100 (Fig. 3).

We quantified cobenefits of afforestation of irrigated grass crops on water availability based on data from hydrology and agricultural simulations of future grass crop area and related irrigation demand (20). Afforestation of 127,000 ha of grass cropland with Douglas fir could decrease irrigation demand by 222 and 233 billion $\text{m}^3 \cdot \text{y}^{-1}$ 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 $\text{mm} \cdot \text{y}^{-1}$ and 516 $\text{mm} \cdot \text{y}^{-1}$. Under current climate conditions, the observations suggest an increase in annual water availability of 260 billion $\text{m}^3 \cdot \text{y}^{-1}$ 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 ob-
servations related to climate, vulnerability, impacts, adaptation,

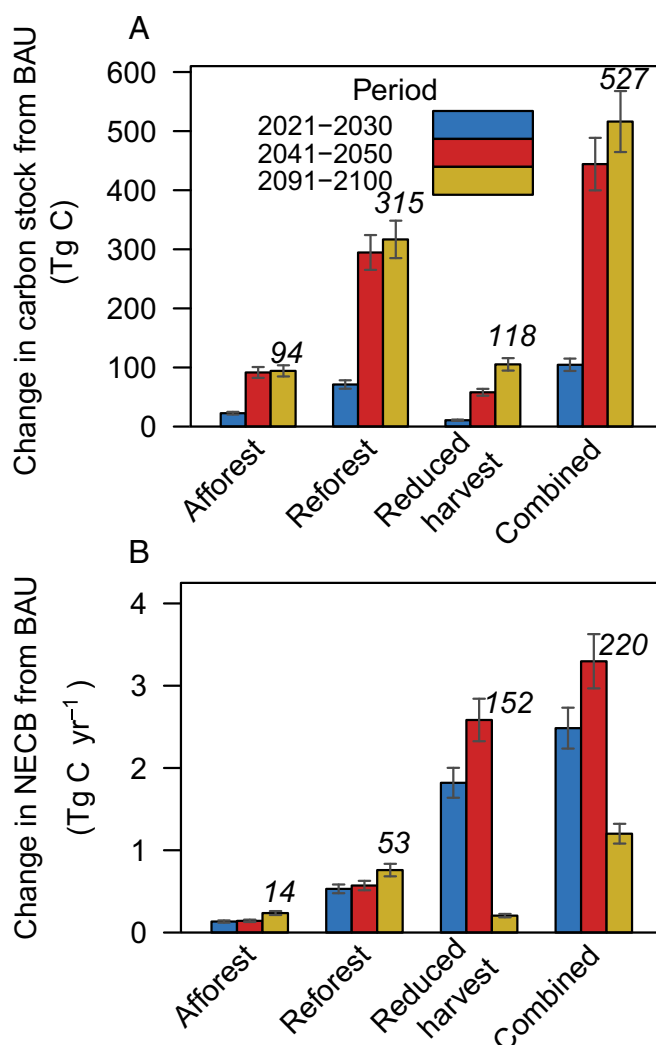


Fig. 3. Future change in carbon stocks and NECB with mitigation strategies relative to BAU management. The decadal average change in forest carbon stocks (*A*) and NECB relative to BAU (*B*) are shown. Italicized numbers over bars indicate mean forest carbon stocks in 2091–2100 (*A*) and cumulative change in NECB for 2015–2100 (*B*). Error bars are $\pm 10\%$.

and mitigation into a common framework, melding biophysical with social components (22). We developed a framework to examine a suite of mitigation actions to increase forest carbon sequestration and reduce forest sector emissions under current and future environmental conditions.

Harvest-related emissions had a large impact on recent forest NECB, reducing it by an average of 34% from 2001 to 2015. By comparison, fire emissions were relatively small and reduced NECB by 12% in the Biscuit Fire year, but only reduced NECB 5–9% from 2006 to 2015. Thus, altered forest management has the potential to enhance the forest carbon balance and reduce emissions.

Future NEP increased because enhancement from atmospheric carbon dioxide outweighed the losses from fire. Lengthened harvest cycles on private lands to 80 y and restricting harvest to 50% of current rates on public lands increased NECB the most by 2100, accounting for 90% of total emissions reduction (Fig. 3 and Tables S5 and S6). Reduced harvest led to NECB increasing earlier than the other strategies (by 2050), suggesting this could be a priority for implementation.

Our afforestation estimates may be too conservative by limiting them to nonforest areas within current forest boundaries and 127,000 ha of irrigated grass cropland. There was a net loss of 367,000 ha of forest area in Oregon and Washington combined from 2001 to 2006 (23), and less than 1% of native habitat remains in the Willamette Valley due to urbanization and agriculture (24). Perhaps more of this area could be afforested.

The spatial variation in the potential for each mitigation option to improve carbon stocks and fluxes shows that the reforestation potential is highest in the Cascade Mountains, where fire and insects occur (Fig. 4). The potential to reduce harvest on public land is highest in the Cascade Mountains, and that to lengthen harvest cycles on private lands is highest in the Coast Range.

Although western Oregon is mesic with little expected change in precipitation, the afforestation cobenefits of increased water availability will be important. Urban demand for water is projected to increase, but agricultural irrigation will continue to consume much more water than urban use (25). Converting 127,000 ha of irrigated grass crops to native forests appears to be a win-win strategy, returning some of the area to forest land, providing habitat and connectivity for forest species, and easing irrigation demand. Because the afforested grass crop represents only 11% of the available grass cropland (1.18 million ha), it is not likely to result in leakage or indirect land use change. The two forest strategies combined are likely to be important contributors to water security.

Cobenefits with biodiversity were not assessed in our study. However, a recent study showed that in the mesic forests, cobenefits with biodiversity of forest species are largest on lands with harvest cycles longer than 80 y, and thus would be most pronounced on private lands (26). We selected 80 y for the harvest cycle mitigation strategy because productivity peaks at 80–125 y in this region, which coincides with the point at which cobenefits with wildlife habitat are substantial.

Habitat loss and climate change are the two greatest threats to biodiversity. Afforestation of areas that are currently grass crops would likely improve the habitat of forest species (27), as about 90% of the forests in these areas were replaced by agriculture. About 45 mammal species are at risk because of range contraction (28). Forests are more efficient at dissipating heat than grass and crop lands, and forest cover gains lead to net surface cooling in all regions south of about 45° latitude in North American and Europe (29). The cooler conditions can buffer climate-sensitive bird populations from approaching their thermal limits and provide more food and nest sites (30). Thus, the mitigation strategies of afforestation, protecting forests on public lands and lengthening harvest cycles to 80–125 y, would likely benefit forest-dependent species.

Oregon has a legislated mandate to reduce emissions, and is considering an offsets program that limits use of offsets to 8% of

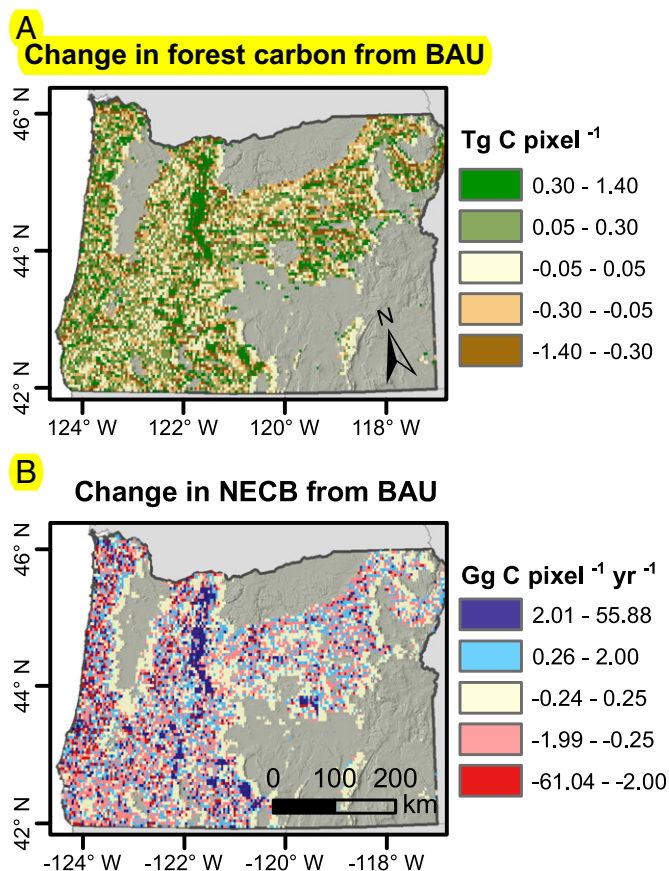


Fig. 4. Spatial patterns of forest carbon stocks and NECB by 2091–2100. The decadal average changes in forest carbon stocks (A) and NECB (B) due to afforestation, reforestation, protected areas, and lengthened harvest cycles to continued BAU forest management (red is increase in NECB) are shown.

the total emissions reduction to ensure that regulated entities substantially reduce their own emissions, similar to California's program (19). An offset becomes a net emissions reduction by increasing the forest carbon sink (NECB). If only 8% of the GHG reduction is allowed for forest offsets, the limits for forest offsets would be 2.1 and 8.4 million metric tCO₂e of total emissions by 2025 and 2050, respectively (Table S6). The combination of afforestation, reforestation, and reduced harvest would provide 13 million metric tCO₂e 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 CO₂ 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 CO₂ 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 m³·y⁻¹ for 238,679 ha and is projected to be 412 and 405 billion m³ 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 m³·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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Strategic Forest Reserves can protect biodiversity in the western United States and mitigate climate change

Beverly E. Law¹ , Logan T. Berner², Polly C. Buotte³, David J. Mildrexler⁴  & William J. Ripple¹

Forest preservation is crucial for protecting biodiversity and mitigating climate change. Here we assess current forest preservation in the western United States using spatial data and find that beyond the 18.9% (17.5 Mha) currently protected, an additional 11.1% (10.3 Mha) is needed to achieve 30% preservation by 2030 (30 × 30). To help meet this regional preservation target, we developed a framework that prioritizes forestlands for preservation using spatial metrics of biodiversity and/or carbon within each ecoregion. We show that meeting this preservation target would lead to greater protection of animal and tree species habitat, current carbon stocks, future carbon accumulation, and forests that are important for surface drinking water. The highest priority forestlands are primarily owned by the federal government, though substantial areas are also owned by private entities and state and tribal governments. Establishing Strategic Forest Reserves would help protect biodiversity and carbon for climate adaptation and mitigation.

¹Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA. ²EcoSpatial Services L.L.C., Flagstaff, AZ, USA. ³Energy and Resources Group, University of California Berkeley, Berkeley, CA, USA. ⁴Eastern Oregon Legacy Lands, Joseph, OR, USA. ✉email: lawb@oregonstate.edu

We are in the midst of climate and biodiversity emergencies¹, and pledges have been made by the world's governments to address both. Studies suggest that countries must ramp up climate pledges by 80% to avoid the most catastrophic effects of climate change². International, national, and state biodiversity targets have been established to include protection of 30% of the land by 2030 (30 × 30), and 50% by 2050 (50 × 50)^{3,4}, a timeframe over which accelerated abrupt ecological disruption is expected⁵. In addition to the targets, the United States (US) stated its understanding of the role of natural climate solutions in climate mitigation and resilience in its Nationally Determined Contributions in line with Article 4 of the Paris Agreement⁶. Nevertheless, only 6.1% of forestland in the conterminous US is protected at the highest level (Supplementary Table 1), with 0.2% in strict nature reserves to protect biodiversity, 4.8% in Wilderness areas, and 1.1% in National Parks⁷. How do we achieve our preservation targets given the pressing need to increase carbon removals from the atmosphere, make substantial reductions in carbon emissions, protect biodiversity, and slow the accelerating species losses?

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and the Intergovernmental Panel on Climate Change (IPCC) jointly recognized the intertwined nature of climate and biodiversity⁸. Their landmark report highlights the synergies and trade-offs between protection of biodiversity and climate change adaptation and mitigation, and recommend measures that can be jointly taken⁸. Global studies have identified terrestrial areas that, if preserved, would stem biodiversity loss, prevent carbon emissions from land conversion, and enhance natural carbon removal from the atmosphere^{9–11}. Although global studies provide estimates of the role of natural climate solutions to store carbon¹² or benefit biodiversity and carbon storage¹⁰, regional analyses with finer resolution information are needed at a scale appropriate to inform decision-making. Our analysis here is among the first to apply

recommendations of the IPBES-IPCC report to forests in a specific geographic region.

Emissions from land cover and land use change now exceed half of removals from the atmosphere by all terrestrial ecosystems¹³. Much attention has been on reducing deforestation and degradation in tropical forests because of their large extent¹⁴, high biodiversity¹⁵, and carbon density¹⁶, and because tropical deforestation and degradation are the second largest source of anthropogenic emissions after fossil fuel emissions¹³. Deforestation and degradation result in habitat loss that is a major cause of species extinctions, and contribute to warming that amplifies risk of species extinction¹⁷. Little attention has been given to the nexus of high carbon density and biodiversity forests in the temperate region, and their importance to climate mitigation and adaptation.

Across forests of the western US an earlier study found that medium to high carbon density forests (carbon per unit ground area) with low vulnerability to mortality from fire or drought by 2099 also had high amounts of critical habitat for threatened and endangered species¹⁸. The study focused on high carbon priority areas for protection that had low vulnerability to mortality, but did not prioritize areas for biodiversity, identify preservation opportunities within each ecoregion, or distinguish land ownerships as a factor for decision-making.

Here, we develop and apply a regional framework to identify forest areas in the western US (Fig. 1) for permanent protections that if preserved, would stem further biodiversity loss, prevent emissions from forest conversion, and safeguard natural carbon stocks and accumulation. This regional framework is unique in that it evaluates the current extent of protected areas and then explicitly determines ways to reach specific forest preservation targets based on three preservation priority scenarios (carbon and/or biodiversity; Fig. 2). We focus on the following questions:

- (1) How much forestland is currently protected in each western state and how much additional forestland would need to be protected to reach the 30 and 50% targets?
- (2) Which forestlands are the highest priority for preservation to meet these targets if prioritized based on forest carbon and/or biodiversity scenarios?
- (3) Who owns the forestlands that have the highest preservation priority under each scenario?
- (4) If these targets were reached, then for each scenario how much forest carbon and species habitat would occur in protected areas compared with present?

The spatial extent of the analysis is 92.46 Mha of forest land in the western US. We first determined current forest preservation status and how much additional forest would be needed to meet the 30 × 30 and 50 × 50 targets in the western US. Specifically, we identified the regional extent of forests at 1 km resolution using a geospatial dataset produced by the US Forest Service (USFS) Forest Inventory and Analysis program (FIA)¹⁹ and determined current preservation status using the Protected Areas Database of the United States (PAD-US version 2.1) from the US Geological Survey (USGS) Gap Analysis Project (GAP)²⁰. To identify forests with the highest preservation priority, we developed a forest preservation priority ranking (forest PPR) system using geospatial data related to forest biodiversity, carbon, and future vulnerability to drought or wildfire (Fig. 2). To ensure protection for the many facets of regional biodiversity and promote regional connectivity, we computed the forest PPR components for each grid cell relative to other grid cells in the same ecoregion within each state. Forest biodiversity was characterized based on terrestrial vertebrate (hereafter *animal*) and tree species richness derived from species habitat distribution models produced by the USGS GAP²¹ and USFS FIA²², respectively. Current forest ecosystem carbon

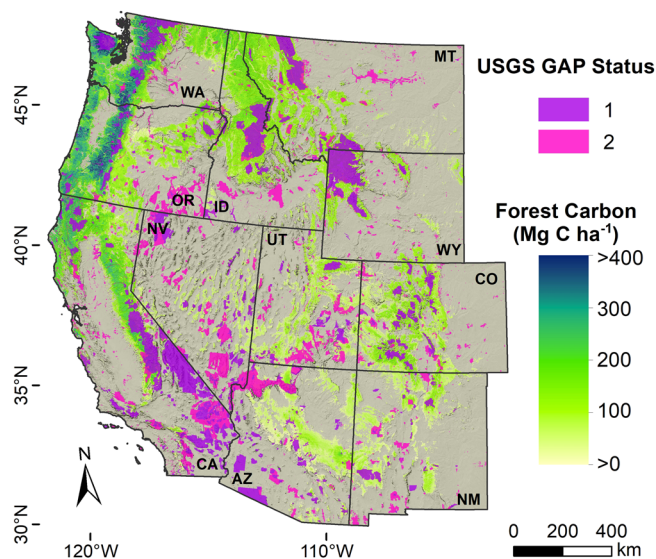


Fig. 1 Current protected lands and forest ecosystem carbon stocks (Mg C ha^{-1}) across the western US. Protected lands shown here are those with GAP Status 1 or 2 from the Protected Areas Database of the United States (PAD-US v. 2.1)²⁰. These statuses reflect areas with permanent protection from anthropogenic conversion of natural land cover. The forest carbon stocks were spatially imputed from inventory measurement by the USFS FIA²³. The protected lands shown here include forestlands and non-forestlands.

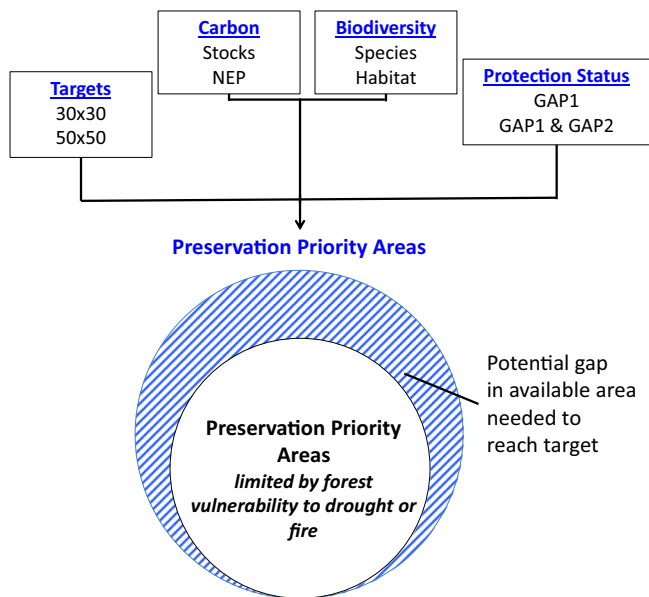


Fig. 2 Analysis framework for prioritizing areas for forest carbon and/or biodiversity preservation across the western US. Regional framework evaluates the current extent of protected areas and then explicitly determines ways to reach specific forest preservation targets based on three preservation priority scenarios (carbon, biodiversity, carbon, and biodiversity).

stocks (2000 to 2009) were quantified using a dataset produced by the USFS FIA²³, while potential forest carbon accumulation from 2020 to 2050 was quantified using cumulative net ecosystem production simulated with a region- and species-specific parameterized version of the Community Land Model version 4.5 (CLM4.5)²⁴. These previous simulations used climatic changes predicted by two global climate models forced by representative concentration pathway 8.5 emissions¹⁸. Future forest vulnerability to drought or wildfire was also derived from these simulations²⁵ and allowed us to compute forest PPRs both including and excluding forests with high vulnerabilities. High vulnerability to future mortality indicates future increases in tree mortality rates which reduces overall carbon storage capacity and has the potential to trigger transitions from forest to non-forest, however explicit vegetation transitions were not simulated. After identifying forests with the highest preservation priority for meeting preservation targets under each prioritization scenario (i.e., biodiversity and/or carbon), we then assessed who owns these forests using ownership data from PAD-US. We also evaluated current and potential protection of not only animal and tree species habitat, but also current carbon stocks, near future carbon accumulation, and forests important for surface drinking water.

Our analysis reveals that to achieve 30% permanent protection of forestland in the region by 2030, an additional 10.3 Mha (11.1%) would need to be protected at the highest levels (herein referred to as GAP 1 and GAP 2). We find that meeting preservation targets would help protect regional forest carbon, biodiversity, and surface drinking water. Establishing Strategic Forest Reserves on public lands would provide climate mitigation, biodiversity protection, and water security.

Results

Current extent and additional protected area needed to meet targets. Protected areas are defined by the USGS GAP as lands dedicated to and actively managed for the preservation of biological diversity, recreation, and cultural uses. GAP status 1 and

GAP status 2 are the highest levels of protection with mandated management plans to maintain a natural state (Supplementary Table 1). In GAP 1 areas, ecological disturbances are allowed to proceed, while GAP 2 areas may receive uses or management practices that degrade the quality of existing natural communities, including suppression of natural disturbance like wildfire. Protecting 30% by 2030 using both GAP 1 and 2 means the targeted lands will have met these criteria for permanent protection and have mandatory management plans that do not allow extractive uses (e.g., logging, livestock grazing, mining).

Our analysis showed that about 7.6% (23.2 Mha) of the land area in the region is protected at the highest level (GAP 1), of which about half (55%, 13 Mha) is forest. About 14.0% of regional forest area is GAP1 and thus to achieve 30% protection by 2030, an additional 16.0% (14.8 Mha) of forest area needs to be protected (Supplementary Table 2). If the analysis is relaxed to include both GAP 1 and GAP 2, then 18.9% forest area is currently protected and an additional 11.1% (10.3 Mha) of forest area would need to be protected by 2030 (Table 1).

Permanently protected land area (GAP 1 and 2) covers an average of 13.2% of each state, but ranges from 6.2% in New Mexico to 23.9% in California (Fig. 1; Table 1). Similarly, permanently protected areas cover an average of 20.2% of forest area in each state, but range from 10.1% in Oregon to 41.9% in Wyoming (~1 to 3 Mha per state). To protect 30% of forest area by 2030 and 50% by 2050, each state would need to increase protection by 0–19.9% and 8.1–36.8%, respectively, while region-wide protection would need to increase by 11.1% and 31.1% to achieve these targets (Table 1).

The area required to protect habitat and ecosystems from being imperiled is estimated to be about half of a typical region or ecoregion²⁶. Of the 28 ecoregions in the western US that are at least 1% forested, 21% ($n = 6$) have at least 30% of their forest area permanently protected as GAP 1 or 2, while only 7% ($n = 2$) have at least half of their forest area protected at these levels (Supplementary Table 3).

Highest priority areas for preservation of carbon and biodiversity. Forest PPRs were derived from carbon and biodiversity priority ranks at 1 km spatial resolution computed when both including and excluding forestland with high future vulnerability as simulated with CLM4.5, and summarized by ecoregion and state. The areas with the highest forest PPRs are primarily in the mountain ranges (Fig. 3a), particularly in the Pacific Northwest. Forests with high carbon priority have high biodiversity priority when highly vulnerable forests are excluded (Spearman's correlation within ecoregions median $r = 0.52$; Figs. 3, 4). However, there are important areas of high biodiversity that do not have the highest carbon rankings. Prominent examples include the Klamath Mountains in southern Oregon and northern California, the east slope of the Cascades in Washington, some of the Sky Island ranges in Nevada and Utah, Arizona, and the Colorado front range (Fig. 3). The Sky Islands are isolated mountain ranges above the desert or grasslands that connect the subtropical Sierra Madre of Mexico with the temperate Rocky Mountains, creating unique biodiversity.

Future increases in tree mortality rates, represented by high future vulnerability to drought and/or fire²⁵, could destabilize carbon²⁷ and biodiversity^{28,29}. Much of the southwest US, and portions of the Sierra Mountains and northwestern Wyoming are highly vulnerable to future drought and/or fire, (Fig. 3d, Table 2). Forests in the Pacific Northwest, which currently support high carbon and biodiversity, are less vulnerable to future mortality (Fig. 3). Areas that are highly vulnerable to future mortality, though concentrated in the water-limited forests of the southwest

Table 1 Current extent of forest, protected lands, and additions needed to meet preservation targets for each state and the broader western US.															
State	Land	Protected lands		Forest		Protected forest		Additions needed to meet preservation targets							
								All lands				Forest			
		Mha	%	Mha	%	Mha	%	30% target	%	50% target	%	30% target	%	50% target	%
AZ	29.53	3.81	12.9	7.67	26.0	1.01	13.2	5.0	17.1	11.0	37.1	1.3	16.8	2.8	36.8
CA	40.92	9.76	23.9	11.97	29.3	2.83	23.6	2.5	6.1	10.7	26.1	0.8	6.4	3.2	26.4
CO	26.96	2.61	9.7	9.50	35.2	1.56	16.4	5.5	20.3	10.9	40.3	1.3	13.6	3.2	33.6
ID	21.64	3.16	14.6	9.53	44.0	1.91	20.0	3.3	15.4	7.7	35.4	1.0	10.0	2.9	30.0
MT	38.07	3.41	9.0	9.57	25.1	2.15	22.5	8.0	21.0	15.6	41.0	0.7	7.5	2.6	27.5
NM	31.47	1.95	6.2	6.74	21.4	0.87	12.9	7.5	23.8	13.8	43.8	1.2	17.1	2.5	37.1
NV	28.63	4.40	15.4	3.60	12.6	0.97	26.9	4.2	14.6	9.9	34.6	0.1	3.1	0.8	23.1
OR	25.12	2.93	11.7	12.68	50.5	1.28	10.1	4.6	18.3	9.6	38.3	2.5	19.9	5.1	39.9
UT	21.98	2.81	12.8	6.93	31.5	1.1	15.9	3.8	17.2	8.2	37.2	1.0	14.1	2.4	34.1
WA	17.43	2.62	15.0	10.00	57.4	2.01	20.1	2.6	15.0	6.1	35.0	1.0	9.9	3.0	29.9
WY	25.32	3.62	14.3	4.27	16.9	1.79	41.9	4.0	15.7	9.0	35.7	-0.5	-11.9	0.3	8.1
Region	307.07	41.08	13.4	92.46	30.1	17.48	18.9	51	16.6	112.4	36.6	10.3	11.1	28.8	31.1
Land includes inland waters and was considered currently protected with a GAP status of 1 or 2. States include Arizona (AZ), California (CA), Colorado (CO), Idaho (ID), Montana (MT), New Mexico (NM), Nevada (NV), Oregon (OR), Utah (UT), Washington (WA), and Wyoming (WY).															

US, contain a range of current carbon and biodiversity rankings (Fig. 3). Notable high vulnerability areas with high biodiversity occur in the Southern Rockies, the Sierra Nevada, and Greater Yellowstone Ecosystem (Fig. 3). General spatial patterns of 30 and 50% preservation priority appear to be similar between inclusion and exclusion of high vulnerability areas, though fine scale differences are evident for several states in the Southwest (Fig. 4).

Land ownership under high preservation priority scenarios. Regional forestlands with the highest preservation priority are primarily owned by the federal government followed by private entities, tribal governments, and state governments, though the relative proportions vary by target and priority (Fig. 5), as well as among individual states (Supplementary Figs. 1 and 2). The federal government owns more than half (61–62%) of high preservation priority forestland in the region, while states own 4 to 5% (Fig. 5), comprising the lands most readily available for permanent protections under GAP 1 and 2. Private entities own about a quarter of these forestlands, with the bulk of those lands in industrial management and a substantial percentage managed for multiple values. Inventoried Roadless Areas (IRAs) comprise 13–18% of regional high priority forestland and 24–28% of the high priority lands owned by the federal government. Interestingly, a larger proportion of high biodiversity priority lands and a smaller portion of high carbon priority lands is in private ownership (Fig. 5). Across targets, there is minimal difference in who owns forestlands needed to achieve 30% or 50% forest preservation targets. There are also minimal differences regardless of whether forestlands with high future vulnerability to droughts and fires were not masked from analysis (Supplementary Figs. 3–5).

Forest ownership of high preservation priority forestlands differs among states. Private entities own over 25% of high preservation priority forestland in California, Colorado, Oregon, Utah, and Washington. Tribal governments own ~45% of high preservation priority forestland in Arizona, by far the highest of any state in the region (Supplementary Figs. 1 and 2). Again, across targets by state, there is minimal difference in ownership of forestlands needed to achieve 30% or 50% forest preservation targets.

Forest carbon, habitat, and surface drinking water added by protected area scenarios. Protected forestlands (GAP 1 and 2) currently (2000–2009) store ~2.25 Pg C, or 20% of the total forest ecosystem carbon in the western US (~11.34 Pg C; Fig. 6a, Supplementary Fig. 6). These protected forests could accumulate another ~0.45 Pg C by 2050 as they continue to grow and mature (Fig. 6b, Supplementary Fig. 6). Depending on preservation priority, if 30% of forestlands were preserved, they would currently store 3.60–3.94 Pg C (32–35% of total) and could accumulate another 0.74–0.91 Pg C by 2050. Similarly, if 50% of forestlands were preserved, they would currently store 5.78–6.21 Pg C (51–56% of total) and could accumulate another 1.20–1.47 Pg C by 2050. Preserving 50% of forestlands would triple the amount of carbon that is currently protected. Prioritizing jointly for carbon and biodiversity leads to only slightly (2–4%) lower preservation of current carbon stocks and near-future carbon accumulation compared with prioritizing for carbon alone.

Generally, less than 20% of each animal and tree species’ forest habitat is currently protected (GAP 1 or 2) in the region (Fig. 7a). The median percentage of forest habitat currently preserved for amphibian, bird, mammal, and reptile species is ~18% for each taxa and 14% for tree species. If prioritized jointly for carbon and biodiversity, then preserving 30% of forestlands would increase median forest habitat protection to ~30% for species of each taxa, while preserving 50% of forestlands would further increase this to ~50% for species of each taxa (Fig. 7b). If 50% of forestlands were preserved, then most (82–95%) animal and tree species would

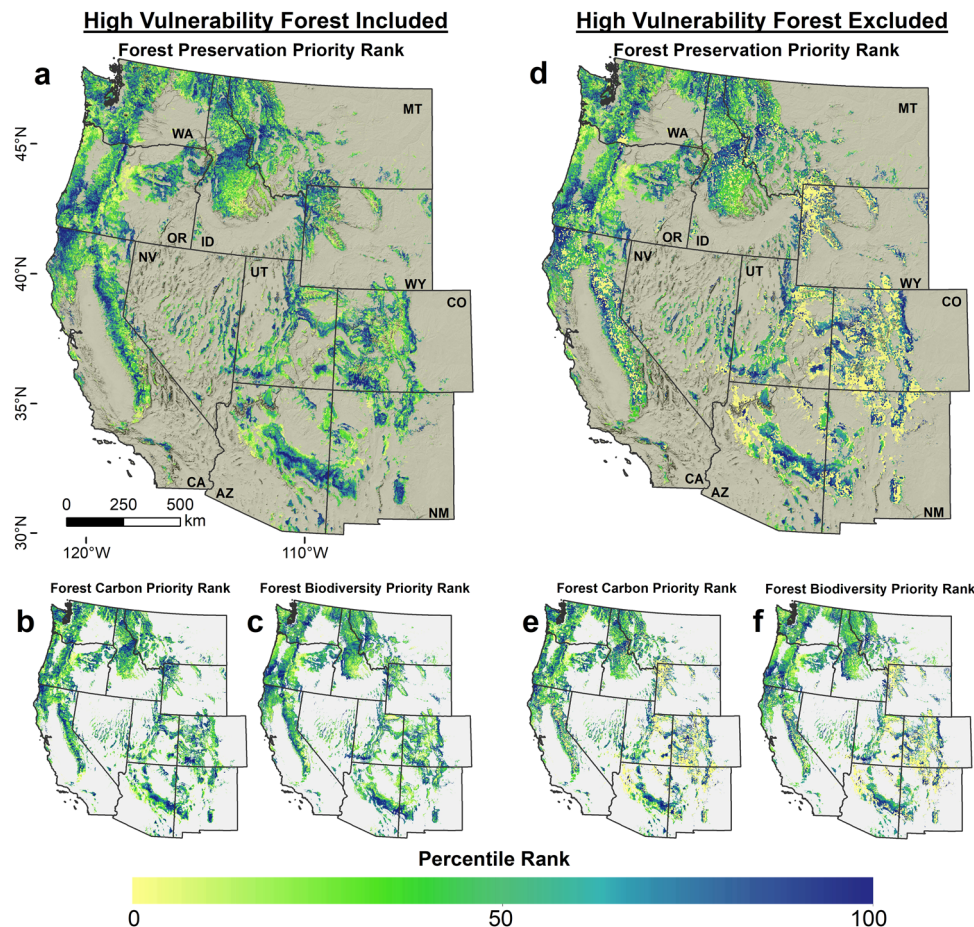


Fig. 3 Forest preservation, carbon, and biodiversity priority ranking for the western US. **a, d** Forest preservation priority ranks were derived from **b, e** forest carbon priority ranks and **c, f** forest biodiversity priority ranks for each ecoregion within every state. High future vulnerability to drought or fire could destabilize forest carbon and biodiversity, thus priority ranks were computed when both including (left columns) and excluding (right columns) forestland with high future vulnerability as simulated with CLM4.5.

have at least 30% of their forest habitat protected. Prioritizing jointly for carbon and biodiversity leads to slightly lower forest habitat protection than if prioritized only for biodiversity.

Threatened or endangered species would also benefit from increased forest preservation. For instance, currently ~26% and ~22% of gray wolf (*Canis lupus*) and Canada lynx (*Lynx canadensis*) forest habitat is protected in the region, but ~36 and 33% would be protected if 30% of forestlands were preserved. Furthermore, currently ~14% and ~15% of marbled murrelet (*Brachyramphus marmoratus*) and spotted owl (*Strix occidentalis*) regional forest habitat is protected, but ~28% and ~31% would be protected by reaching this preservation target. Protecting 50% of forestlands would lead to over half of these species' regional forest habitat being preserved.

Forestlands account for 56% of the most important areas (top 75%) for surface drinking water in the region (Supplementary Table 4). Only ~19% of the most important forestlands for surface drinking water are currently preserved as GAP 1 or 2. However, reaching 30% or 50% forest preservation targets would mean preserving about 33 and 53%, respectively, of the forestlands that are most important for surface drinking water, after excluding high vulnerability forests.

Discussion

Preservation is crucial for mitigating ongoing climate change and stemming loss of biodiversity^{10,12,30}, thus international efforts are

underway to protect 30% of land and water by 2030 (30 × 30) and 50% by 2050 (50 × 50). Here we assessed current preservation in the western US and show that 13.4% (41.08 Mha) of land area is protected (GAP 1 or 2; IUCN Ia–VI), including 18.9% (17.48 Mha) of regional forestland (Table 1). To meet the 30 × 30 or 50 × 50 targets in this region, an additional 10.3 Mha or 28.8 Mha of forestland would need protection. We developed and applied a geospatial framework to explicitly identify forestlands that could be strategically preserved to help meet these targets. We propose that Strategic Forest Reserves could be established on federal and state public lands where much of the high priority forests occur, while private entities and tribal nations could be incentivized to preserve other high priority forests. We further find that preserving high priority forests would help protect (1) ecosystem carbon stocks and accumulation for climate mitigation, (2) animal and tree species' habitat to stem further biodiversity loss, and (3) surface drinking water for water security. Progress has been made, but much work needs to be done to reach the 30 × 30 or 50 × 50 targets in the western US.

To meet preservation targets, new permanent protections are needed at the highest levels for forests in the western US. Permanent protection is best met on federal and state public lands with additional land designated as wilderness areas, wild and scenic rivers, and national monuments, and by a new category of Strategic Forest Reserves for climate mitigation and adaptation. We found that about 65% of regional high priority forest occurs on federal and state lands, highlighting important roles for federal

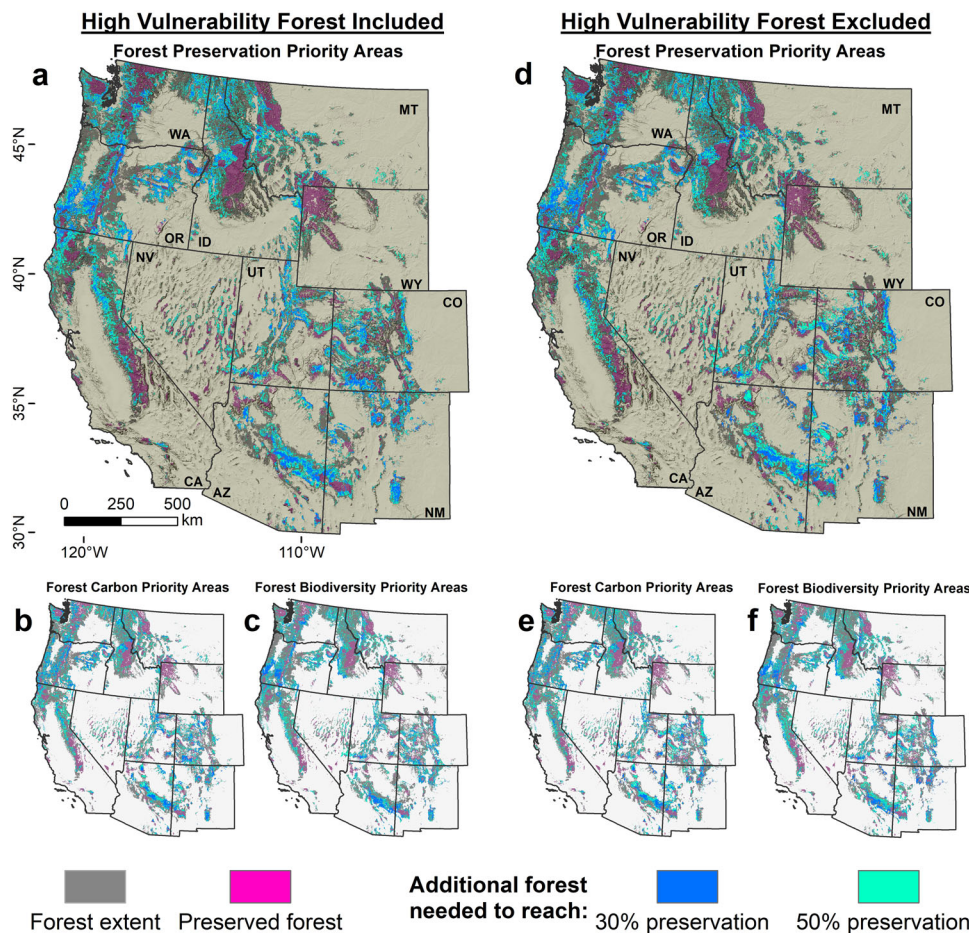


Fig. 4 Currently preserved forestlands and additional forestlands identified to meet preservation targets across the western US. Preservation targets include preserving 30 and 50% of forestland in each state. Preservation priority areas are presented for three scenarios that include **a, d** overall forest protection priority, as well as constituent **b, e** forest carbon priority and **c, f** forest biodiversity priority. High future vulnerability to drought or fire could destabilize forest carbon and biodiversity, thus protection priority areas were identified when both including (left columns) and excluding (right columns) forestland with high future vulnerability as simulated with CLM4.5. These forest priority areas were identified by sequentially combining the highest ranked forestlands within each state (Fig. 3) until each protection target was met. Currently protected forestlands shown here are GAP 1 and 2.

Table 2 Forestland simulated to have high future vulnerability to fire, drought, and fire or drought (sum) from 2020 to 2050 for each state in the western US.								
State	Forest		High future vulnerability to...					
			Fire		Drought		Either	
	Mha	%	Mha	%	Mha	%	Mha	%
AZ	7.67	26.0	0.14	1.8	2.80	36.5	2.93	38.2
CA	11.97	29.3	2.42	20.2	0.07	0.6	2.49	20.8
CO	9.50	35.2	2.09	22.0	2.84	29.9	4.77	50.2
ID	9.53	44.0	1.22	12.8	0.19	2.0	1.41	14.8
MT	9.57	25.1	1.59	16.6	0.11	1.1	1.70	17.8
NM	6.74	21.4	1.22	18.1	2.00	29.7	3.10	46.0
NV	3.60	12.6	0.03	0.8	0.65	18.1	0.68	18.9
OR	12.68	50.5	0.57	4.5	0.19	1.5	0.75	5.9
UT	6.93	31.5	0.77	11.1	1.73	25.0	2.41	34.8
WA	10.00	57.4	0.22	2.2	0.01	0.1	0.23	2.3
WY	4.27	16.9	1.56	36.5	0.67	15.7	2.22	52.0
Region	92.46	30.1	11.82	12.8	11.28	12.2	22.71	24.6

Forest vulnerability was assessed using simulations from the Community Land Model 4.5 conducted as part of an earlier study²⁵.

and state governments. We also found that private entities and tribal nations own about 25 and 10%, respectively, of regional high priority forest. Strategic Forest Reserves could be established on federal lands through executive action, regulation and rule-making and could be a low-cost way to simultaneously meet goals of protecting climate and biodiversity. Private and tribal lands present substantial opportunities for increasing carbon storage and protecting biodiversity through incentives, voluntary conservation measures, and fair market acquisition. To help meet preservation targets, federal and/or state governments could fund private entities and tribal nations to establish permanent conservation easements that protect carbon rich and biodiverse forests from resource extraction. Federal and state governments must lead efforts to protect forest carbon and biodiversity, though private entities and tribal nations could make important contributions to these efforts in the western US.

To qualify for inclusion in meeting preservation targets, lands should have protection that meets GAP 1 or 2 standards. These standards include permanent protection from conversion of natural land cover and a binding management plan that provides for maintaining a natural state (Supplementary Table 1). Lowering the standard of land protections to include GAP 3 or GAP 4 has gained interest, but it comes with a cost to species and

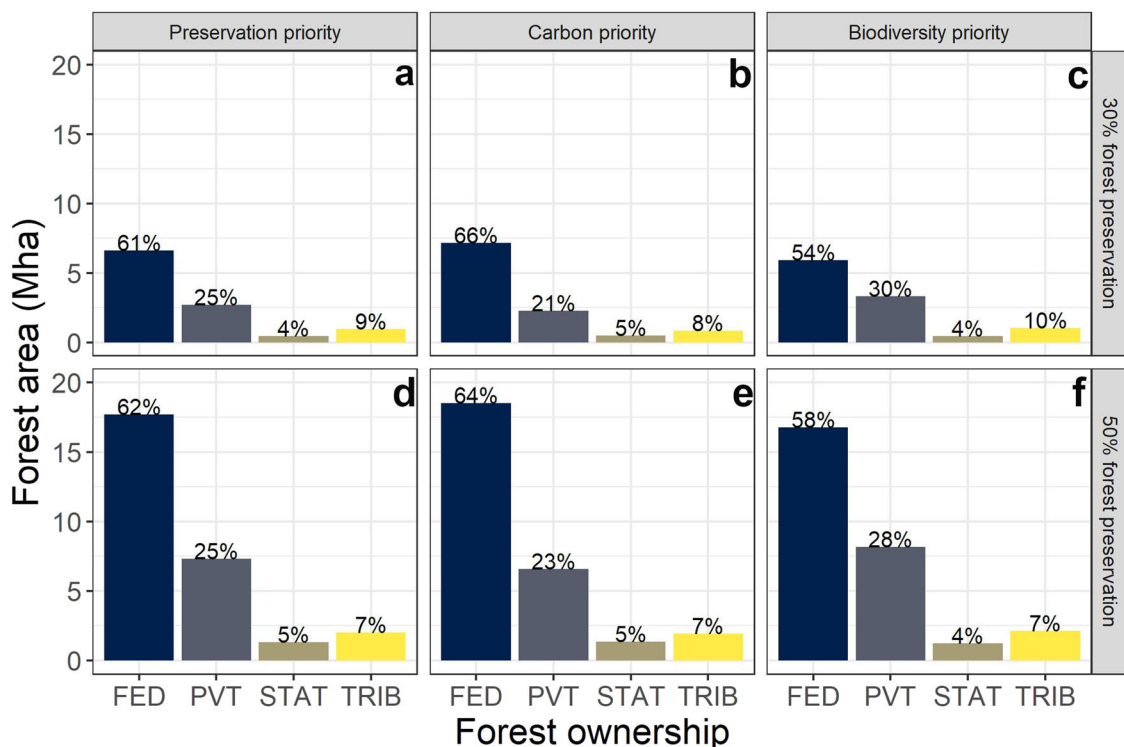


Fig. 5 Current ownership of forestlands in the western US needed to achieve two preservation targets. Forest ownership is presented for each preservation target (rows) and priority (columns). Preservation targets include **a–c** 30% and **d–f** 50%. Preservation priorities include **a, d** overall forest protection priority, **b, e** forest carbon priority, and **c, f** forest biodiversity priority. Forest owners include the U.S. Federal Government (FED), Private (PVT), State Governments (STAT), and Tribal Governments (TRIB). The figure excludes ownership classes that hold <2% of high preservation priority forestland (e.g., Non-Governmental Organizations). State-level summaries are provided in Supplementary Figs. 1 and 2. Similar patterns are evident when forestlands with high future vulnerabilities are included in the analysis (Supplementary Figs. 3–5). Land ownership data from the PAD-US²⁰.

ecosystem resilience. For example, livestock grazing covers a large portion (121 Mha) of federal public lands in the region^{31,32} and causes a major decrease in biodiversity due to processes such as degradation and competition³³. Logging also has deleterious impacts on biodiversity³⁴ and is a large source of carbon emissions in the western US, particularly in the Pacific Northwest^{35,36}. Lands used to meet preservation targets should have the same level of protection as Wilderness areas without grazing, and be permanently protected from roads, logging, and other development. Wilderness areas are cost-effective cornerstones of intact landscapes that provide clean water, fish and wildlife habitat, and climate change mitigation, while also supporting sustainable recreation economies worth billions of dollars annually^{28,30}. Recreation can be compatible with permanent protection so long as it does not include use of off-highway vehicles that have done considerable damage to ecosystems, fragmented habitat, and severely impacted animals including threatened and endangered species³⁷. Forestlands used to meet preservation targets should be managed for preservation of biodiversity, carbon, and water supplies by preserving older, mature forests and limiting resource extraction.

It is possible to elevate the preservation status of GAP 3 areas on federal lands by phasing out livestock grazing, mining, and logging and strengthening protection via administrative rule. Inventoried Roadless Areas (IRAs) are key GAP 3 federal areas that have already been identified and are available for permanent protection. The National Forest System (NFS) includes approximately 16.8 Mha of IRAs in the western US, or 71% of all IRAs on NFS lands in the nation³⁸. These are among the most wild and undeveloped areas not only in the nation but also within their respective states³⁸. We found that IRAs comprise 13–18% of

regional high priority forest and 24–28% of the high priority forest owned by the federal government, underscoring the crucial biodiversity and carbon benefits that these forests provide. IRAs currently provide clean drinking water for millions of people, support salmon populations and wildlife, and reduce isolation between protected areas^{39,40}. However, IRAs are an administrative designation of the USFS and not legislatively established by the US Congress, thus they are not considered part of the US system of protected areas (GAP 1 or 2)³⁸. There is also large potential to meet preservation targets by protecting un-inventoried roadless areas (e.g., ~2 Mha in Oregon), many of which are candidates for protection and contiguous with IRAs or existing protected areas.

Forest protection is the lowest cost climate mitigation option. Forest carbon accumulation should not be considered as an offset that allows additional fossil fuels to be burned. This is a weakness of current “net zero” accounting that should be modified by separating emissions reduction from carbon removal from the atmosphere⁴¹. Accounting and incentives could be applied to each approach to ensure the targets are met at local to international scales.

Establishment of Strategic Forest Reserves on non-federal public and private land could have important implications for international climate change mitigation agreements. For example, the Paris Agreement encourages trade in offsets. The trade in offsets has set up some potential problems, particularly when offsets are secured by storing more carbon on non-federal public land and private land but tallied twice, once when traded in markets (especially by international emitters) and again when reported in the national reporting instruments, such as NDC stock taking. Although the Paris Agreement is clear that double-counting must be avoided under Article 6,

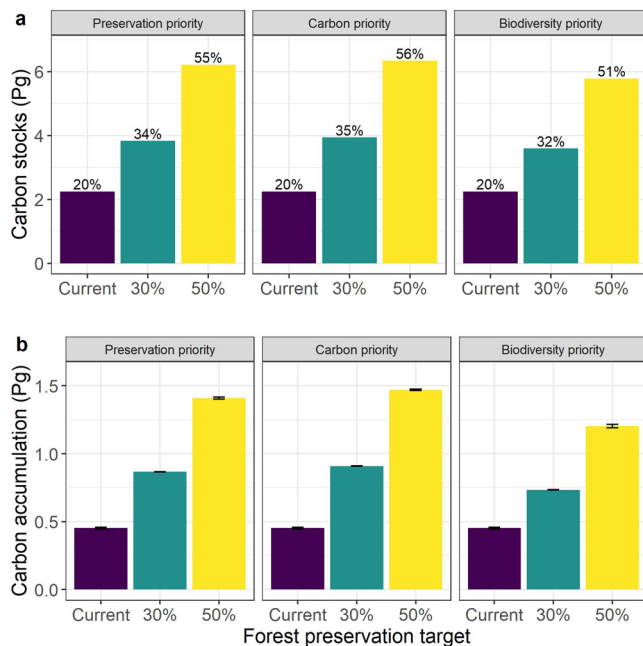


Fig. 6 Forest ecosystem carbon stocks and near-term carbon accumulation in current and potentially preserved forestlands by preservation target and priority. **a** Forest ecosystem carbon stocks including carbon in live and dead trees and soil. Black text above each bar denotes the percentage of total region-wide carbon stocks that is currently or would be preserved by reaching the preservation targets. **b** Forest carbon accumulation from 2020 to 2050 simulated using CLM4.5 forced by the IPSL and MIROC climate models assuming no harvest on preserved forestlands. Bars denote multi-model average carbon accumulation and error bars show the range among simulations. **a, b** The forestlands contributing to the preservation targets (e.g., 30%, 50%) include currently protected forestland. Currently preserved forestlands shown here are GAP 1 and 2. The forest ecosystem carbon stock data are from the USFS FIA²³ and the forest carbon accumulation data are from Buotte et al.⁶⁶.

the extent that double-counting is avoided depends on how accounting rules are operationalized. If emissions reductions are double-counted, it results in an increase in global emissions. If 40% of reserve actions are taken on non-federal public land and private land, this may have implications for emerging voluntary markets as the increased demand in markets could depress the value of those options. While economic and accounting issues are beyond the scope of this study, they exist and need to be addressed as policy commitments are made.

Our study shows that strategically increasing the extent of forest protection would help safeguard climate, biodiversity, and drinking water in the western US. Forest protection is needed to prevent forest loss and degradation, reduce greenhouse gas emissions, and maintain large carbon sinks. Avoiding loss and restoring carbon- and species-rich ecosystems is of highest importance for combined climate change mitigation and biodiversity protection⁸. We find that currently only ~20% of regional forest carbon stocks are in protected areas but that ~35% of carbon stocks could be protected by meeting the area-based 30 × 30 target. Protecting existing forest carbon stocks⁴² and allowing forests to continue to grow are effective means of preventing carbon emissions and removing carbon dioxide from the atmosphere (Supplementary Fig. 7)^{11,12,36,43}. Protecting high priority forests also creates co-benefits for adaptation to climate change for people and nature, such as higher genetic, species, and ecosystem diversities, resilience to climate extremes, and increased water availability²⁸.

Preserving high priority forests across the region would increase the amount of protected habitat for animal and tree species and promote landscape connectivity, thus helping maintain viable populations and ecological functions for climate adaptation^{44,45}. We found that generally less than 20% of each animal and tree species' regional forest habitat is currently protected, yet this could increase to ~30% and ~50% for each species if the 30 × 30 and 50 × 50 targets were met by preserving high priority forests. To ensure increased protection for the many facets of regional biodiversity, we prioritized forests for preservation within each ecoregion because these delineate distinct biotic (e.g., vegetation, wildlife) and abiotic (e.g., soils, climate) conditions^{46,47}. Distributing protection across ecoregions also promotes regional connectivity. Nevertheless, our current analysis did not incorporate metrics of forest connectivity³⁹ or fragmentation⁴⁸, thus isolated forest "patches" (i.e., one or several grid cells) were not ranked lower for preservation priority than forests that were part of large continuous corridors. Similarly, forest heterogeneity within each 1 km grid cell was not considered. Extensive road systems are common on private and federal public lands and fragment large expanses of forest that are recovering from a century of high-grade logging⁴⁸. Many of these fragmented forests are nevertheless important for carbon and biodiversity. Further efforts could combine landscape metrics with the forest PPR system to incorporate effects of connectivity and fragmentation (e.g., values of large contiguous patches versus smaller isolated patches of forest) on forest preservation priority. To best preserve biodiversity, new protected areas should be well-distributed across the region, include climate refugia^{49,50}, and have connecting corridors and road crossings to facilitate species movement and gene flow^{39,44,51}.

Climate and land use change have contributed to animal population declines in the western US^{34,52}, leading to an increase in species listed under federal protection⁵³. These environmental changes contributed to declining bird populations in about half of assessed species ($n = 108$) across the western US since the 1980s (mean trend = -0.84% per year)³⁴. For instance, destruction and fragmentation of old-growth forest habitat caused marbled murrelet and spotted owl populations to decline in the Pacific Northwest, leading them to be state and federally listed^{54,55}. We find that only ~15% of their forest habitat is currently protected and that preserving high priority forests would protect additional habitat that could aid population recovery. In addition to birds, large threatened carnivores such as gray wolves and Canada lynx would benefit from expanding regional forest protection. Gray wolves are a keystone species in the region and can trigger trophic cascades to plants with beneficial effects for biodiversity and streams⁵⁶. Canada lynx is a cold-adapted species and increases in temperature and wildfires threaten their persistence in parts of the western US⁵⁷. Animals at the southern edge of their species ranges may be particularly vulnerable to warming and thus protection of additional forest habitat may allow them to persist in higher elevations and move northward to a climate more suitable for survival⁵⁷. Expanding forest protection to meet preservation targets could help stem loss of regional biodiversity.

Besides safeguarding climate and biodiversity, preserving high priority forests would help protect clean water, thus providing a crucial ecosystem service given mounting concerns over water security in the western US^{58,59}. Anthropogenic warming is contributing to a megadrought in the Southwest⁶⁰ and lower mountain snowpack across much of the region⁶¹, with future warming expected to exacerbate water insecurity^{58,59,62}. We found that despite covering only 30% of the region, forests account for over half of the most important (top 75%) areas for regional surface drinking water. However, only 19% of these specific forestlands are currently protected (GAP 1 or 2). Forests

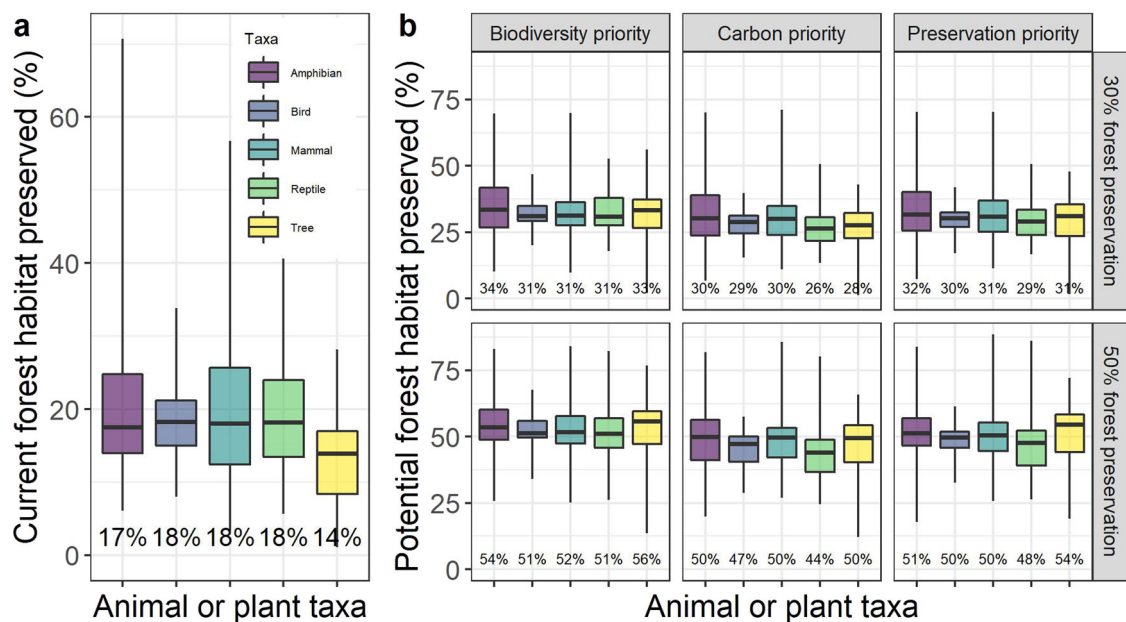


Fig. 7 Current and potential forest habitat preservation for animal and plant species summarized by taxa. **a** The percentage of each species' regional forested habitat that currently occurs on protected (GAP 1 or 2) forestlands in the western USA, grouped by taxa. **b** The percentage of each species' forested habitat that would be preserved based on several preservation targets (i.e., 30% or 50%) and priorities (i.e., carbon and/or biodiversity). Data for animal species habitat from the USGS GAP²¹ and for tree species habitat from the USFS FIA²³. For each boxplot, the intra-box line depicts the median, while the box extends from the 25th to 75th percentiles, and the whiskers extend from the 5th to 95th percentiles. Black text within each box denotes the median percentage of protected habitat across species of that taxa.

help ensure surface drinking water quality^{63,64} and thus meeting the preservation targets would provide co-benefits for water security in an era of growing need.

Forest vulnerability to future drought and fire should be considered when identifying areas for biodiversity and climate protection^{18,25,65}. Drawing on prior mechanistic model simulations from CLM4.5^{25,66}, we find the highest forest vulnerability is likely to occur in parts of the Southwest (e.g., New Mexico, Arizona, Colorado; 2.98–4.77 Mha forest) whereas the lowest forest vulnerability occurs in the Pacific Northwest (e.g., Oregon, Washington; 0.23–0.75 Mha forest). The Southwest is projected to become increasingly hotter and drier over the coming century, leading to continued increases in wildfire and drought-induced tree mortality that could destabilize forest carbon and biodiversity^{25,62,67–69}. Lower forest vulnerability in the Pacific Northwest means that permanence of protection is more likely to be achieved. From a policy perspective, highly vulnerable forests might not be high priorities for preservation because of potential shifts from forest to non-forest, though from a biodiversity perspective it is important to recognize that maintaining protection of these vulnerable forests may encourage species persistence in topographically complex climate refugia and facilitate species migration to areas that may be more suitable for survival⁴⁹.

Wildfire is an important ecological process and together with climate change is a key driver of ecosystem change. Annual burn area increased in the western US over the past three decades due to warming and drying^{70,71} and more human-caused ignitions⁷². As warm dry ecoregions continue to get warmer and drier^{60,62}, the fire regime may change to large high-severity fires that could convert more structurally homogeneous dry forests to non-forest ecosystems⁷³. In other ecoregions, fires may continue as a patchwork of mixed severities⁷⁴ that is better for forest regeneration and biodiversity⁷⁵. Moreover, mixed-severity fires mostly combust surface litter, duff, shrubs and small trees⁷⁶, with regional fires leading to lower carbon losses than harvest or beetles^{35,77,78}. Differences in fire regimes among ecoregions are

important parts of the decision-making process. For example, forests in parts of Montana and Idaho are projected to be highly vulnerable to future wildfire but not drought, thus fire-adapted forests climatically buffered from drought may be good candidates for preservation. Moist carbon rich forests in the Pacific Coast Range and West Cascades ecoregions are projected to be the least vulnerable to either drought or fire in the future²⁵, though extreme hot, dry, and windy conditions led to fires in the West Cascades in 2020. It is important to recognize that forest thinning to reduce fire risk has a low probability of success in the western US⁷³, results in greater carbon losses than fire itself, and is generally not needed in moist forests^{79–82}. Predicting future occurrence and timing of large disturbance events remains difficult, thus to better inform land management, efforts are needed to improve the ability of terrestrial biosphere models to simulate fire, drought, and other ecosystem processes^{83,84}.

In summary, we not only show that additional forest protection is needed to meet preservation targets (i.e., 30 × 30, 50 × 50) in the western US, but also determine where it would be most effective to preserve additional forest for climate mitigation and adaptation goals that minimize further species loss and ecosystem disruption. Our prioritization framework helps ensure preservation opportunities are distributed across the region, thereby protecting many facets of regional biodiversity, promoting connectivity, and providing local opportunities for engagement in decision-making. Drought and wildfire are becoming more common in this region and could destabilize forest carbon and biodiversity in some areas; thus, our framework incorporates ecosystem model simulations to identify forests with high future vulnerability and reduces their priority for protection. Meeting preservation targets would increase protection of forest carbon stocks and accumulation, animal and tree species' habitat, and surface drinking water in the western US. We focus on forestlands, but note these lands often include a mosaic of non-forest ecosystems (e.g., grasslands, wetlands, shrublands) that are also important for biodiversity preservation and carbon storage and accumulation.

Developing a broader landscape PPR system that includes non-forest ecosystems would require standardized spatial datasets related to current ecosystem carbon stocks (e.g. ref. ⁸⁵), habitat distribution for non-woody plant species and ideally invertebrate species, and multi-taxa simulations of potential future ecological dynamics. To help inform efforts to meet preservation targets, our new forest prioritization datasets can be combined with local knowledge and finer-scale local analyses using higher resolution spatial datasets. Next steps are to apply this framework across countries, include non-forest ecosystems, simulate future ecological conditions at higher spatial resolution, and account for how preservation prioritization is affected by uncertainty in underlying geospatial datasets. Natural climate and biodiversity solutions will be most effective when simultaneously implemented with ambitious reductions in all human-caused greenhouse gas emissions.

Methods

General data processing and analysis. An important step in spatial conservation prioritization is selecting a spatial resolution. High spatial resolution prioritization is needed to inform land management but spatial resolution is often constrained by the availability of existing species and ecosystem datasets⁸⁶. We derived the forest PPR using existing spatial datasets that were originally gridded at 30 m, 250 m, and 4000 m spatial resolution over the 92.46 Mha (924,600 km²) of forest land in the western US (Table 3). The coarsest resolution datasets were CLM4.5 simulations of future carbon accumulation and vulnerabilities from 2020 to 2050^{18,66}. It is crucial to consider future carbon accumulation and vulnerabilities when evaluating potential contributions of forests to climate change mitigation and biodiversity protection^{18,65}; however, CLM4.5 and other land surface model simulations are very computationally intensive and rarely available even at a 4000 m spatial resolution. The CLM4.5 simulations were thus the primary factor constraining the spatial resolution of our analysis. We selected a 1 km spatial resolution for this analysis as a balance between the fine resolution (30–250 m) and coarse resolution (4000 m) datasets currently available. While a finer spatial resolution (e.g., 250 m) would have been preferable, we were not confident that future forest carbon accumulation or vulnerabilities would be adequately captured by further down-scaled CLM4.5 simulations. Moreover, a 1 km resolution is amenable to large-scale conservation planning that considers multiple facets of biodiversity and ecosystem function across a subcontinent and lends itself to comparisons with other conservation prioritization datasets produced at 1 km resolution (e.g. ref. ³⁹). We performed the spatial analysis on a 1 km resolution grid in an Albers Equal Area projection using the statistical software R (version 4.0)⁸⁷. Data were processed using *raster*⁸⁸, *rgdal*⁸⁹, and *gdalUtils*⁹⁰, handled using *data.table*⁹¹, and visualized using *ggplot2*⁹² libraries. Maps were created using Esri ArcMap 10.8 software.

Assessing current preservation status of regional forests relative to pre-servation targets. We assessed the current extent and preservation status of forestland in the western US, as well as the additional forestland that would need to be protected to reach 30 and 50% preservation targets. We characterized the current forest extent using a 250 m resolution forest type dataset created by the United State Forest Service (USFS) Forest Inventory and Analysis (FIA) program using forest inventory, MODIS satellite, and ancillary geospatial datasets¹⁹. We characterized land preservation status using the Protected Areas Database of the United States (PAD-US version 2.1). The PAD-US is the official national inventory of protected areas in the United States and is produced by the USGS GAP²⁰. The PAD-US includes spatial information on the known protected areas for public and private lands in all 50 states, along with the status of each protected area according

to guidelines developed by the International Union for the Conservation of Nature (IUCN). Conservation status is characterized by GAP status codes that describe management intent to conserve biodiversity. GAP 1 and 2 signify areas with permanent protection from anthropogenic land cover conversion and management plans to maintain a fully or primarily natural state. The GAP 1 generally corresponds to IUCN Category Ia, Ib, and II, and GAP 2 to IUCN Categories III through VI (Supplementary Table 1). We clipped the forest extent and PAD-US datasets to the region, majority aggregated forest extent to 1 km resolution, and gridded the PAD-US GAP status code at 1 km resolution using the lowest GAP status in the case of overlap. We then assessed the total land and forest area of each state that currently has permanent protection (GAP 1 or 2). Moreover, we computed the additional area needed if the goal is to protect 30 and 50% of total land and forest area in each state.

Prioritizing forestlands for preservation based on carbon and/or biodiversity.

After identifying the additional forest area needed to reach 30 and 50% preservation targets, we then sought to prioritize unprotected forestlands for preservation based on carbon and/or biodiversity (three scenarios). We derived both carbon and biodiversity priority ranks for each forested grid cell in the region and also derived a forest preservation priority rank (“forest PPR”) for each grid cell that incorporated metrics of both forest carbon and biodiversity.

We defined forest carbon metrics that included both current forest ecosystem carbon stocks and simulated near-future forest carbon accumulation from 2020 through 2050. The USFS FIA mapped forest ecosystem carbon stocks at 250 m resolution across the contiguous U.S. using inventory plot, MODIS satellite, and ancillary geospatial datasets²³. This dataset reflects forest conditions during the period from 2000 to 2009 and is the most recent spatial dataset on forest ecosystem carbon stocks available from the USFS FIA. We determined current forest carbon stocks for each 1 km grid cell by summing the carbon stocks of the 16 underlying 250 m resolution grid cells.

Forest carbon accumulation was simulated across the western US from 1979 to 2099 by Buotte, et al.²⁵ using a modified version of the CLM4.5²⁴. The CLM is the land surface component of the Community Earth System Model⁹³, and calculates multiple biophysical and biogeochemical processes, including surface heat fluxes, photosynthesis, evaporation, transpiration, carbon allocation to plant tissue, decomposition, and nitrogen cycling. The CLM4.5 was modified to represent 13 coniferous forest types commonly found in the region, and to allow soil moisture stress to increase leaf shed²⁵. Forest carbon cycling was simulated at ~4 km resolution for two time periods: 1979–2014 and 2015–2099. The historical simulations (1979–2014) were performed using historical CO₂ concentrations, climate, and harvest such that the simulations represent present-day stand ages. The future simulations (2015–2099) were forced by downscaled climate data from the IPSL-CM5A-MR and MIROC5 general circulation models following representative concentration pathway 8.5 concentrations of anthropogenic greenhouse gas emissions. Previous comparisons between simulation output and observational data sets showed that simulated aboveground carbon was highly correlated ($R^2 > 0.80$) with observation-based estimates across forest types and ecoregions²⁵. Potential future forest carbon accumulation was estimated by running the CLM4.5 with no harvest after 2014 and then summing annual net ecosystem production from 2020 onward, thus allowing forest carbon accumulation to be determined by forest type, soil properties, climate, and wildfires. We estimated potential forest carbon accumulation for each 4 km grid cell by summing annual net ecosystem production from 2020 to 2050 and then disaggregated these data to 1 km resolution for analysis.

We defined metrics of biodiversity using tree species richness and terrestrial vertebrate species richness by taxa. The USFS FIA mapped live tree basal area for 324 tree species at 250 m resolution across the contiguous U.S. using inventory plot data along with MODIS satellite and environmental datasets²². This is a subset of the over 1000 tree species found in the USA. The USGS GAP modeled current habitat distribution for 1718 terrestrial vertebrate species at 30 m resolution across the contiguous U.S. using a suite of geospatial predictors²¹. This nominally includes

Table 3 Spatial datasets used to derive the forest preservation priority ranking system.				
Category	Metric	Period	Original resolution (m)	Reference
Ecosystem	Ecoregions (level 3)	--	--	46
	Forest extent	2000–2004	250	19
Biodiversity	Amphibian species habitat (n = 97 species)	2000	30	21
	Bird species habitat (n = 483 species)	2000	30	21
	Mammal species habitat (n = 339 species)	2000	30	21
	Reptile species habitat (n = 170 species)	2000	30	21
	Tree species habitat (n = 78 species)	2000–2009	250	22
	Forest carbon stocks	2000–2009	250	23
Carbon	Forest carbon accumulation	2020–2050	4000	25
	Vulnerability to drought	2020–2050	4000	25
Vulnerability	Vulnerability to fire	2020–2050	4000	25

all terrestrial amphibian, bird, mammal, and reptile species found during summer and/or winter in the contiguous U.S., though stopover habitats for migratory species are not included. We selected the tree and vertebrate species that occurred in the study domain, converted live tree basal area to species presence or absence, and then aggregated each species habitat map to 1 km resolution such that a grid cell was considered to have habitat if it included any modeled habitat at a finer spatial resolution. For each species, we masked out habitat on non-forelands, resulting in our analysis including 78 tree species and 1089 terrestrial vertebrate species. We then estimated tree and vertebrate taxa (e.g., amphibian) species richness by counting the number of species with habitat in each forested grid cell. We did not include terrestrial invertebrates, non-woody plants, or non-vascular plants because there was not the necessary spatial data.

Recognizing the importance of spatially distributed preservation¹¹, we computed forest carbon, biodiversity, and preservation priority ranks for each grid cell relative to other grid cells in the same ecoregion within each state. There are 35 level III ecoregions in our study domain that represent land areas with distinct biotic (e.g., vegetation, wildlife) and abiotic (e.g., soils, climate) conditions⁴⁶. The forest carbon priority ranks were derived by computing for each grid cell the percentile ranks of current ecosystem carbon stocks and near-future carbon accumulation, summing the resulting ranks, and then re-ranking grid cells based on these summed ranks. The forest biodiversity priority ranks were derived in a similar manner using vertebrate and tree species richness ranks, with vertebrate species richness ranks computed from the ranked sum of percentile ranks for each vertebrate taxa (i.e., amphibians, birds, mammals, and reptiles). Finally, the forest preservation priority rank was derived for each grid cell as the ranked sum of forest carbon and biodiversity priority ranks.

Ongoing warming and drying could increase forest vulnerability to drought or fire in parts of the western US thereby destabilizing forest carbon and biodiversity^{25,65}. Water-limited forests in the Rocky Mountains, Southwest, and Great Basin regions were expected to be the most vulnerable to future drought-related mortality and the Sierra Nevada and portions of the Rocky Mountains were expected to be most vulnerable to fire in the next decades²⁵. Therefore, we derive and compare preservation priority rankings with and without forests with high future vulnerability to drought or fire.

Determining ownership of forestlands with high preservation priority. We determined who currently owns unprotected forestlands that have the highest priority for meeting preservation targets. The PAD-US (version 2.1) dataset includes the geographic boundaries of public lands and their ownership (e.g., Federal Government, State Government), as well as of private conservation lands that are voluntarily provided by authoritative sources²⁰. This dataset does not include the geographic boundaries of other private lands, but these boundaries are included in an older, off-shoot version of the dataset created by the Conservation Biology Institute (CBI) (i.e., PAD-US CBI Edition version 2)⁹⁴. We gridded both versions of the PAD-US dataset at 1 km resolution and filled data gaps in the PAD-US using the PAD-US CBI Edition. The PAD-US also is occasionally missing information on who owns public lands but the database generally has information on their management type. In these cases, we filled unknown ownerships with the corresponding management type. We then extracted ownership information for each grid cell that was identified as having high priority for meeting each preservation target and priority. Lastly, for each preservation target and priority we computed the total area of these high priority forestlands that occurred in each ownership category.

Evaluating how meeting preservation targets contributes to protecting forest carbon, biodiversity, and surface drinking water. We evaluated current protection (GAP 1 or 2) of forest carbon, biodiversity, and important areas for surface drinking water as well as how protection would increase by meeting each preservation target if forests were prioritized for carbon and/or biodiversity. Specifically, we estimated total current ecosystem carbon stocks and potential near term carbon accumulation (2020–2050) for currently protected forestlands and if preservation targets were met following each prioritization scenario. We again relied on carbon stock and accumulation datasets from the USFS FIA²³ and Community Land Model 4.5 simulations⁶⁶, respectively. For biodiversity, we determined the current amount of each animal and tree species' habitat^{21,22} that occurs in regional forestlands, as well as the percentage each species' forest habitat that is currently protected. We then determined how much of each species' forest habitat would be protected by reaching the preservation targets using each prioritization scenario and summarized these data by taxa (i.e., amphibians, birds, mammals, reptiles, and trees). We also assessed how meeting the preservation targets would contribute to protection of forest habitat for four select threatened animal species, including grey wolves (*Canis lupus*), Canada lynx (*Lynx canadensis*), marbled murrelet (*Brachyramphus marmoratus*), and spotted owl (*Strix occidentalis*). Moreover, we assessed current and potential protection of the most important areas (top 75%) for surface drinking water in the region using the Forests to Faucets (version 2) dataset from the USFS⁹⁵. The USFS estimated surface drinking water importance for each of the country's sub-watersheds based on surface water supply, flow paths, and consumer demand. We clipped this dataset to the study domain, rasterized the Important Areas for Surface Drinking Water attribute at 1 km resolution, and identified the most important areas (top 75%) for surface drinking water in the

region. We then used spatial overlays to assess the extent to which the most important areas occurred on current protected forestlands and potential future protected lands under each preservation target and prioritization scenario.

Data availability

The forest preservation priority datasets generated as part of this research are publicly archived with PANGAEA (<https://www.pangaea.de/>). The datasets that support the findings of this study are publicly available. The Protected Area Database of the United States (PAD-US v. 2.1) dataset is available from the USGS (<https://www.sciencebase.gov/>). The forest extent dataset is available from the USFS (<https://data.fs.usda.gov/geodata/>). The forest ecosystem carbon stock dataset is available from the USFS (<https://doi.org/10.2737/RDS-2013-0004>). The CLM4.5 forest carbon cycle simulations are available from the ORNL DAAC (<https://doi.org/10.3334/ORNLDAAAC/1662>). The vertebrate species habitat data are available from the USGS (<https://gapanalysis.usgs.gov/>). The tree species basal areas data are available from the USFS (<https://doi.org/10.2737/RDS-2013-0013>). The surface drinking water data are available from the USFS (https://www.fs.fed.us/ecosystems/services/FS_Efforts/forests2faucets.shtml).

Code availability

All custom scripts written for this analysis are publicly archived on GitHub (https://github.com/ecospatial-services/wus_forest_conservation).

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Author contributions

B.E.L., L.T.B., and P.C.B. designed the study. Community Land Model output was provided by P.C.B. Data acquisition, analysis, and visualization were conducted by L.T.B. Ideas were contributed by W.J.R. and D.J.M. Writing was led by B.E.L. and L.T.B. with input and edits from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Beverly E. Law.

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Creating Strategic Reserves to Protect Forest Carbon and Reduce Biodiversity Losses in the United States

Beverly E. Law ^{1,*}, William R. Moomaw ², Tara W. Hudiburg ³, William H. Schlesinger ⁴, John D. Sterman ⁵ and George M. Woodwell ⁶

¹ Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

² The Fletcher School and Global Development and Environment Institute, Tufts University, Medford, MA 02155, USA; william.moomaw@tufts.edu

³ Department of Forest, Rangeland, and Fire Sciences, University of Idaho, Moscow, ID 83844, USA; thudiburg@uidaho.edu

⁴ Cary Institute of Ecosystems Studies, Millbrook, NY 12545, USA; schlesingerw@caryinstitute.org

⁵ MIT Sloan School of Management, Massachusetts Institute of Technology, Cambridge, MA 02139, USA; jsterman@mit.edu

⁶ Woodwell Climate Research Center, Falmouth, MA 02540, USA; gwoodwell@woodwellclimate.org

* Correspondence: bev.law@oregonstate.edu

Abstract: This paper provides a review and comparison of strategies to increase forest carbon, and reduce species losses for climate change mitigation and adaptation in the United States. It compares forest management strategies and actions that are taking place or being proposed to reduce wildfire risk and to increase carbon storage with recent research findings. International agreements state that safeguarding biodiversity and ecosystems is fundamental to climate resilience with respect to climate change impacts on them, and their roles in adaptation and mitigation. The recent Intergovernmental Panel on Climate Change report on impacts, mitigation, and adaptation found, and member countries agreed, that maintaining the resilience of biodiversity and ecosystem services at a global scale is “fundamental” for climate mitigation and adaptation, and requires “effective and equitable conservation of approximately 30 to 50% of Earth’s land, freshwater and ocean areas, including current near-natural ecosystems.” Our key message is that many of the current and proposed forest management actions in the United States are *not consistent* with climate goals, and that preserving 30 to 50% of lands for their carbon, biodiversity and water is feasible, effective, and necessary for achieving them.

Keywords: carbon dioxide; biodiversity; preservation targets; climate mitigation; climate adaptation; deforestation proforestation



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1. Introduction

The climate is changing rapidly at an accelerating rate in every region of the planet. Immediate and sustained actions are needed to reduce dangerous and amplifying warming feedbacks. To avoid catastrophic, irreversible release of heat trapping methane and carbon dioxide, it is essential that natural land and ocean sinks remove and store substantially more atmospheric carbon dioxide to halt Arctic warming that is increasing over 3 times faster than the planetary average [1,2]. The next 10 to 30 years are a critical window for climate action, when severe ecological disruption is expected to accelerate [2–4]. Analysis of country-based pledges to reduce emissions in the nationally determined contributions (NDCs) suggests that emissions reductions should increase by 80% above the combined NDCs to keep temperature increases below the proposed 2 °C limit [5], and even greater reductions are required to remain below 1.5 °C. It is worth noting that these limits are warmer than the current temperature increase of 1.1 °C, meaning that the consequences for all climate-related changes will be more severe if those limits are reached or breached.

Forests play an important role in storing carbon, along with oceans, wetlands, and peatlands. Forests account for 92% of all terrestrial biomass globally, storing approximately 400 gigatons carbon [6]. Despite regional negative effects of climate change on the net amount of carbon removed from the atmosphere annually by land ecosystems, their removal of carbon dioxide from the atmosphere has remained fairly constant over the last 60 years at about 31% of emissions, with forests contributing the most [7]. Forests can play an important role in capturing and storing immense amounts of carbon. Reducing emissions from energy systems, deforestation, forest degradation, and other sources while increasing accumulation of carbon by natural systems are the primary means by which we will control atmospheric carbon dioxide (CO₂).

Here we present the status of science on forest management to mitigate climate change, and protect water and biodiversity in the United States, as well as the importance of Strategic Reserves to accomplish national and international goals of reducing biodiversity losses, and increasing the forest carbon reservoirs using natural climate solutions.

As discussed in more detail below, functionally separating carbon, water, and biodiversity and considering them independently leads to actions that inadvertently reduce the values of each, and can increase carbon emissions. This is why the 2021 report by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services and the Intergovernmental Panel on Climate Change (IPBES-IPCC) [8] stresses that climate change and biodiversity need to be examined together as parts of the same complex problem when developing climate mitigation and adaptation solutions [9,10].

The IPCC Assessment Report 6 confirms the findings of a growing body of research that maintaining ecosystem integrity and its biodiversity are essential to an effective response to a changing climate [1]. The Summary for Policy Makers, which is approved line by line by all IPCC member governments *including the United States*, summarizes current adaptation and mitigation climate science as follows:

“Summary for Policy Makers.D.4 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).”

“Summary for Policy Makers.D.4.1 Building the resilience of biodiversity and supporting ecosystem integrity can maintain benefits for people, including livelihoods, human health and well-being and the provision of food, fibre and water, as well as contributing to disaster risk reduction and climate change adaptation and mitigation.” The formal definition of ecosystem integrity refers to the “ability of ecosystems to maintain key ecological processes, recover from disturbance, and adapt to new conditions.”

Many current U.S. forest management practices that optimize resource extraction are inconsistent with this scientific consensus, are worsening both climate change and biodiversity loss, and decreasing multiple ecosystem services of U.S. forests. Strategies to mitigate and adapt to climate change have been proposed by scientists [8] and policy-makers or those implemented by land managers and industries, and recent research has quantified their effectiveness and inadequacies. The strategies include:

- Avoiding deforestation and forest degradation—keeping forests intact;
- Reducing carbon loss by increasing harvest intervals and decreasing harvest intensity;
- Carbon storage in long-lived forest products (e.g., in combination with shorter harvest intervals);
- Burning trees for bioenergy;
- Thinning to reduce fire risk or severity and thus carbon losses.

We provide a synthesis of literature on evaluation of these strategies, as well as the importance of protecting the many values of forests, including carbon accumulation, biodiversity, and water availability. We focus on two regions of the U.S., the Pacific Coast, and southeast regions, which account for about 45% of the total U.S. forests’ living biomass and removals by harvest [11].

2. Strategies

2.1. Avoid Deforestation and Forest Degradation, and Decrease Harvest-Related Carbon Losses

Primary forests are defined as forests composed of native species in which there are no clearly visible indications of human activities and ecological processes have not been significantly disturbed [12]. Multiple values are found at higher levels in intact forests of a given type, including habitat for endangered species, water security, and accumulated forest carbon stocks that keep carbon out of the atmosphere, and provide moderation of air and surface temperature through evapotranspiration [13,14]. Only 7% of the forest area in the U.S. is considered intact, with the exception of the nearly 68,000 km² Tongass National Forest in southeast Alaska, of which about 20,000 km² is defined as productive old-growth. Most of its 900 watersheds are near natural conditions, and its carbon-rich rainforests have similar carbon densities to the Pacific Northwest U.S. rainforests [15–17]. It is the largest intact temperate rainforest in the world, yet logging of old-growth continues while the USDA is in the process of restoring the roadless protections. The 2001 Roadless Rule prohibits road construction and timber harvesting on almost 30 million hectares of inventoried roadless areas (IRAs) on National Forest System lands, and is intended to provide protection for multiple uses.

Federal lands managed by the U.S. Forest Service (FS), the National Forest System (NFS), and the Bureau of Land Management (BLM) are managed under a multiple use—sustained yield model [18,19]. The statute directs the agencies to “balance multiple uses of their lands and ensure a sustained yield of those uses in perpetuity” [20]. The forest management plans describe where timber harvesting may occur as well as measures of sustainable harvest levels. The balance of these uses on federal lands has been an ongoing point of contention with the public [20].

Most timber harvesting occurs on private lands [11], however, there is increasing pressure to allow more timber cutting on federal lands. In the Pacific Northwest (PNW), removals declined on public lands after the peak in the late 1980s [11], partly due to implementation of the Northwest Forest Plan on public lands that aimed to protect endangered species in old-growth forests. The result was a strong increase in forest carbon accumulation on public lands over the next 17 years, while private lands remained near zero carbon accumulation, accounting for losses due to wildfire and harvesting [21].

Most forests in the U.S. have been harvested multiple times, and many managed forests are harvested well before reaching maturity. As of 2014, 51% of timber land in the south was less than 40 years old compared with 20% in the north and 22% in the west. In contrast, 56% of northern timber land was more than 60 years old, compared with 27% in the south and 69% in the west [11]. Since then, harvest ages have decreased in some cases because of changes in forest products (e.g., increasing production of cross-laminated timber, wood for bioenergy), thinning to reduce wildfire risk or severity, or removals after fire or beetle kill. Consequently, forest carbon densities are much lower than their potential, and could accumulate much more carbon and avoid carbon emissions associated with harvest [22].

Evaluation of strategies to mitigate climate change showed that forests can store more carbon if the harvest interval is lengthened on private lands and harvest is reduced on public lands in Oregon (Figure 1) [15]. A comparison of strategies showed that reducing harvest by half on public forests to allow them to continue to accumulate carbon (cumulative net ecosystem carbon balance, NECB) while increasing harvest rotation age from 40 years back to 80 years in forests with relatively low vulnerability to drought and fire under future climate conditions contribute the most to increasing forest carbon and reducing emissions. Far less effective are reforestation—just one-third as much carbon accumulation—and lastly, afforestation—just one-tenth as much carbon accumulation—that can compete with land usage for agriculture and urban development. This finding is supported by a recent National Academy report on “Negative Emissions” or atmospheric CO₂ removal options that finds the potential for afforestation and reforestation in limiting atmospheric CO₂ to be modest [23].

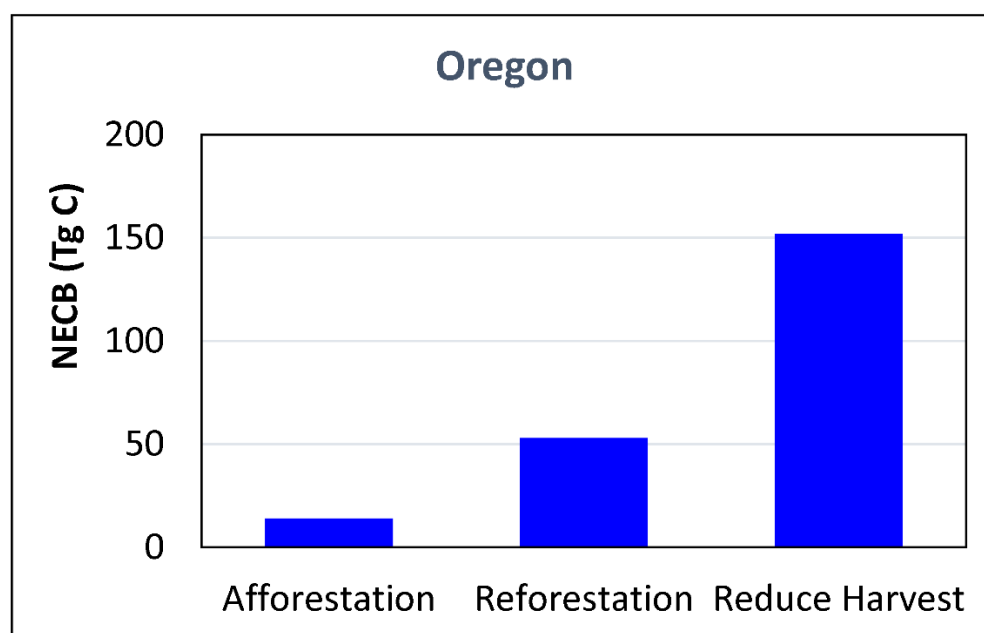


Figure 1. Land-use strategies to mitigate climate change across Oregon. Values on *y*-axis are cumulative change in net ecosystem carbon balance (NECB) from 2015 to 2100. Reduced harvest is a combination of restricted harvest by half on federal lands, and increased harvest intervals to 80 years on private lands. Data are from observation-based modeling [15].

A global study of 48 forests of all types found that among “mature multi-aged forests” half the living aboveground carbon was in the largest diameter 1% of the trees [24]. A study of six National Forests in Oregon found that trees of 53 cm DBH or greater comprised just 3% of the total stems, but held 43% of the aboveground carbon [25]. The U.S. Forest Service decided to drop a restriction on harvesting large trees in this category (Federal Register Document 2021-00804; <https://www.govinfo.gov/content/pkg/FR-2021-01-15/pdf/2021-00804.pdf>, accessed 20 April 2022), an action at odds with climate and biodiversity goals. Contrary to common belief, older forests continue to accumulate large quantities of carbon in trees and forest soils. Globally, forests older than 200 years continue to accumulate carbon at a rate of 1.6 to 3.2 Mg C ha^{−1} yr^{−1} [26].

Thus, temperate forests with high carbon and lower vulnerability to mortality have substantial additional capacity for climate mitigation. On a global level, it is estimated that forests could hold twice as much carbon as they currently do if managed differently [27]. While planting trees is desirable, that will contribute relatively little to carbon accumulation out of the atmosphere by 2100 compared to reducing harvest (See Figure 1). For example, if the Bonn Challenge of restoring 350 Mha by 2030 is given to natural forests, they would store an additional 42 Pg C by 2100, whereas giving the same area to plantations would store only 1 Pg C [15,28].

The potential for additional carbon accumulation is also being degraded by current management practices [29]. It was estimated that the “current gross carbon sink in forests recovering from harvests and abandoned agriculture to be −4.4 GtC/y, globally” [30]. This is more than the current difference between anthropogenic emissions and land and ocean annual accumulation out of the atmosphere (3.4 GtC/y) [7].

Mature and old forests generally store more carbon in trees and soil than young forests, and continue to accumulate it over decades to centuries [15,16,25] making them the most effective forest-related climate mitigation strategy. For example, restricting harvest by half on federal forests and changing the harvest cycle to 80 years across Oregon would increase forest carbon stocks 118 Tg C by 2100 [15,16,25]. Converting mature and older forests to younger forests results in a significant loss of total carbon stores, even when wood products are considered [31,32]. For example, a comparison of carbon stored in an unharvested

versus harvested mature forest using the Forest-GHG life cycle assessment model to track harvested carbon from forest to landfill [31] shows that the unharvested forest has a much higher carbon density 120 years later, even when carbon in wood products is summed with the post-harvest carbon storage (Figure 2).

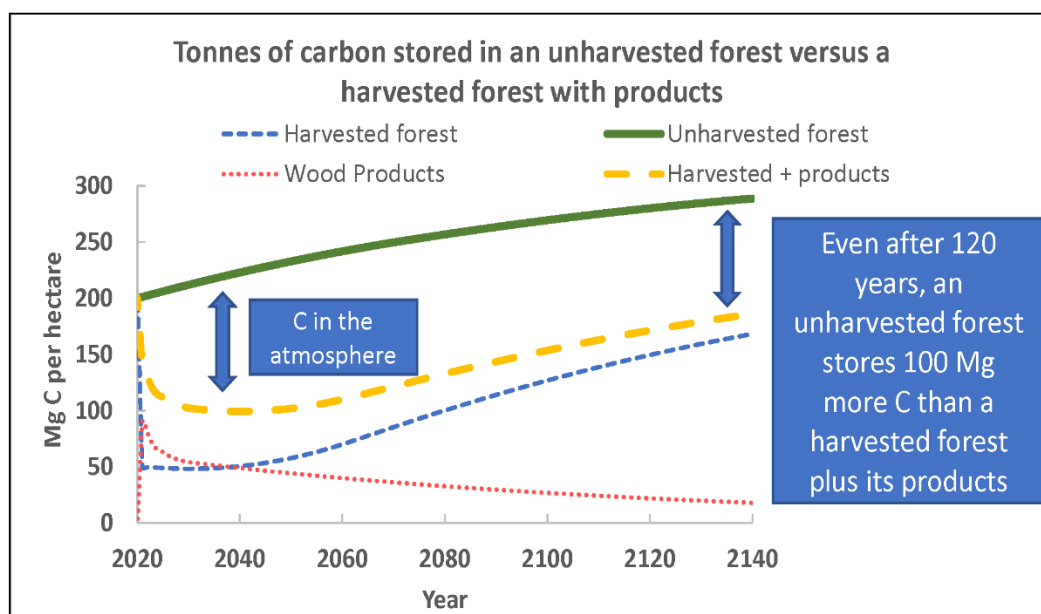


Figure 2. A mature forest with a carbon density of 200 tons of carbon per hectare (green line) is harvested (blue line) in 2020. This results in an immediate reduction of live tree carbon stocks. Approximately half of the aboveground carbon is removed and taken to the mills (as wood) while the other half remains behind in slash piles (leaves, bark, branches, etc.) and in the dead belowground roots. The slash is burned on-site and the carbon is immediately emitted to the atmosphere. The roots decompose over the next few decades, emitting carbon to the atmosphere. The carbon taken to the mill as wood is processed into short- and long-term wood products (red line), that decay over years to centuries, eventually returning the carbon to the atmosphere. Estimates comparing the carbon benefits of wood products to alternative materials have been found to overestimate the benefit by factors of between 2- and 100-fold by not counting the full life cycle carbon and the shorter durability of wood relative to alternative materials [33].

2.2. Harvesting Forests for Bioenergy Production

Utilizing wood biomass as a substitute for coal *increases* CO₂ emissions and *worsens* climate change for many decades or more [34]. Meeting U.S. national emissions reduction goals requires net emissions to drop by approximately 50% by 2030, reach net zero by 2050, and be net negative beyond 2100 [2,4].

Although wood and coal release comparable amounts of carbon dioxide per unit of primary energy [35], wood chips and pellets burn less efficiently. For example, a 500-megawatt power plant burning wood pellets emits an estimated 437,300 tons of CO₂-C annually, whereas the same plant burning coal would emit 392,000 tons/year [36]. The situation is worse if wood displaces other fossil fuels: wood releases about 25% more CO₂ per unit of primary energy than fuel oil, and about 75% more CO₂ than fossil (natural) gas [35]. Further, greenhouse gas emissions from the wood supply chain exceed those of the coal supply chain: Approximately 27% of harvested carbon equivalent is used to produce dry pellets [37], while coal processing adds just about 11% to emissions [38]. Therefore, the immediate impact of wood bioenergy is an increase in CO₂ emissions, creating a “carbon debt”, even when wood displaces coal, the most carbon intensive fossil fuel. The harvested forests can regrow, repaying the debt, but regrowth is uncertain and takes time.

Regrowth takes time: The time between the combustion of wood and the potential, *eventual* removal of that excess CO₂ by regrowth is known as the carbon debt payback time [39]. For forests in the eastern U.S., which supply much of the wood for pellet production and national and international export, carbon debt payback times range from many decades to a century or more, depending on forest age at harvest, species, and climate zone [38,40].

Carbon debt payback times are longer in the young forests prevalent in the U.S. because harvesting wood from growing forests also prevents the CO₂ removal that would have occurred had trees not been harvested and burned [41]. If a 40-year-old forest was harvested and burned, releasing its carbon immediately to the atmosphere, under ideal conditions, it would take another 40 years to remove the added carbon from the atmosphere and restore the initial carbon stocks in the regrown forest, known as “slow in, fast out” [42–44]. However, if not harvested, the same forests would have continued to accumulate significantly more carbon, thereby further reducing the amount in the atmosphere. Shorter rotation times between harvests for bioenergy leave the greatest amount of CO₂ in the atmosphere [40].

Forests of the southeastern and southcentral U.S. are the largest source of wood for commercial scale bioenergy, mostly for use in Europe. If allowed to continue growing (proforestation), they could remove significant additional atmospheric CO₂ and accumulate the additional carbon in trees and soils [22].

Note that wood bioenergy harvest worsens climate change even if the harvested forests are managed sustainably, because the average total stock of carbon on the land is lower than prior to harvest, and the carbon lost from the land is added to the atmosphere, worsening climate change [38,40]. Moreover, reforestation following harvest of a diverse bottomland hardwood forest that provided habitat for multiple animal species would, in most cases, be converted to a pine monoculture plantation.

Eventual carbon neutrality does not mean *climate neutrality*. The excess CO₂ from wood bioenergy worsens global warming immediately upon entering the atmosphere. The harms caused by that additional warming are not undone even if regrowth eventually removes all the excess CO₂. Global average surface temperatures will not immediately return to previous levels and may persist for a millennium or more [45]. The Greenland and Antarctic ice sheets melt faster, sea level rises higher, accelerated permafrost thaw releases more methane, wildfires become more likely, storms intensify more, and extinction is greater than if the forest had not been harvested and the wood had not been burned [45]. Recent simultaneous temperature spikes of tens of degrees Celsius in the Arctic and Antarctica demonstrate that unprecedented warming signals are already occurring, resulting in some changes, such as sea-level rise, that are irreversible for centuries to millennia [1]. Even eventual full forest recovery and carbon removal will not replace lost ice, lower sea level, undo climate disasters, or bring back communities lost to floods or wildfires.

2.3. Thinning to Reduce Fire Risk or Severity and Carbon Loss

2.3.1. Broad-Scale Thinning to Reduce Fire Severity Conflicts with Climate Goals

A reaction to the recent increase in the intensity and frequency of wildfires is to thin forests to reduce the quantity of combustible materials. However, the amount of carbon removed by thinning is much larger than the amount that might be saved from being burned in a fire, and far more area is harvested than would actually burn [42,46–49]. Most analyses of mid- to long-term thinning impacts on forest structure and carbon storage show there is a multi-decadal biomass carbon deficit following moderate to heavy thinning [50]. For example, thinning in a young ponderosa pine plantation showed that removal of 40% of the tree biomass would release about 60% of the carbon over the next 30 years [51]. Regional patchworks of intensive forest management have increased fire severity in adjacent forests [49]. Management actions can create more surface fuels. Broad-scale thinning (e.g., ecoregions, regions) to reduce fire risk or severity [52] results in more carbon emissions than fire, and creates a long-term carbon deficit that undermines climate goals.

As to the effectiveness and likelihood that thinning might have an impact on fire behavior, the area thinned at broad scales to reduce fuels has been found to have little relationship to area burned, which is mostly driven by wind, drought, and warming. A multi-year study of forest treatments such as thinning and prescribed fire across the western U.S. showed that about 1% of U.S. Forest Service treatments experience wildfire each year [53]. The potential effectiveness of treatments lasts only 10–20 years, diminishing annually [53]. Thus, the preemptive actions to reduce fire risk or severity across regions have been largely ineffective.

Effective risk reduction solutions need to be tailored to the specific conditions. In fire-prone dry forests, careful removal of fuel ladders such as saplings and leaving the large fire-resistant trees in the forest may be sufficient and would have lower carbon consequences than broad-scale thinning [54]. The goals of restoring ecosystem processes and/or reducing risk in fire-prone regions can be met by removing small trees and underburning to reduce surface fuels, not by removal of larger trees, which is sometimes done to offset the cost of the thinning. With continued warming and the need to adapt to wildfire, thinning may restore more frequent low-severity fire in some dry forests, but could jeopardize regeneration and trigger a regime change to non-forest ecosystems [53].

While moderate to high severity fire can kill trees, most of the carbon remains in the forest as dead wood that will take decades to centuries to decompose. Less than 10% of ecosystem carbon enters the atmosphere as carbon dioxide in PNW forest fires [21,46]. Recent field studies of combustion rates in California's large megafires show that carbon emissions were very low at the landscape-level (0.6 to 1.8%) because larger trees with low combustion rates were the majority of biomass, and high severity fire patches were less than half of the burn area [55,56]. These findings are consistent with field studies on Oregon's East Cascades wildfires and the large Biscuit Fire in southern Oregon [57,58].

To summarize, harvest-related emissions from thinning are much higher than potential reduction in fire emissions. In west coast states, overall harvest-related emissions were about 5 times fire emissions, and California's fire emissions were a few percent of its fossil fuel emissions [59]. In the conterminous 48 states, harvest-related emissions are 7.5 times those from all natural causes [60]. It is understandable that the public wants action to reduce wildfire threats, but false solutions that make the problem worse and increase global warming are counterproductive.

2.3.2. Change Focus from Broad-scale Thinning to the Home Ignition Zone

Over the past century, public agencies have been responsible for managing fire risk and protecting communities, however, their focus has been on suppression, fuel reduction, and prevention. Yet, of all the ignitions that crossed jurisdictional boundaries, more than 60% originated on private property and 28% in national forests [61]. These findings are in stark contrast to the common narrative that wildfires start on remote public land and then move into communities [62].

Hardening home structures in areas with high risk of wildfires such as the wildland-urban interface has been found to be the most effective means to reduce property damage from wildfires [63]. Many rural homes use propane tanks that explode from the intense heat. Safer energy options for homeowners would reduce the spread from house to house and the loss of the structures. Community safety experts and wildfire risk managers indicate that focus should be on addressing the home ignition zone by using fire-resistant designs, more intensive fuel reduction close to buildings, and preventing new developments in high fire-risk areas [64]. Incentives are misaligned because zoning and approval of building locations are functions of local governments, but responding to fires, and shouldering those costs, are the responsibility of state and federal agencies. Additionally, a large number of the most destructive fires have been ignited by poorly maintained powerlines [65]. Buried lines and better maintenance could reduce the frequency of wildfires.

2.3.3. Post-Fire Harvest versus Natural Regeneration

After fires, the remaining live and dead trees in the burn area and those on the periphery provide seed sources for natural regeneration [66]. Fires also provide ash which can act as a natural fertilizer, providing macro- and micronutrients for regrowth. Natural regeneration allows germination of genetic- and species-diverse seeds, and resprouting of shrubs that provide important habitat as forests recover. The diversity of early successional species also increases the resilience of the ecosystem to future disturbance, and accumulates additional carbon [67]. Natural and managed regeneration failures have occurred, particularly in dry regions [67–69], but here we are referring to the diversity of seed stock in natural regeneration compared to planting of less diverse seedling sources. Although there is enthusiasm about participating in reforestation, tree planting must be done carefully to ensure appropriate species selection for specific sites, whereas natural growth has more likelihood of re-establishing local biodiversity [67].

The complex early seral forest habitats that develop after high severity burns are important to a broad range of wildlife [70]. Post-fire harvest and felling of live and dead trees can harm soil integrity, hydrology, natural regeneration, slope stability, and wildlife habitat [71]. Large standing dead, live yet possibly dying, and downed trees help forests recover and provide habitat for more than 150 vertebrates in the PNW [72].

In burned watersheds, post-fire logging worsens conditions that have resulted from a century of human activity [73,74] and impedes the rate of recovery. In sum, post-fire treatments can cause a significant loss of ecosystem services [75].

3. Solutions

To mitigate climate change and avoid additional irreversible changes, we must reduce energy consumption through greater end-use efficiency gains and shift to carbon-free energy sources (e.g., solar and wind) [76], and simultaneously increase removal and accumulation of additional carbon from the atmosphere in forests, wetlands, and soils.

Global studies have identified areas for protection of intact forests that would stem biodiversity loss and prevent land conversion to other uses [77,78]. A recent study suggests assessment of ecosystem integrity represented by faunal intactness (no loss of species), habitat intactness, and functional intactness (no reduction in faunal densities below ecologically functional densities) [1]. However, global analyses can miss important local to regional ecological features that affect species and thus, the potential for protections. A global meta-analysis showed that most vulnerable bird species need large intact forests, although relatively small fragments can still have substantial biodiversity value if protected at the highest levels (IUCN categories I–VI) [79]. To address this issue, the International Union for Conservation of Nature (IUCN) developed a policy [80] for defining forests of conservation value:

“While primary forests of all extents have conservation value, areas of greater extent warrant particular attention where they persist, as they support more biodiversity, contain larger carbon stocks, provide more ecosystem services, encompass larger-scaled natural processes, and are more resilient to external stresses. The significance of large areas of primary forests has been highlighted by the global mapping of Intact Forest Landscapes (IFL) greater than 500 km² in extent. While suitable for many purposes, other thresholds may be more suitable at regional and national levels that reflect local ecological factors.” (IUCN Policy Statement on Primary Forests, https://www.iucn.org/sites/dev/files/content/documents/iucn_pf-ifl_policy_2020_approved_version.pdf, accessed on 22 April 2020).

Much focus has been on protecting some notable primary forests [81] such as the Amazon, but that should not distract our attention from the need to retain significant intact forests within North America. There is more carbon stored in the world’s temperate and boreal forests combined than in all remaining tropical forests [81]. There are ecosystems in many ecoregions that meet the conditions for protecting half of forestlands [82]. Bird populations are good indicators of ecosystem integrity. A net population decline of 2.9 billion birds in North America occurred between 1970 and 2017, of which forest-dependent

species accounted for over one-third of the total, indicating a loss of insects and rapid recent degradation of forest ecosystem integrity [83,84].

Areas in the lower 48 states with high concentrations of imperiled forest- and non-forest species with small ranges in the west and east should be considered for protection (Figure 3) [85].

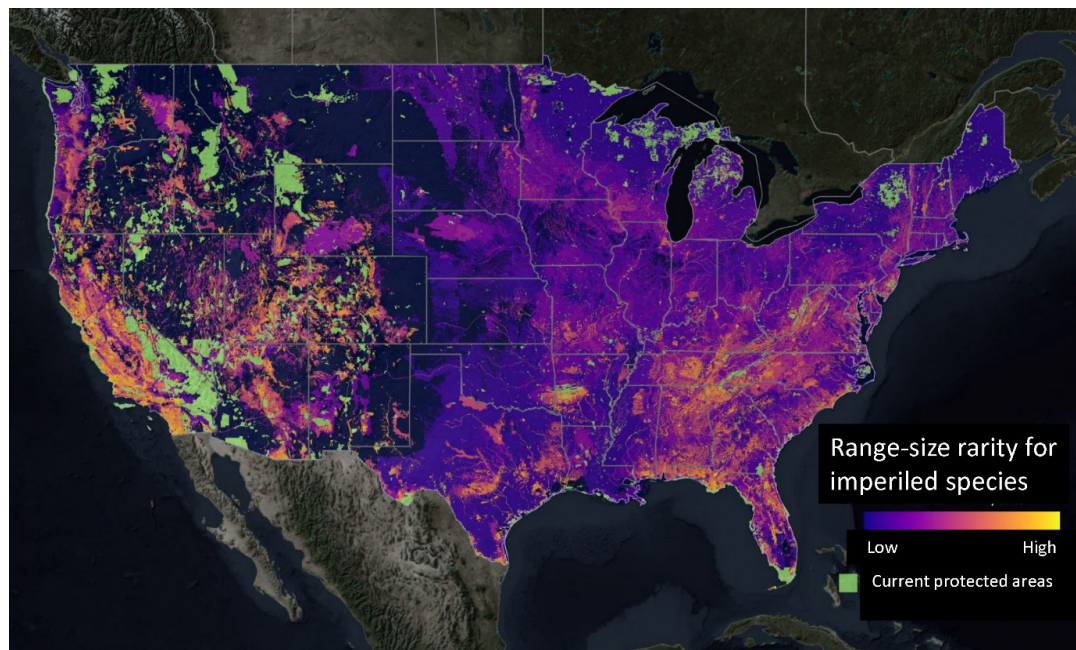


Figure 3. Summed range-size rarity of forest and non-forest species in the lower 48 states that are protected by the Endangered Species Act and/or considered to be in danger of extinction. Species include vertebrates (birds, mammals, amphibians, reptiles, freshwater fishes), freshwater invertebrates, pollinators, and vascular plants. High values (yellow) are areas where species with small ranges (and thus fewer places where they can be conserved) are likely to occur; the presence of multiple imperiled species contributes to higher scores. (Image produced by NatureServe; <https://livingatlas.arcgis.com>, accessed 21 April 2022).

Instead of regularly harvesting on all of the 70% of U.S. forest land designated as “timberlands” by the U.S. Forest Service, setting aside sufficient areas as Strategic Reserves would significantly increase the amount of carbon accumulated between now, 2050 and 2100, and reestablish greater ecosystem integrity, helping to slow climate change and restore biodiversity. The 2022 IPCC AR6 report stated that “Recent analyses, drawing on a range of lines of evidence, suggest that maintaining the resilience of biodiversity and ecosystem services at a global scale depends on effective and equitable conservation of approximately 30% to 50% of Earth’s land, freshwater and ocean areas, including currently near-natural ecosystems (high confidence).” Continuing commercial timber harvest on a portion of the remaining public lands and tens of millions of hectares of private lands would continue to adequately supply a sustainable forestry sector.

Preserving and protecting mature and old forests would not only increase carbon stocks and growing carbon accumulation, they would slow and potentially reverse accelerating species loss and ecosystem deterioration, and provide greater resilience to increasingly severe weather events such as intense precipitation and flooding.

Domestic livestock grazing occurs on 85% of public lands in the western U.S. and is a significant source of greenhouse gas emissions (12.4 Tg CO₂ equivalents per year). Due to overgrazing, it was estimated to decrease aboveground biomass carbon by about 85% when converted from forests and woodlands to grass-dominated ecosystems [86]. Discontinuing or greatly reducing this practice would be an important climate mitigation strategy.

High carbon forests in the western U.S. are highly biodiverse ecosystems that store and provide water to millions of people and to major agricultural regions, and are more resilient to climate change [9]. The PNW and Alaska stand out as having the largest mature and old forests with immense carbon stores and high biodiversity that meet the IPCC criteria of meriting protection to remove significant additional carbon from the atmosphere. A majority of these areas are on public lands with the potential for permanent protection consistent with the highest international standards, and could be complemented with additional protections on private and indigenous lands [87]. These forests are critical for greater future carbon accumulation, and are an essential source of clean drinking water [9]. Forests dominate the drinking water supply in the U.S. that must be protected at the source [88,89]. For example, forests account for almost 60% of the most important areas for surface drinking water in the western U.S., yet only about 19% are protected at the highest levels. Other regions of the U.S. such as the southeast host some of the greatest biodiversity on the continent, and require protection for their forest carbon, biodiversity, and water.

Across the eleven western U.S. states, a framework was applied to prioritize protection of high carbon and biodiversity forest areas to meet the 30×30 and 50×50 preservation targets (Figure 4). Out of 92.5 Mha of forestland in the region, 14% is currently protected at the level equivalent to wilderness areas, IUCN classification Ia to II, and 5% is protected at IUCN classifications III to VI, which allows practices that degrade existing natural communities, such as road building and suppression of natural disturbances [90]. To achieve 30% protection of forest area by 2030, an additional 10 Mha would need to be protected at these levels. To meet the 50% target by 2050, an increase of 29 Mha is required. The analysis examined, removing from consideration, areas that are at high risk of mortality from wildfire or drought under future climate conditions (Figure 5) [91] to determine if there was sufficient qualifying area to protect. The prioritization used an ecoregion approach [82] to determine relative importance for protection of biodiversity and/or carbon within each ecoregion. Ecoregions are delineated based on similarity of a range of abiotic and biotic characteristics (topography, climate, soils, vegetation), e.g., EPA Level III [92]. Ecoregion-based conservation was evaluated in a range of habitats, and is recognized as a strong basis for the need to conserve about half of each region [82]. A similar framework could be applied in other regions, with additional data such as species endemism, if available.

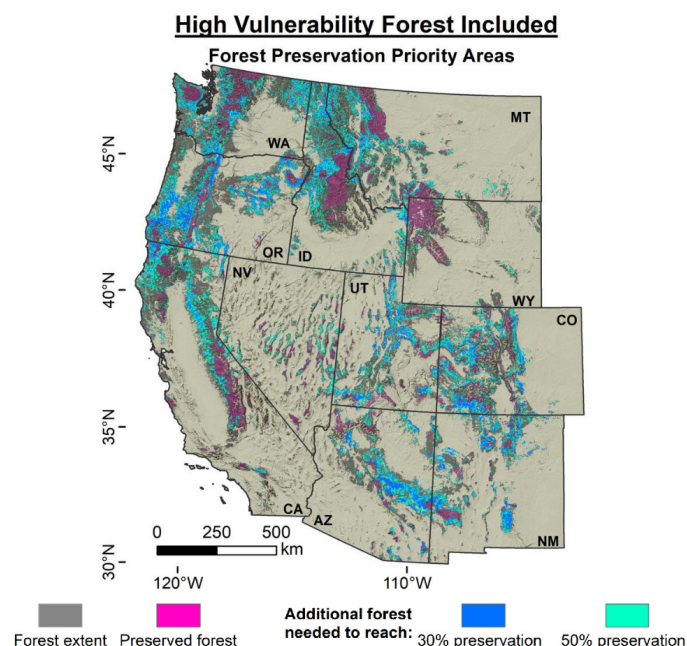


Figure 4. Forestlands that are currently preserved, and additional areas identified as high priority for protection of biodiversity and forest carbon for climate mitigation across the western U.S. Adapted from [5].

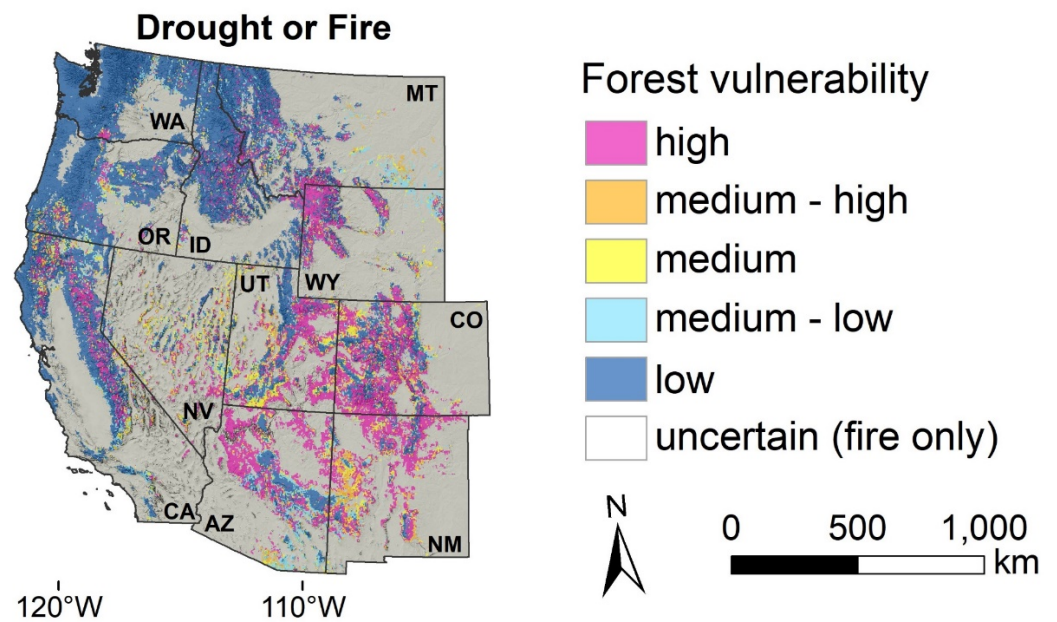


Figure 5. Vulnerability of forestlands to either drought or fire under future climate scenarios to year 2050. Adapted from [83].

The strategic reserves defined within each ecoregion would protect carbon, water, and biodiversity, and recognize the value of forested landscapes that are diverse in structure and function. Across the climate gradient from mesic to drier ecoregions, portions can be impacted by wildfire, but they are still important to protect their biodiversity, allowing species to persist (e.g., in refugia), migrate, and reorganize with a changing climate. An example is the Klamath Mountains ecoregion in Oregon and California, which has high biodiversity partly because of its unique geology. It is one of the top four temperate coniferous forests in species richness globally. Its vulnerability to forest fires should not disqualify it from protecting the rich diversity of plant and animal species from human degradation [70].

4. Conclusions

Maintaining forest ecosystem integrity is “*fundamental*” to resilient development and climate mitigation and adaptation. Current extractive management practices on all forests designated as “timberlands” are inconsistent with slowing, and eventually achieve lower “atmospheric concentrations of greenhouse gases that will avoid dangerous anthropogenic interference with the climate system” [93]. Many of the existing forest management practices allegedly protect forests and homes from wildfire and are having severe adverse effects on forest ecosystem integrity and resilience, and are worsening climate change and diminishing biodiversity. Forest bioenergy adds significantly more CO₂ to the atmosphere than fossil fuels. Its use is based upon a mistaken assumption that it is necessary to shift to renewable energy than to reduce heat-trapping gas emissions such as carbon dioxide, rather than to reduce emissions from all sources including forest bioenergy for electricity.

Climate change mitigation and biodiversity protection is an essential component of forest management decision-making. To avoid dangerous anthropogenic interference with the climate system, provide water security, and stem biodiversity losses, permanent Strategic Climate and Biodiversity Reserves need to be established quickly, and their integrity monitored and maintained.

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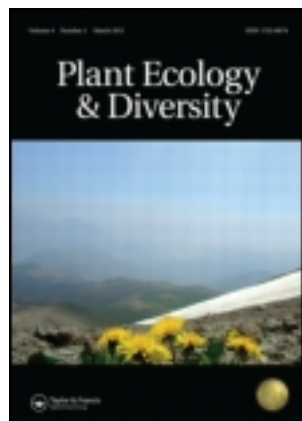
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Thinning effects on forest productivity: consequences of preserving old forests and mitigating impacts of fire and drought

Beverly E. Law^a, Tara W. Hudiburg^a & Sebastiaan Luyssaert^b

^a Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA

^b Laboratoire des Sciences du Climat et de l'Environnement, CEA CNRS UVSQ, Centre d'Etudes Orme des Merisiers, Gif Sur Yvette, France

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Thinning effects on forest productivity: consequences of preserving old forests and mitigating impacts of fire and drought

Beverly E. Law^{a*}, Tara W. Hudiburg^a and Sebastiaan Luyssaert^b

^aDepartment of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA; ^bLaboratoire des Sciences du Climat en de l'Environnement, CEA CNRS UVSQ, Centre d'Etudes Orme des Merisiers, Gif Sur Yvette, France

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Background: Management strategies have been proposed to minimise the effects of climate change on forest resilience.

Aims: We investigated the Pacific Northwest US region forest carbon balance under current practices, and changes that may result from management practices proposed for the region's 34 million ha of forests to mitigate climate change effects.

Methods: We examined the relationship between net primary production (NPP) and biomass, using plot data, and estimated the effects of proposed clear-cut harvest of young mesic forests for wood products and bioenergy while preserving mesic mature/old forests for biodiversity (Sparing), thinning all forests (Sharing) and a combination of sparing mesic mature and old, clearing mesic young and thinning dry forests (Sparing/Sharing).

Results: The forests of the region were found highly productive (NPP 163 Tg C year⁻¹) and a strong carbon sink with net ecosystem production of 45 Tg C year⁻¹. Observations indicated the relationship between NPP and biomass was not significantly different for thinned versus unthinned stands, after accounting for site quality and precipitation effects. After simulating proposed management to mitigate climate change, regional NPP was reduced by 35% (Sparing), 9% (Sharing) and 29% (Sparing/Sharing) compared with current practices.

Conclusions: Applying management practices appropriate for current forest conditions to mitigate future climate change impacts can be accomplished, but at a cost of reducing NPP. Sparing all forests >50 years old resulted in the largest NPP reduction, but the impact could be reduced by clearing only a subset of young forests.

Keywords: disturbance; drought; fire; forest carbon processes; harvest

Introduction

Climate change is expected to include warming, changes in precipitation regimes and lengthen forest growing seasons which can exacerbate drought stress and contribute to disturbance from insects (Kurz et al. 2008a, 2008b), pathogens and wildfire (Westerling et al. 2006). These disturbance agents often occur in sequence, further complicating understanding of potential trajectories of change in carbon cycling. In addition, natural disturbances can be amplified by anthropogenic activities, increasing the vulnerability of forests (Raffa et al. 2008). There is much uncertainty about how and where to mitigate these effects at the local to regional scales. A question is, if forests are thinned to minimise the effect of potential drought and fire, how does this affect forest carbon stocks, productivity and vulnerability to mortality?

Natural disturbances affect forest carbon dynamics for years to decades. Recent large-scale events such as hot/dry years across Europe and the USA, and large-scale forest mortality from insects in Canada have given us a window to the future on terrestrial ecosystem responses. After a drought, the effects on moisture reserves, soil nutrients and plant carbohydrates lead to longer-term effects in plant carbon cycling, and potentially mortality. Photosynthesis, respiration and net ecosystem production (NEP, net primary production (NPP) minus heterotrophic respiration) decline

in most cases in drought years (Ciais et al. 2005; Reichstein et al. 2007), and carry-over effects of multiple years of drought can lead to depressed carbon uptake in subsequent years (Thomas et al. 2009). Declines in NEP following major disturbances can result in the forest becoming a net carbon source for an average of 15–20 years until productivity increases again and decomposition of dead material decreases (Luyssaert et al. 2008; Amiro et al. 2010). Direct and carry-over effects, mortality and consequently species competition in response to drought are strongly related to the survival strategies of species (van der Molen et al. 2011).

Previous studies in the Pacific Northwest US region suggest that in semi-arid regions, old forests can respond positively to thinning treatments to alleviate drought stress (Kolb et al. 2007). In one ponderosa pine study, basal area increment of individual trees increased two to threefold 5 years after thinning, water stress was reduced compared with unthinned trees, and this was sustained for up to 15 years after the basal area was reduced by 60–80% (McDowell et al. 2003). Thus, it is reasonable to suggest that thinning of semi-arid forests that are at high risk of crown fires and drought effects could improve sustainability of semi-arid forests.

Forest thinning and other management practices are thought to reduce mortality and increase growth, and have

*Corresponding author. Email: bev.law@oregonstate.edu

therefore been proposed and implemented to minimise the effects of drought, warmer temperatures and longer growing seasons expected with climate change. However, inventory analysis, field studies and simulations indicate that thinning forests to increase climate adaptability or alter fire behaviour would increase forest carbon emissions and losses (Campbell et al. 2007; Mitchell et al. 2009; Hudiburg et al. 2011). In addition, it is proposed that mature (>50 years) and old forests should be protected for biodiversity and natural adaptation to climate change (e.g. landscape connectivity for species migration), while continuing to harvest younger stands for wood products and bioenergy as an alternative energy source. Forest resilience and sustainability are paramount, and the carbon consequences of such mitigation activities need to be determined.

Given that several functions (i.e. biodiversity conservation, adaptability to climate change, mitigating climate change through carbon sequestration and mitigating the effects of climate change on forests through decreasing stand susceptibility to fire and drought stress) need to be simultaneously realised, implementation of forest management needs to account for large-scale considerations. One such large-scale consideration is whether these functions are best realised through land sharing or land sparing. Land sharing is a management strategy that would aim to integrate biodiversity conservation with forest production on the same land by using wildlife-friendly methods. Land sparing, on the other hand, would separate land for conservation (e.g. preserves) from land used for production (e.g. intensive plantations; Phalan et al. 2011).

Our goal was to examine changes in productivity that could result from typical land sharing and land sparing harvest practices proposed for Pacific Northwest US forests to mitigate climate change impacts on forests. Our objectives were to examine (1) the regional NPP and NEP that are influenced by historic and current management practices; (2) the effect of precipitation, forest age and thinning on the relationship between NPP and biomass within ecoregions using experimental and inventory data; and (3) the regional effect on NPP of: (a) clear-cut harvesting young forests (on a 50-year cycle, converting a portion of the landscape to short rotation) and setting aside mature and old forests (i.e. land sparing forests >50 years) in all ecoregions; (b) thinning all ecoregions at a moderate level (i.e. land sharing); and (c) sparing mesic mature/old, clear-cutting mesic young and thinning all dry forests (<650 mm annual precipitation) to reduce fire and drought stress in the latter (Sparing/Sharing).

Materials and methods

Study area

We conducted this study in forests of the Pacific Northwest US region, which consists of the states of Washington (WA), Oregon (OR) and northern California (CA). California and Oregon have a similar amount of forested area, with 12.8 and 12.2×10^6 hectares,

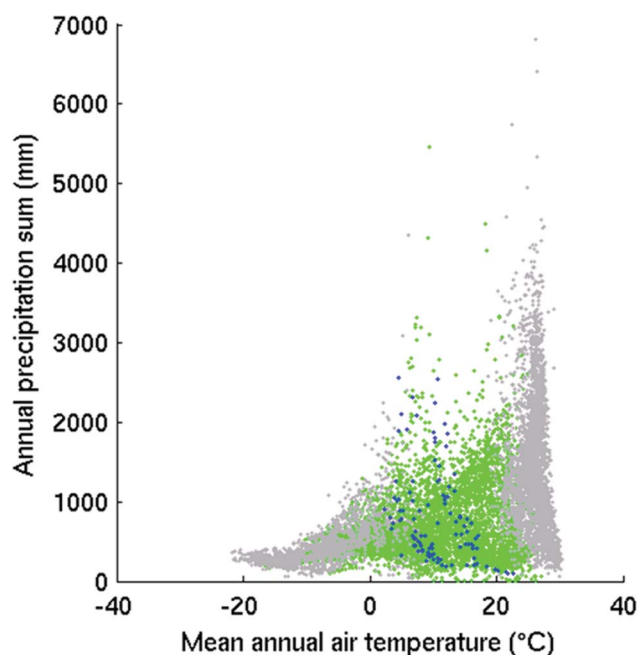


Figure 1. Regional climate range and variability of mean annual temperature ($^{\circ}\text{C}$) and annual precipitation sum (mm). Light grey dots represent global temperature and precipitation regimes, darker grey dots represent temperate climates and the darkest dots represent the forest type averages across the study region.

respectively, and Washington has 9.0×10^6 forested hectares, for a regional total of 34 million hectares. Wilderness areas and reserves were excluded from the analysis, which partly explains the differences in forest area, as Washington has more protected areas.

There is a strong climatic and vegetation gradient from the mild mesic coastal forests (mean annual precipitation $2500 \text{ mm year}^{-1}$) to the semi-arid pine and cold desert juniper woodlands (300 mm year^{-1} ; Figure 1). Primary species in the mesic area are Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and coastal redwood (*Sequoia sempervirens* (D. Don) Endl.) (Franklin and Halpern 2000). These forests have the potential to live for over 1000 years, and the mesic ecoregions have some of the highest biomass accumulation and productivity levels in the world (Hudiburg et al. 2009; Keith et al. 2009).

Data sources

Our primary data sources were the Forest Inventory and Analysis (FIA) dataset, plot data from our own productivity and thinning studies, and remote sensing data products. FIA data are collected annually on all types of forest land across the US. The FIA inventory has a probability-based design consisting of 0.404 ha plots systematically gridded across the landscape, encompassing a representative range of stand ages, disturbance histories, ownerships and land cover types. The FIA data were combined with Landsat-based mapping of vegetation type, fire and fuel characteristics, and 200 supplementary plots (Sun et al. 2004; Hudiburg et al. 2009) to produce mapped estimates

of current total forest NPP and NEP over the Pacific Northwest US region (details of computation methods in Hudiburg et al. 2011). Forest NPP included all trees regardless of stature, and understory shrubs. Wood NPP (bole, bark, branches and coarse root) was estimated as the difference between the biomass of each component at current and previous time steps using tree increment core data. Foliar NPP was estimated as the foliage biomass divided by the average leaf retention time using species-specific look-up tables constructed for the supplemental plot data. Fine root NPP was estimated as fine root biomass multiplied by average fine root turnover. We defined NEP as the difference between annual NPP and heterotrophic respiration. While direct measurements of soil respiration were not available on FIA plots, we were able to calculate NEP using a mass-balance approach and supplementary plot data where soil and root carbon pools were measured (Hudiburg et al. 2011; Campbell et al. 2009):

$$\begin{aligned} \text{NEP} = & \text{Above-ground NPP} - \text{dead wood decomposition} \\ & - \text{litterfall} + \Delta\text{root} + \Delta\text{soil C.} \end{aligned} \quad (1)$$

Plot means of current NPP and NEP were scaled to regional and state totals, using spatially explicit forest cover, ecoregion and succession class data products available in 30 m \times 30 m resolution from LandFire Landsat-derived products (USGS 2009). Ecoregions denote areas within which ecosystem characteristics are generally similar (geology, physiography, vegetation, climate, soils, land use, wildlife and hydrology; Omernik 1987, 2004). There are 18 ecoregions in the Pacific Northwest US region (Table 1). The remote sensing product LandFire has five succession classes associated with vegetation development (A, early development, post-replacement; B, mid-development closed; C, mid-development open; D, late development closed; E, late development open). We chose to use pixels labelled as 'A' or 'B' for selection of areas which were considered less than ca. 50 years. Plot values were aggregated by climatic region (ecoregion), forest type and age class (succession class), and this look-up table was used to assign a value to each associated 30 m pixel.

We examined the effects of thinning on the relationship between NPP and biomass using plot-level data from thinning experiments and inventories. The effects of thinning on NPP have often been studied as a function of stand age. Where such an approach may be appropriate for plantation-type management or stand-level studies, it can be challenging for large-scale studies or to compare stands under different management strategies because thinning can occur at different stand ages. For this reason, we studied the effect of thinning on the relationship between NPP and stand biomass. Because the relationship is also affected by forest type, precipitation and site quality, we included these variables in our analysis. This information was used to prescribe growth after thinning in the regional analysis.

One thinning experiment was in the Northern Sierras of California, where ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) was replanted in 1961 after stand-replacing fire. The area experiences average annual air temperature of 12 °C, and precipitation of 950 mm, most of which occurs outside the growing season. After the fire, the area was harvested, root-raked and windrowed into debris piles, and then planted. The stands were thinned once from below, removing 50% of the basal area, resulting in reduction of basal area from 40 to 20 m² ha⁻¹ (Campbell et al. 2009). The thinning regime applied was not atypical of fuel-reduction practices in mature ponderosa pine in the region. We examined the relation between total NPP and biomass of the untreated stands ($n = 4$) with those 3 years after a single thinning treatment ($n = 5$) and those 16 years after a single thinning treatment ($n = 5$). All stands were measured at the same time and were ca. 30 years old.

We also analysed data from observational plots, thinned and unthinned mature (40–80 years) ponderosa pine stands in the Metolius, Oregon watershed, a drier region with 30-year mean annual precipitation of 360 mm (Law et al. 2001). These studies allowed us to determine if the relationship between NPP and biomass changed for an extended period (ca. 10 years) after thinning in pine forests subject to summer drought but with different annual precipitation, as is expected for mitigating drought effects. In addition, we examined the relationship between NPP and biomass for thinned and unthinned plots within ecoregions (Omernik 1987) using inventory data after analysis of the influence of precipitation and age.

Projecting post-treatment C-balances

We aimed to project post-treatment NPP and compare it with that of current practices across the Pacific Northwest US region to examine the change in productivity associated with proposed management actions to mitigate climate change impacts on forests. Thinning treatments specific to mesic and dry forest were applied on the current forests to estimate their future biomass and NPP. Over 8000 inventory plots in all forest types across the whole region were virtually thinned according to stand density reduction requirements, and the new biomass values were calculated. The aforementioned relationships between NPP and biomass, accounting for forest type and ownership (site quality) and precipitation, were then applied to estimate future NPP.

The basal area removals, maximum bole size and areas treated were determined for three treatment levels: (1) clear-cut harvest young forests (on a 50-year cycle, converting a portion of the landscape to short-rotation) and set aside mature and old forests (i.e. Sparing forests > 50 years old) in all ecoregions; (2) thinning all ecoregions at moderate level (i.e. Sharing); and (3) spare mesic mature and old forests, clear-cut mesic young forests and thin all dry forests (< 650 mm annual precipitation) (i.e. Sparing/Sharing). The Sparing treatment essentially converts most previously harvested lands into short-rotation forests, and protects mature and old mesic forests for

Table 1. Ecoregion characteristics including dominant forest types, total area, total number of plots and number of thinned plots, mean annual precipitation (MAP), and regressions for predictions of NPP from biomass (B), forest type (FT), precipitation (P) and ownership (O); organised by MAP (high to low). Regressions were conducted for each ecoregion separately.

Ecoregion ¹ (mean forest age)	Forest (ha)	Total plots, thinned plots	Dominant forest types	MAP	Parameters (r^2)
CR (62)	4812627	1008, 127	Douglas-fir, Sitka Spruce, Redwood, Western Red Cedar, Fir-hemlock	1742	B + O(0.62)
WC (105)	4329871	987, 63	Douglas-fir, Hemlock, Mixed Conifer, Red Fir, Western Red Cedar	1688	B + P + O(0.56)
KM (105)	3748465	1103, 68	Mixed Conifer, Mixed Evergreen, Red Fir, Douglas-fir, Riparian, Oak	1549	B + FT + O(0.57)
NC (104)	2311424	452, 32	Fir-Hemlock, Mixed Conifer, Spruce-Fir, Western Red Cedar, Riparian	1548	B + FT + P + O(0.58)
PL (50)	1102015	164, 0	Douglas-fir, Riparian, Western Red Cedar, Sitka Spruce	1304	B + FT (0.73)
WV (45)	538681	105, 0	Douglas-fir, Hemlock, Riparian	1280	B + FT (0.68)
SM (113)	730051	167, 0	Mixed Evergreen, Mixed Conifer, Mixed Oak, Oak Woodland, Riparian	1064	B + FT + P(0.52)
SN (116)	1022645	1215, 124	Mixed Conifer, Red Fir, Ponderosa Pine, Mixed Oak-Conifer, Pine	915	B + FT + P + O(0.53)
CO (97)	2688165	447, 19	Pine, Mixed Conifer, Redwood, Oak Woodland and Savanna	652	B + FT + P(0.69)
EC (92)	3545116	1032, 144	Ponderosa Pine, Mixed Conifer, Juniper, Pine, Red Fir	630	B + FT + P + O(0.62)
NR (73)	1514359	329, 50	Mixed conifer, Riparian, Spruce-Fir, Ponderosa Pine	613	B + FT + P(0.70)
BM (93)	3312268	827, 62	Mixed Conifer, Ponderosa Pine, Juniper, Spruce-Fir	552	B + FT + O(0.72)
CB (135)	352650	105, 0	Pinyon-Juniper, Ponderosa Pine, Pine	445	B + P (0.56)
CV (na)	170243	na	Oak, Pine, Riparian, Salt Desert Scrub, Mixed Oak Savanna	412	Na
CP (67)	253667	63, 13	Mixed Conifer, Ponderosa Pine, Riparian	330	B + O(0.60)
NB (115)	478106	95, 3	Juniper, Aspen, Pinyon-Juniper, Ponderosa Pine, Mountain Mahogany	304	B (0.42)
MB (122)	93889	35, 0	Pinyon-Juniper, Mixed Oak Woodland	185	B + FT (0.47)
SB (na)	2175	na	Pinyon-Juniper	110	Na

¹BM, Blue Mountains; CB, Central Basin; CO, California Chaparral and Oak Woodlands; CP, Columbia Plateau; CR, Coast Range; CV, Central California Valley; EC, East Cascades; KM, Klamath Mountains; MB, Mohave Basin; NB, North Basin and Range; NC, North Cascades; NR, Northern Rockies; PL, Puget Lowlands; SB, Sonoran Basin; SM, Southern California Mountains; SN, Sierra Nevada; SR, Snake River; WC, West Cascades; WV, Willamette Valley.

biodiversity and other ecosystem values. The thinning treatment in dry ecoregions (dry portion of Sharing and Sharing/Sparing treatments) removes smaller trees and some larger trees to provide at least 9 Mg of dry biomass ha^{-1} (4.5 Mg C ha^{-1}) of merchantable biomass (Skog et al. 2008), with the expectation that the merchantable biomass would help pay for removal of small trees that are potential fuel ladders to the crowns of larger trees. All treatments exclude public forest reserves. A treatment period of 20 years was assumed to be the amount of time required to treat the entire landscape in the Sharing treatment. Pixels were harvested over a 20-year period, so that only 5% of the treatable area was treated each year in all three scenarios. It is also a common timeframe of policy actions and verification of expected results. FIA plots with stand densities greater than 300 trees ha^{-1} and located on forestland capable of producing 10 Mg of merchantable wood $\text{ha}^{-1} \text{year}^{-1}$ were thinned according to each treatment.

New plot mean biomass values were scaled to state and ecoregion boundaries to determine the removal totals.

Biomass removal levels were defined by current or proposed practices (USDA 2010), and treatments were designed to reduce crown fire potential by thinning from below (Stephens et al. 2009). Synthesis of fuel treatment studies showed that stand basal area was reduced by an average of 48% (Evans and Finkral 2009); however, Johnson et al. (2007) indicated that 30–55% basal area removal plus surface fuel treatment was necessary in dry forests to alter potential fire behaviour from crown fire to surface fire under severe fire weather conditions. This level of treatment was predicted to maintain surface fire behaviour for 30–40 years, depending on rate of understory growth, after which additional fuel treatment would be needed. We used 40% basal area removal for the dry ecoregions (maximum 60 cm diameter at breast height (DBH)), for LandFire map areas identified as having a mean

fire return interval of less than 40 years and precipitation < 650 mm.

We analysed data for changes in NPP by biomass, forest type, ecoregion, site quality and climatic conditions. We used the ecoregion-specific relationships between NPP and biomass on the previously thinned inventory and experimental plots to predict post-treatment NPP. In the wetter ecoregions (Coast Range and West Cascades), NPP tends to increase linearly at first with increasing biomass then reach a maximum where it remains fairly constant (Figure 2). In some of the drier ecoregions, NPP does not appear to reach a maximum and continues to increase. For this reason, linear regressions were only fit to plots that had not reached maximum NPP. After the plots were virtually thinned or clear-cut, the new biomass was used to predict a new NPP using the ecoregion-specific equations, producing the following year's new biomass. This was repeated until the new NPP equalled the plot NPP before treatment (law of constant final yield). For comparisons with current practices, we assumed that current landscape level NPP was constant and incremented the current plot biomass for each year using the observed NPP. The change in NPP due to external factors (e.g. N deposition) is the

same for the three treatments, and we are reporting differences among treatments, so this assumption should affect the treatments equally. The total NPP resulting from the treatments were compared with total values for current management practices after 20 years.

Monte Carlo simulations were used to conduct an uncertainty analysis using the mean and standard deviations for NPP calculated by several approaches. Three alternative sets of allometric equations were used to estimate the uncertainty due to variation in region and/or species-specific allometry. The full suite of species-specific equations that use tree diameter (DBH) and height (preferred) were compared with a DBH-only national set, and to a grouped forest type set. Finally, the total uncertainty was combined with the uncertainty in land cover estimates (10%) using the propagation of error approach (National Research Council 2010).

Results

Current terrestrial carbon fluxes

The region was found to be highly productive and a strong carbon sink. The current NPP for CA, OR and WA was

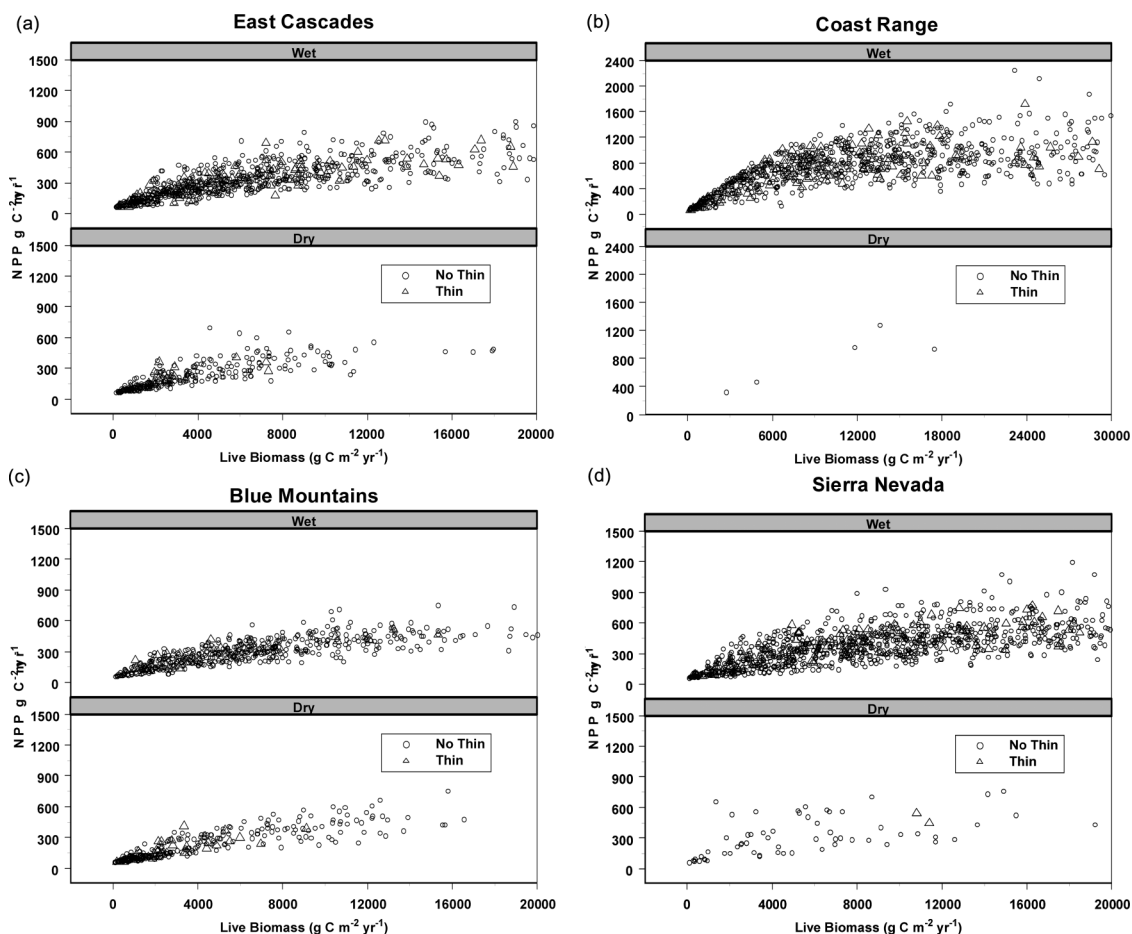


Figure 2. Relationship between NPP and biomass using inventory plot data for selected mesic (precipitation >650 mm year⁻¹) and dry (<650 mm year⁻¹) plots in selected ecoregions. (a) East Cascades (630 mm annual precipitation, all three states); (b) Coast Range (1741 mm precipitation, all three states); (c) Blue Mountains (511 mm precipitation, Oregon, Washington); (d) Sierra Nevada (915 mm precipitation, California). Data are for forests <80 years of age. Open symbols are thinned stands.

Table 2. State total and mean carbon fluxes resulting from current practices (Current NPP, NEP, fire emissions and harvest removals) and the three treatment treatments: (1) clear-cut harvest young forests (on a 50-year cycle, converting a portion of the landscape to short rotation) and setting aside mature and old forests (Sparing) in all ecoregions; (2) thin all ecoregions at moderate level (Sharing); (3) spare mesic mature and old, clear-cut mesic young and thin all dry forests (<650 mm annual precipitation) to reduce fire and drought stress in the latter (Sparing/Sharing).

State forested land (million ha)	Washington (9.0)	Oregon (12.2)	California (12.8)
Annual fossil fuel emissions (Tg C year ⁻¹)	21	15	105
Carbon density (Mg C ha ⁻¹)	172 ± 25	150 ± 22	130 ± 18
Current net primary production -NPP			
Total (Tg C year ⁻¹)	44.9 ± 5.2	58.3 ± 6.5	59.9 ± 6.7
Per unit area (g C m ⁻² year ⁻¹)	517 ± 58	477 ± 53	442 ± 50
Current net ecosystem production -NEP			
Total (Tg C year ⁻¹)	11.3 ± 1.2	15.2 ± 1.6	18.1 ± 2.1
Per unit area (g C m ⁻² year ⁻¹)	125 ± 13	125 ± 13	142 ± 16
Current fire emissions ¹ (Tg C year ⁻¹)	0.9 ± 0.1	1.3 ± 0.2	1.8 ± 0.3
Current harvest removals (Tg C year ⁻¹)	5.5 ± 0.4	6.4 ± 0.5	2.7 ± 0.2
Total treatment removals (Tg C year ⁻¹)			
• Thin all (Sharing)	12.0 ± 0.8	14.5 ± 1.0	11.2 ± 0.8
• Cut young, spare old (Sparing)	8.0 ± 0.6	11.0 ± 0.8	8.9 ± 0.6
• Sparing in mesic / Sharing in dry	9.2 ± 0.6	10.0 ± 0.7	7.8 ± 0.6
Treatment NPP (Tg C year ⁻¹)			
• Thin all (Sharing)	41.2 ± 4.6	53.3 ± 6.0	54.4 ± 6.1
• Cut young, spare old (Sparing)	28.5 ± 3.2	36.4 ± 4.1	41.9 ± 4.7
• Sparing in mesic / Sharing in dry	30.9 ± 3.5	40.7 ± 4.6	44.3 ± 4.9
Area treated (million hectares)			
• Thin all (Sharing)	7.1	9.8	7.8
• Cut young, spare old (Sparing)	1.4	2.1	2.0
• Sparing in mesic / Sharing in dry	3.2	5.4	3.1

¹ Fire emissions refers to carbon loss due to direct combustion.

59.9 ± 6.7, 58.3 ± 6.5 and 44.9 ± 5.2 Tg C year⁻¹, totalling 163.0 Tg C year⁻¹ and averaging about 479 g C m⁻² year⁻¹ (Table 2; Figure 3a), based on pixel values (Methods section). NEP for CA, OR and WA was 18.1 ± 2.1, 15.2 ± 1.6 and 11.3 ± 1.2 Tg C year⁻¹, respectively, averaging 125 to 142 g C m⁻² year⁻¹ (Table 2; Figure 3b). NPP was highest in the western coastal portion of the region, which is more mesic with mild temperatures due to the influence of the Pacific Ocean. Current harvest removals were significantly lower in CA (2.7 ± 0.2 Tg C year⁻¹), compared with 5.5 ± 0.4 and 6.4 ± 0.5 Tg C year⁻¹ in WA and OR, respectively.

Observed thinning effects

We wanted to examine the changes in stand-level growth after thinning with our data from two thinning experiments in the region (Metolius 13 stands of which five were thinned, and Forest Hill 14 stands of which 11 were thinned).

Thinning of semi-arid ponderosa pine stands in the Metolius area (annual precipitation 360 mm) showed an increase in the ratio of above-ground NPP (ANPP) to biomass several years later compared with unthinned stands (Figure 4a). A thinning experiment in a 44-year-old ponderosa pine plantation in the Sierra Nevada Mountains, where precipitation is almost three times higher (950 mm) than the Metolius area, did not appear to alter the relationship between NPP and biomass 3 and 16 years after thinning compared with unthinned stands (Figure 4b).

Large-scale analysis of the relationship between current NPP and biomass for inventory plots in several of the ecoregions (Figure 2) showed that the relationship between NPP and biomass was significant in all ecoregions (*P* values < 0.05). The range of observed values in NPP for a given biomass was quite large in some ecoregions, and a substantial portion of this variability could be attributed to spatial variation in precipitation, site quality, species composition and a heterogeneous age structure. For the majority of the ecoregions, the inclusion of forest type, precipitation and/or ownership significantly improved the relationship (*P* values < 0.05; Table 1).

Projected large-scale thinning effects

Harvest removals were highest in the Sharing treatment in all three states compared with the other treatments (Table 2), but were lowest on a per unit treated area basis. In the Sparing/Sharing treatment, the amount of biomass removed from young mesic forests (<50 years) that were clear-cut was much higher than that removed by thinning all drier forests (Figure 5), resulting in 97% and 38% removal of above-ground tree biomass per plot, respectively, which is typical of harvest practices in the region (Skog et al. 2008; Evans and Finkral 2009; Harrod et al. 2009). Removals from thinning the drier ecoregions were highest in the California Central Basin (CB) and California Chaparral and Oak Woodlands (CO) (Figure 5). Biomass removals from clear-cutting young mesic ecoregions were highest in the Washington and Oregon Coast Range (CR),

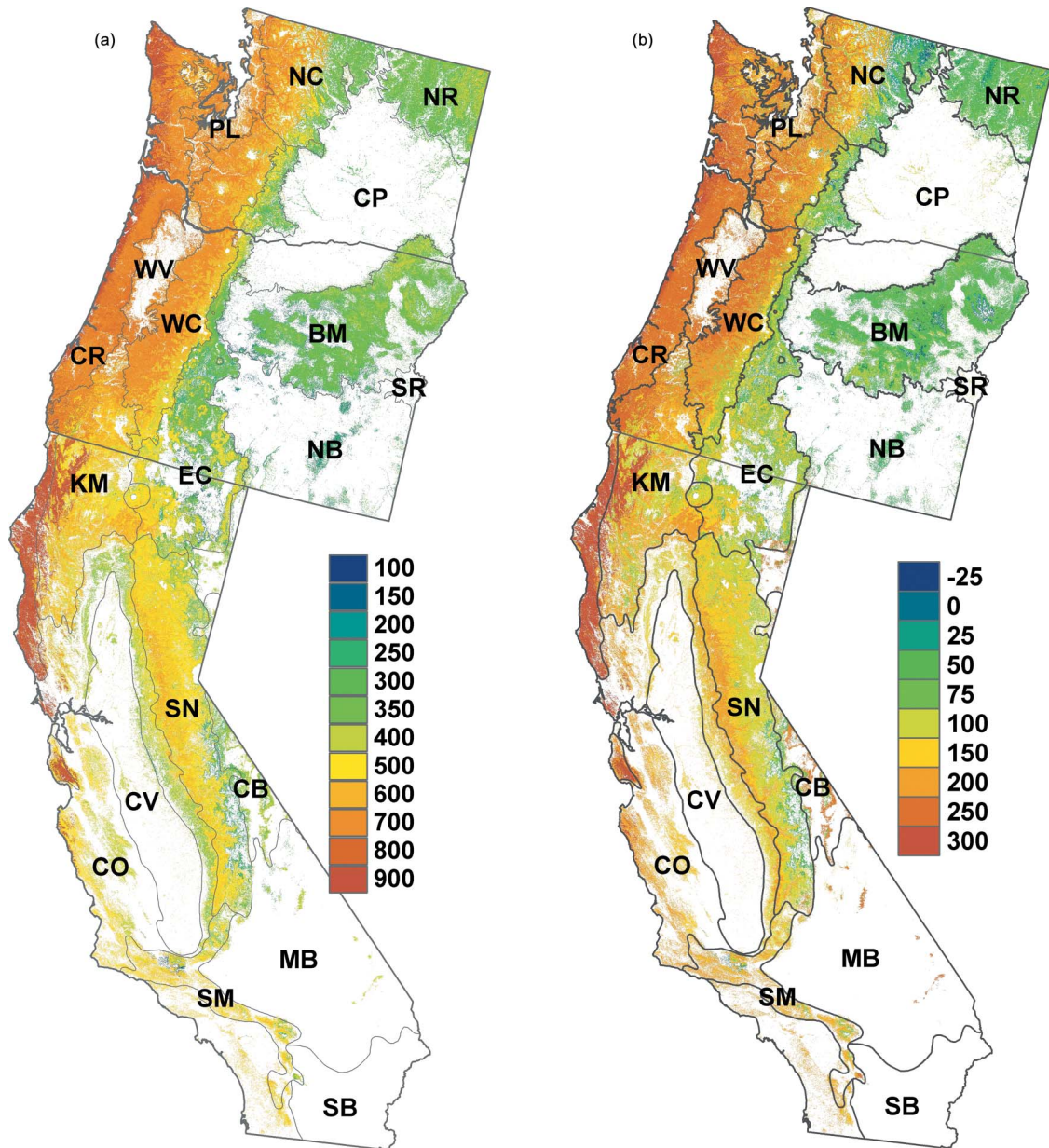


Figure 3. Regional (a) NPP and (b) NEP under current practices (CP) expressed in $\text{g C m}^{-2} \text{ year}^{-1}$. BM, Blue Mountains; CB, Central Basin; CO, California Chaparral and Oak Woodlands; CP, Columbia Plateau; CR, Coast Range; CV, Central California Valley; EC, East Cascades; KM, Klamath Mountains; MB, Mohave Basin; NB, North Basin and Range; NC, North Cascades; NR, Northern Rockies; PL, Puget Lowlands; SB, Sonoran Basin; SM, Southern California Mountains; SN, Sierra Nevada; SR, Snake River; WC, West Cascades; WV, Willamette Valley.

Oregon West Cascades (WC), Oregon Willamette Valley (WV) and Washington Puget Lowland (PL) (Figure 5).

A Sharing treatment (moderately thin all forests) reduced regional NPP by 9% to $149 \text{ Tg C year}^{-1}$ after 20 years. The Sparing treatment (clear-cut all young forests, spare all mature and old forests) reduced regional NPP by 35% to $107 \text{ Tg C year}^{-1}$. In the Sparing/Sharing treatment, where land sparing was applied in the mesic mature/old forests, mesic young forests were clear-cut and thinning was applied in the dry forests as a means of reducing fire and drought stress, regional NPP was reduced by 29% to $116 \text{ Tg C year}^{-1}$. The largest decreases in NPP due to treatment were in California (Table 2), and

specifically the Sierra Nevada, Southern California Mountains and California Oak Woodlands ecoregions (Figure 6), where biomass removals were highest. Other areas of high removals and large decreases in NPP were the West Cascades and North Cascades, where more area in young forests and high productivity per unit area (due to mild climate) in these ecoregions led to large decreases in NPP compared with the other ecoregions.

Mitigating the effects of drought and fire

To mitigate the effects of drought, preventing a reduction in productivity by implementing a large-scale thinning of drier

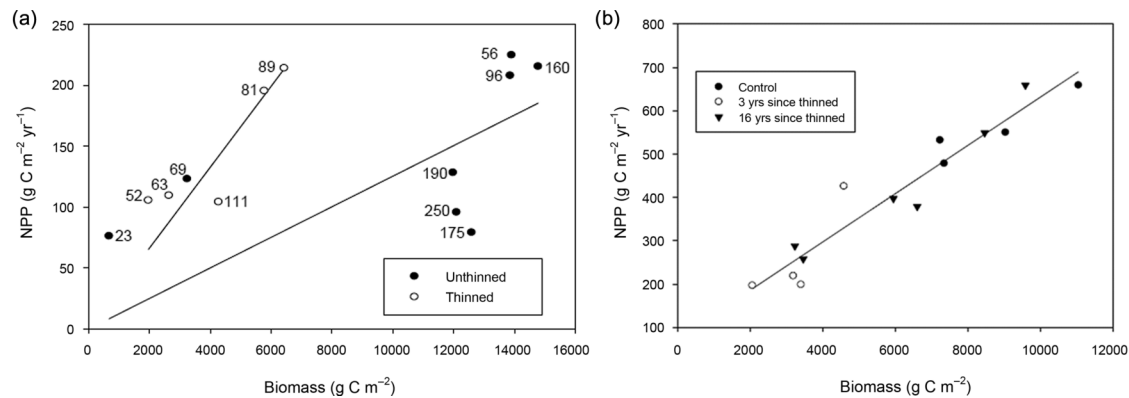


Figure 4. (a) Thinning effects on the relationship between above-ground net primary production (ANPP in g C m⁻² year⁻¹) and biomass (g C m⁻²) in Metolius semi-arid ponderosa pine (360 mm precipitation per year). Regressions are forced through the origin (young and mature plots $r^2 = 0.56$, old plots $r^2 = 0.27$ and overall $r^2 = 0.35$). Points are labelled with the plot mean stand age (years); (b) NPP and biomass 3–16 years post thinning compared with unthinned stands of mature (ca. 35 year) ponderosa pine in the Sierra Nevada Mountains, where annual precipitation is higher at 950 mm year⁻¹. Regressions are lines of best fit forced through the origin.

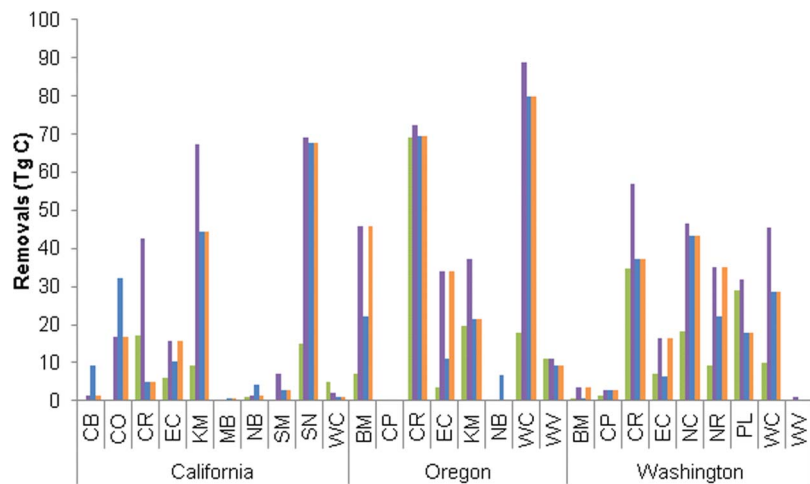


Figure 5. Comparison of current biomass removals (Tg C) in each ecoregion with (1) removals 20 years after thinning all forests (Share); (2) clear-cut young mesic forests and spare all old forests (Spare); and (3) clear-cut mesic young forests, spare mesic old forests and thin all dry forests (Spare mesic / Share Dry).

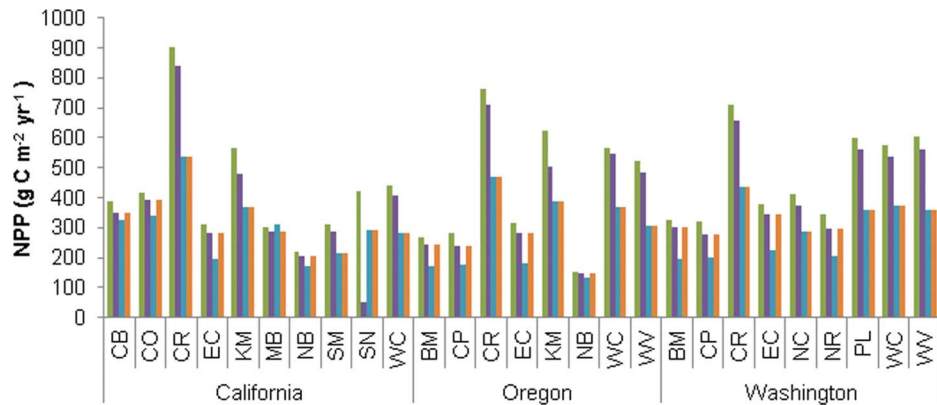


Figure 6. Comparison of current NPP (g C m⁻² year⁻¹) in each ecoregion with (1) NPP 20 years after thinning all forests (Share); (2) clear-cut young mesic forests and spare all old forests (Spare); and (3) clear-cut mesic young forests, spare mesic old forests and thin all dry forests (Spare Mesic / Share Dry).

forests (Sparing/Sharing treatment) had a cost of a 12.5% decrease in NPP (from 41 to 36 Tg C year⁻¹).

The dry ecoregions together have a mean fire return interval of 25–55 years and 1.4 of the 12.4 million ha of dry forest land (11%) are affected by wildfires annually. As a zero-order estimate, this fire-induced loss in productive forest land corresponds to an 11% loss of NPP. Large-scale prevention of forest fires had a cost of 12.5% reduction in NPP over the 20-year treatment period (Sparing/Sharing treatment for dry forest only).

Forest fires are less frequent in the mesic regions (0.9 million ha and <5% of the forested area), but nevertheless preventive thinning has also been proposed in these areas. A Sharing treatment in which both mesic and dry forest were thinned to prevent productivity losses from wild fires results in a 9% reduction of the productivity across all ecoregions that is not offset by productivity loss due to fire under current conditions. This could change if water availability in summer decreases due to warm spring snowmelt water loss that could otherwise be available for growth in summer.

Biodiversity

In the Sparing/Sharing treatment, the amount of area of forests >50 years old that was preserved for biodiversity and adaptive capacity in the mesic forests was 18.3 million ha with 29% reduction in NPP. In the Sparing treatment, which emphasises sparing all forests >50 years old across the region, an additional 10.2 million ha are preserved for a total of 28.5 million ha.

Discussion

Current terrestrial carbon fluxes

In the Pacific Northwest US region, there is a higher frequency of younger stands on private land than on public land and there are more old stands on public land. Mean stand age on private land ranges from 42 years in the Coast Range to ca. 105 years in the California Oak Woodlands and Chaparral. Mean ages on public land range from 60 years in the Willamette Valley to ca. 130 years in the West Cascades, where most of the land is public (Hudiburg et al. 2009).

Our earlier work showed that forests of the west coast region have high biomass and indicated that regional carbon stocks could theoretically increase by 46% if forests were managed for maximum carbon storage (Hudiburg et al. 2009). Mean NPP of 80 forest types in the region was estimated at 100–900 g C m⁻² year⁻¹, within the global range of temperate and boreal forests (100–1600 g C m⁻² year⁻¹; Luysaert et al. 2007).

In the mesic ecoregions, recent changes in age-class distributions were the result of implementation of the Northwest Forest Plan (NWFP) in 1993 to conserve species, such as the northern spotted owl (*Strix occidentalis caurina*) that had been put at risk from extensive harvest of older forests. Simulations showed that the area

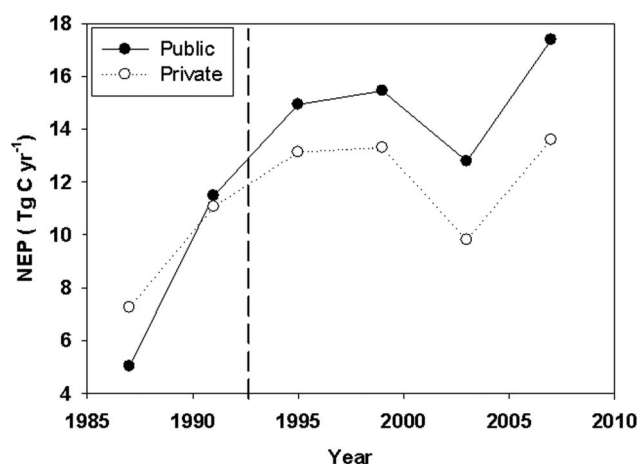


Figure 7. NEP expressed in g C m⁻² year⁻¹ after implementation of the Northwest Forest Plan on public lands in 1993 (after Turner et al. 2011). Data reported separately for public (black circles) and private (white circles) land.

of the NWFP was a carbon source (both public and private ownership) prior to implementation of the NWFP. After implementation, harvest removals were reduced by 82% on public lands and the forests became a carbon sink (Turner et al. 2011). Results from the simulations showed that NEP on public lands prior to implementation averaged 20% lower than that of private lands, and after implementation, NEP on public lands averaged 20% higher than that on private lands (Figure 7). The simulations also suggested that the drought in 2001–2003 had a large impact on NEP in all ecoregions.

Observed thinning effects

Studies have shown that thinning forests initially reduces area-based NPP while increasing NPP of the remaining trees (Law et al. 1992). Over time, regrowth after thinning results in little difference in area-based NPP compared with unthinned stands, all else being equal (Kira et al. 1953).

In the Metolius thinning analysis, the large variation in NPP for high biomass in unthinned stands was likely due to edaphic differences where the lower ANPP values at high biomass are for old forests, including a low-density stand of all old trees. The old, tall semi-arid forests survived many severe droughts and fires, as indicated by the historic fire return interval of 3–38 years in the area (Bork 1985). The thinning study on the same species but wetter climate of northern California showed no change in the relation between NPP and biomass compared with unthinned stands, indicating more rapid recovery from thinning and compensatory effects by understory vegetation, confirming the temporary effect of thinning. Although the two thinning studies were not directly comparable, they support the assumption that thinning can temporarily reduce competition in areas with more severe soil water deficits.

In the large-scale analysis of inventory plots, the inclusion of forest type, precipitation and/or ownership significantly improved the relationship between NPP and

biomass. The relationship with precipitation reflects the large regional variation in water availability. While measures of site quality (i.e. site index defined as species-specific tree height at a reference age) were available for the plot data, adequate spatially explicit regional data layers of height and age were not available for scaling plot data. In a previous analysis with inventory data (Hudiburg et al. 2009), we found a significant difference between the site indexes of publically and privately owned forests due to the historical pattern of private land ownership being located in lower elevation forested areas characterised by higher productivity. When we accounted for ownership (as a surrogate for site quality), the NPP-biomass relationship improved in about half of the ecoregions (Table 1). Thus, we concluded that, in general, over the treatment period of 20 years, there is no long-term thinning response of NPP (i.e. it does not exceed that of unthinned stands).

Projected large-scale thinning effects

The Sharing treatment resulted in the smallest decline in regional NPP after 20 years, and it also had the highest total harvest removals (Table 2). However, on a per-unit-treated-area basis, the Sparing treatment (clear-cutting young forests <50 years) removed 50 times the biomass of the Sharing treatment (thinning). The higher total removals in the Sharing treatment were somewhat offset by more rapid recovery of NPP. This result is due to a combination of much lower initial decline in NPP on thinned versus clear-cut plots and differences in treated area. The Coast Range in Oregon is a good example of this because the total removals are nearly equal for each treatment (Figure 5), but the effect on NPP was quite different (Figure 6). Thinning the same total amount of biomass over a much larger area does not reduce overall NPP as much as clearing all young forests over a smaller area. For the region in general, the larger initial loss in NPP from clearing young forests takes much longer to recover because of the initiation stage of growth.

The large decreases in NPP of the Sparing/Sharing treatment were influenced by historical harvest practices. Harvest had reached a peak on both public and private lands prior to implementation of the NWFP in the early 1990s, which means there were many young forests in some ecoregions, like the historically productive Coast Range and West Cascades, which were subject to clear-cuts in this treatment.

All the proposed large-scale changes in forest management were expected to result in a considerable decrease of NPP over a 20-year time period. Whether the NPP reduction would be reflected in the regional carbon sink (net biome production) ultimately depends on the C-losses through harvest, fire and decomposition.

Mitigating the effects of drought and fire

Our results (Figure 4a, b) support the assumption that thinning temporarily reduces competition in areas with more severe soil water deficits. As a consequence, large-scale thinning of semi-arid regions could mitigate the

effects of summer droughts on forest production. During the 2001–2003 extreme droughts, the Metolius semi-arid mature forest experienced a 40–44% decrease in gross photosynthesis and NEP and a ca. 15% decrease in NPP compared with surrounding years (Thomas et al. 2009). Preventing a reduction in productivity by implementing a large-scale thinning of drier forests (Sparing/Sharing treatment) still led to a 12.5% decrease in NPP. However, if thinning could avoid large-scale dieback of forests due to drought stress, preventive thinning may have a role to play under future climate conditions if a substantial increase in drought stress and frequency is predicted for the dry ecoregions.

The zero-order estimate of fire-induced loss in NPP (11%) was less than that of large-scale prevention of forest fires (12.5%) over the 20-year treatment period (Sparing/Sharing treatment for dry forest only). Currently, high-severity fires responsible for high basal area mortality account for only about 20% of burned areas in the region (Schwind 2008; Meigs et al. 2009). In the Metolius area, NPP several years after fire was only 40% lower in the high versus low-severity burn areas, suggesting compensatory effects of new vegetation growth. Reduced NEP was primarily due to change in NPP, not heterotrophic respiration (Meigs et al. 2009). This and other studies suggest that the net effect of thinning the drier forests would be reduced NPP compared with NPP after fires.

Biodiversity

Treatment effects on biodiversity could not be determined. However, previous studies in the region showed that thinning encouraged growth of important mid-canopy layers of plant species in structurally complex mesic forests (Comfort et al. 2010), and in Sierra mixed conifer forests higher plant species richness was associated with less canopy closure (a measure of thinning intensity; Battles et al. 2001). In addition, light-to-moderate thinning had a neutral-to-positive influence on bird species diversity in the Pacific Northwest (Hayes et al. 1997), and this was likely due to increased shrub and understory layers and structural diversity. A meta-analysis across North America concluded that the magnitude of response to forest thinning is often small for several years after thinning; however, some species of higher conservation concern may be positively or negatively affected by thinning and simple diversity and richness measures may not be sufficient for fully understanding the effects of thinning on biodiversity (Verschuyl et al. 2011).

Current harvest practices treat approximately 1.1% of the total forested area annually and remove a total of $14.6 \pm 1.0 \text{ Tg C year}^{-1}$ from all three states combined, with 44% of this harvest from Oregon alone (Smith et al. 2007). While all of the treatments included considerable harvest increases compared with current management practices, the proposed harvest area ranged from < 1–3.6% of the total forest area annually and did not exceed historical harvest rates (Table 2).

In the Sparing/Sharing treatment, the area of mesic young forests treated with clear-cut harvest (5%/year harvest of area designated for the treatment) was still within historical rates when scaled to the total forest area. In this treatment, the area spared in mesic forests tripled the land area preserved compared with currently preserved land area (4.6 million ha in the region), which is small relative to that in other temperate regions of the world. In the Sparing treatment, the land area preserved increased to 28.5 million ha, over six times current levels; however, the cost in reduced NPP was the highest of all treatments (35% vs. 29% for Sparing/Sharing). Therefore, if the Sparing/Sharing treatment was selected as the best approach for sustaining the region's biodiversity and supporting adaptation and migration through functional connectivity of forest, while reducing drought stress in dry forests by thinning, the cost in terms of productivity would be high (29% reduction in NPP). However, under the current environmental conditions this lower NPP would still sustain a substantial carbon sink (Hudiburg et al 2009; Luysaert et al 2008).

Conclusions

The regional analysis indicates that proposed climate change mitigation actions to reduce impacts in Pacific Northwest US forests that included a treatment of sparing mesic mature forests, clear-cutting mesic young forests (<50 years, reducing harvest cycle from 80 to 50 years, which is already being planned) and thinning all age classes of dry forests to minimise drought and fire impacts on carbon (<650 mm precipitation per year) resulted in a 29% decrease in NPP over the 20-year treatment period compared with NPP resulting from current practices. Emphasising sparing of all old forests, mesic and dry, while clear-cutting all young forests results in the largest reduction in NPP (35%). The impact could be reduced by treating a subset of the young forests, which may also be desirable for facilitating migration of trees to a more favourable climate, and allow recruitment of young into older age classes or acceleration of old-growth structure. Thinning of all forests at a moderate level would have the lowest impact on NPP (9% reduction), but it would not preserve mature and old forests. It could also reduce occurrence of spatial complexity in early successional forests that is similar to that in old-growth forests (Donato et al. 2011). There are trade-offs with each treatment, but this study indicates they come at a cost of reducing regional NPP over 20 years in this region. In particular, thinning or managing for fire suppression may remove more NPP with a longer time-lag for recovery than fire itself. Repeated cycles of thinning in dry forests (20–30-year cycle) and clear-cutting young forests (50-year cycle) would likely lead to less of a reduction in regional NPP over the following 50-year period because NPP of some preserved forests may decrease due to ageing and NPP of the thinned dry forests may not be reduced much further after the initial harvest and regrowth.

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Author contributions

B.L. designed the study, and conducted and guided field studies and analysis. T.H. conducted the regional analysis and statistical analysis on plot data. S.L. contributed to the analysis. B.L., T.H. and S.L. co-wrote the paper.

Notes on contributors

Beverly Law is Professor of Global Change Forest Science. Her areas of research include quantifying and understanding the effects of climate and disturbance on carbon, water and energy exchange with the atmosphere, and effects of forest management to mitigate environmental stress and climate change.

Tara Hudiburg is a Ph.D. student in terrestrial carbon cycling and evaluation of management and policy actions.

Sebastiaan Luyssaert is a climatologist. His research includes the role of forest management in mitigating climate change.

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Mixed-severity wildfire and habitat of an old-forest obligate

DAMON B. LESMEISTER^{1,2,†} STAN G. SOVERN,² RAYMOND J. DAVIS,³ DAVID M. BELL,¹
MATTHEW J. GREGORY,⁴ AND JODY C. VOGELER^{4,5}

¹USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331 USA

²Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA

³USDA Forest Service, Pacific Northwest Region, Corvallis, Oregon 97331 USA

⁴Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331 USA

⁵Natural Resources Ecology Lab, Colorado State University, Fort Collins, Colorado 80523 USA

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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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† **E-mail:** dlesmeister@fs.fed.us

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 km²; 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

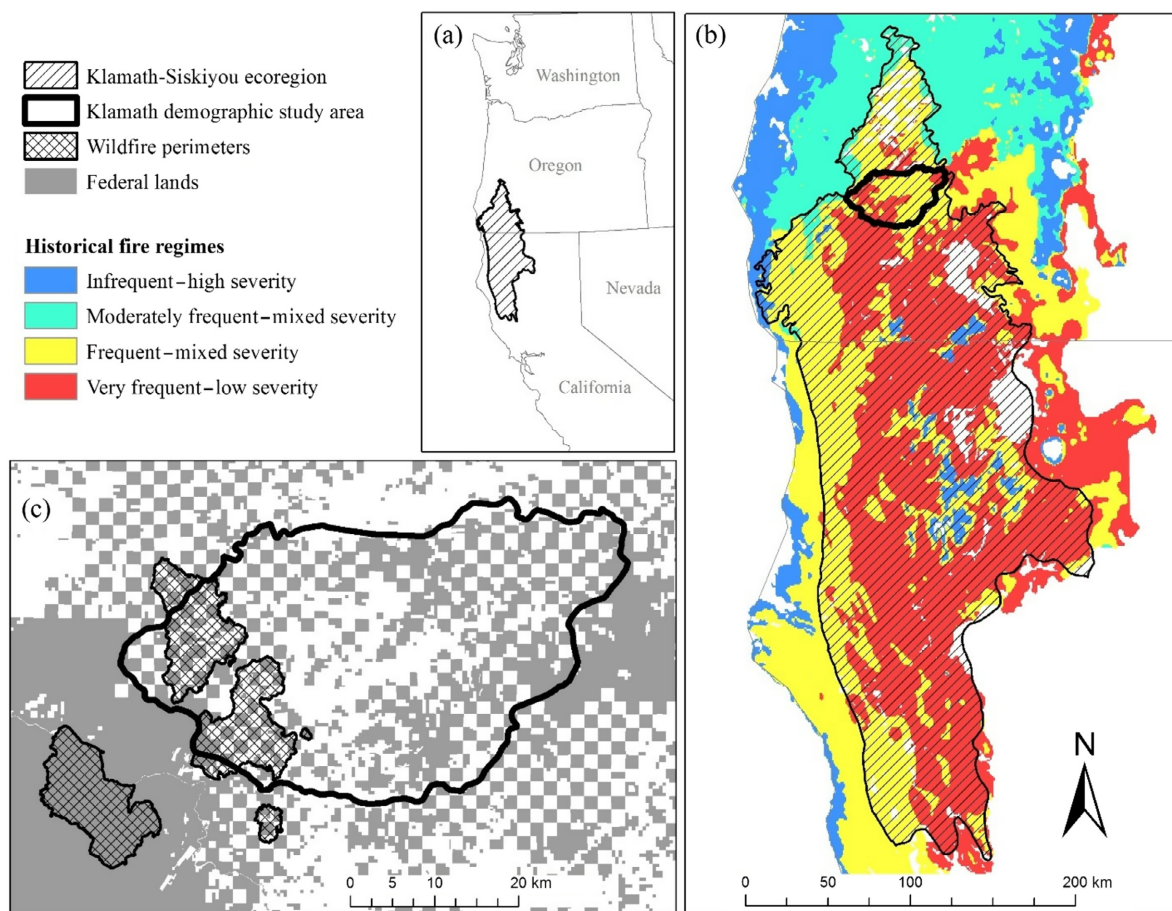


Fig. 1. Maps showing (a) the Klamath-Siskiyou ecoregion of California and Oregon, USA (hatched area); (b) historical fire regimes in the Klamath-Siskiyou ecoregion (Spies et al. 2018), Klamath northern spotted owl demography study area (1422 km²; center = 123.315° W, 42.782° N, heavy black border); and (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

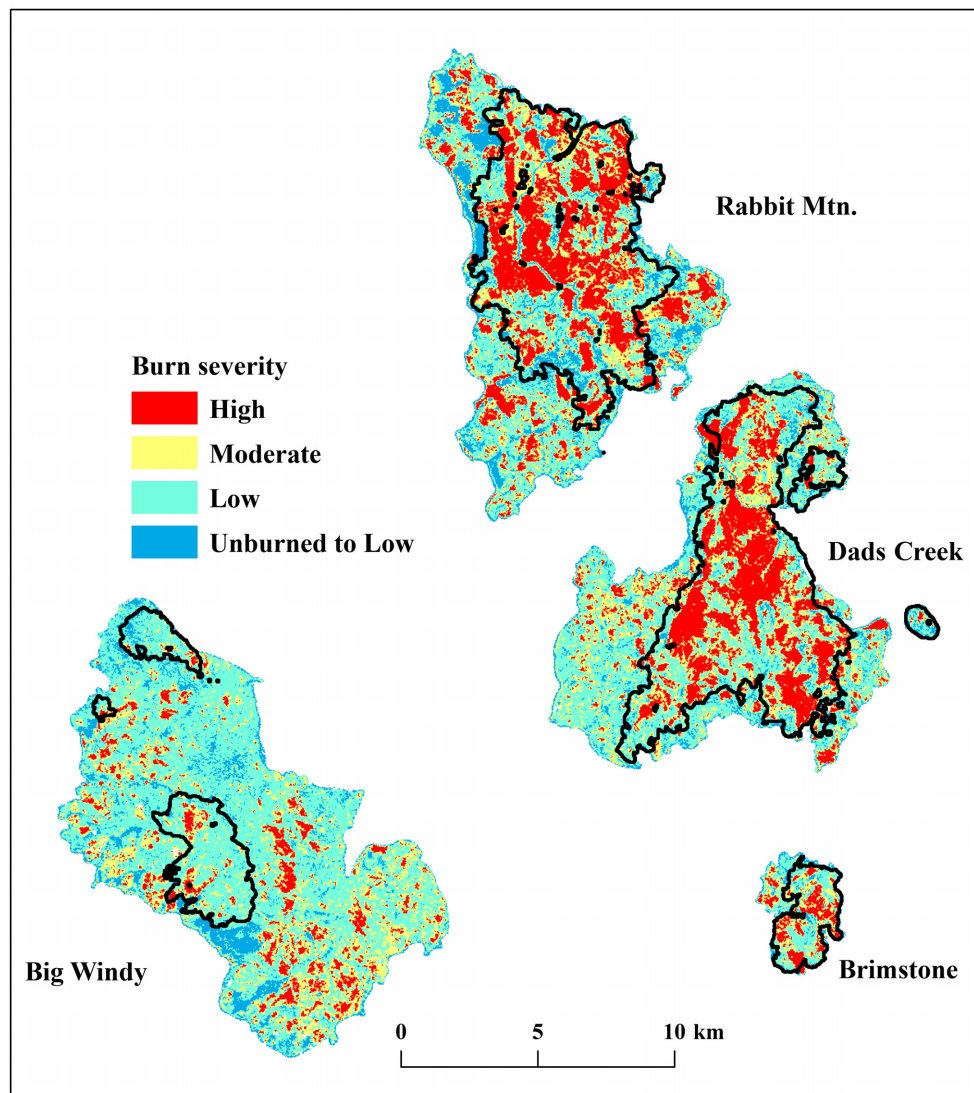


Fig. 2. Map of monitoring trends in burn severity (Eidenshink et al. 2007) data for the Big Windy and Douglas Complex Fires in southwest Oregon, USA, 2013. Severity is based on change in normalized burn ratio (dNBR) from Landsat-8 images from pre- and post-fire. The perimeter of the fires after the fourth 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 $\sim 567,000$ ha. Within this OLC Rogue River collection area, $\sim 50,000$ 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

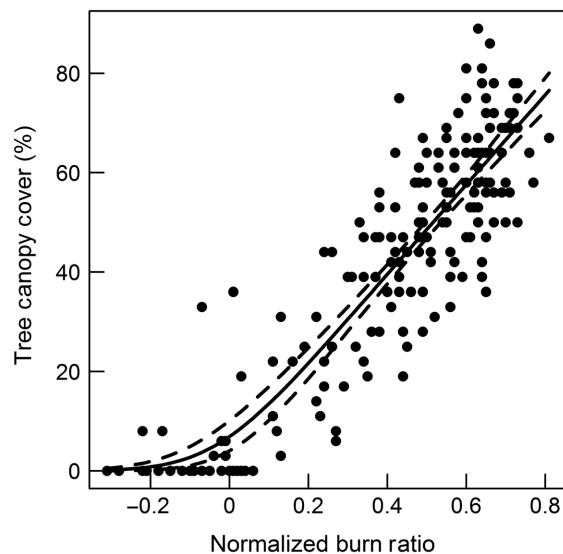


Fig. 3. Mean (solid line) and 95% confidence intervals (dashed lines) for predicted live tree canopy cover as a function of normalized burn ratio within the Douglas Complex and Big Windy Fires in southwest Oregon, USA, in 2013 based on the zero-truncated regression model.

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),

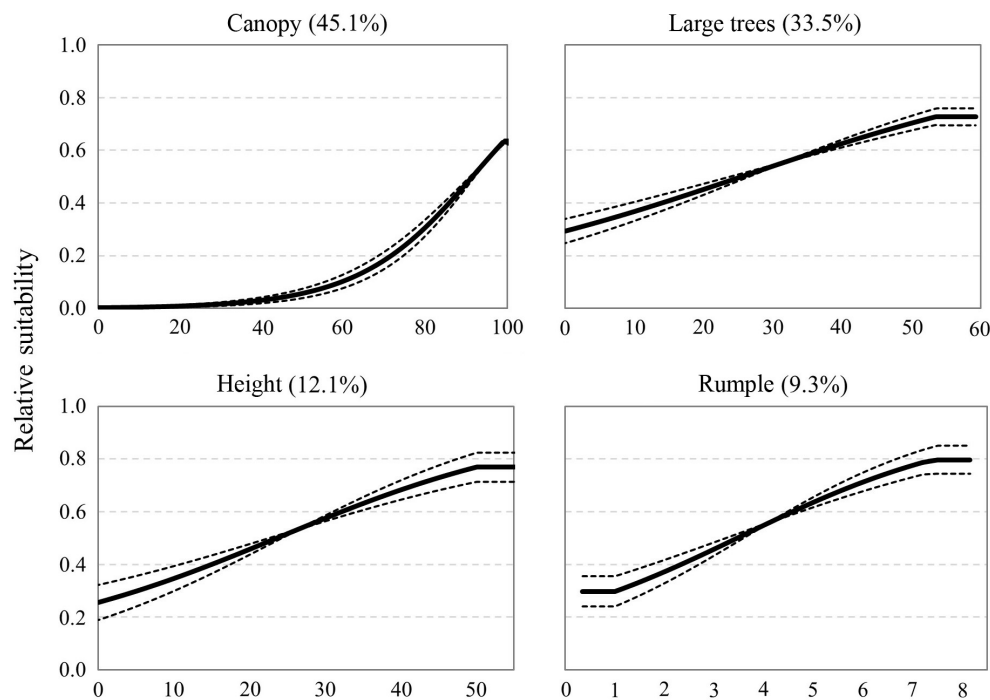


Fig. 4. Variable response functions with percent contribution (%) to pre-fire nesting/roosting habitat suitability model for northern spotted owls in the Klamath demographic study area in southwest Oregon, USA, where the Douglas Complex and Big Windy Fires burned in 2013. The solid line represents the 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 (rump 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

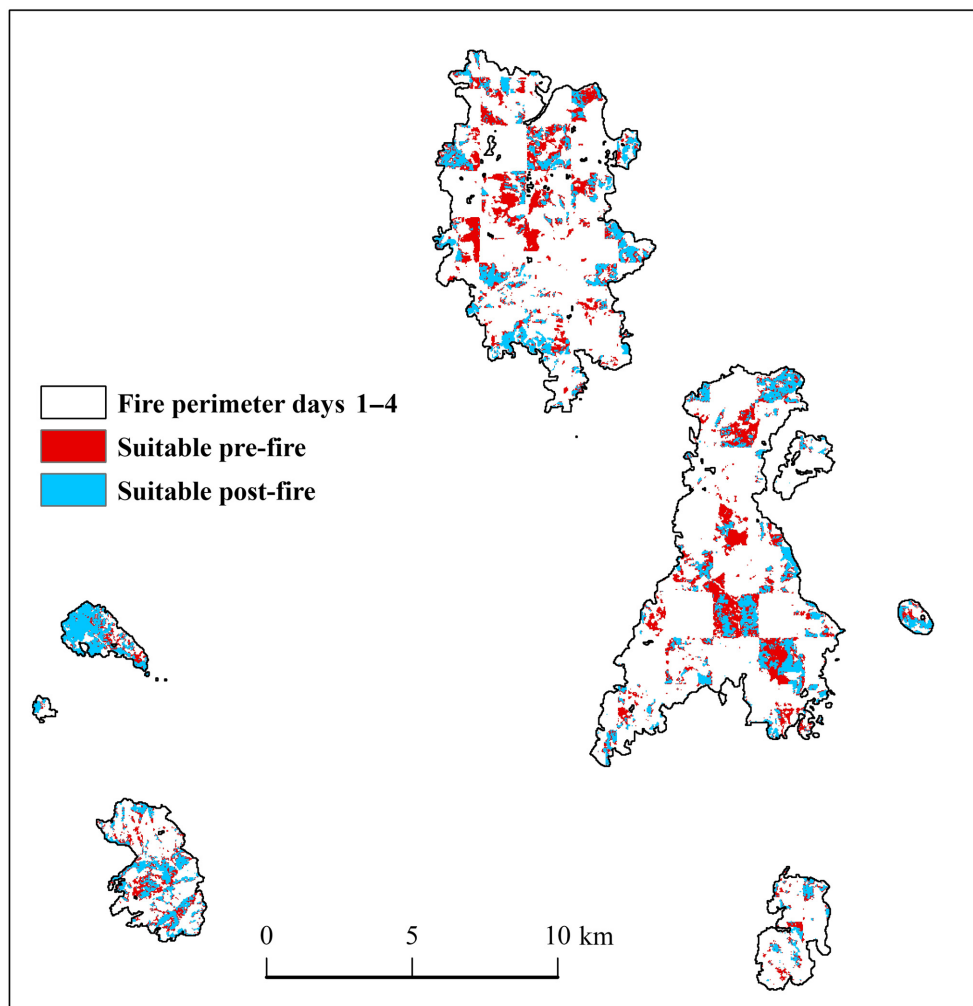


Fig. 5. Patterns of conversion from suitable habitat to unsuitable conditions for northern spotted owl nesting and roosting in the Douglas Complex and Big Windy Fires that burned in southwestern Oregon, USA. Binary classification of nesting/roosting habitat was based on predicted vs. expected ratio threshold 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

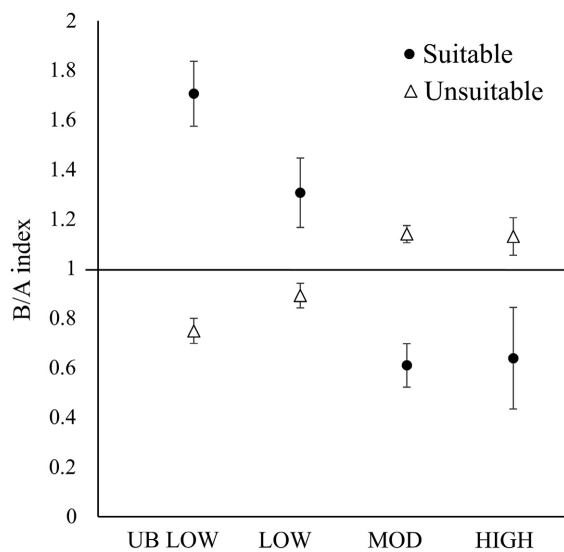


Fig. 6. Ratio of proportion of suitable and unsuitable nesting/roosting habitat that burned (B) at each fire severity to what was available (A) to burn (B/A index) with 95% confidence intervals, Douglas Complex and Big Windy Fires, southwestern Oregon, USA, 2013. We used Monitoring Trends in Burn Severity (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 (Schoenagel 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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ORIGINAL RESEARCH

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Northern spotted owl nesting forests as fire refugia: a 30-year synthesis of large wildfires

Damon B. Lesmeister^{1,2*} , Raymond J. Davis³, Stan G. Sovern^{1,2} and Zhiqiang Yang⁴

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

* Correspondence: damon.lesmeister@usda.gov

¹USDA Forest Service, Pacific Northwest Research Station, 3200 NW Jefferson Way, Corvallis, OR 97331, USA

²Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, OR 97331, USA

Full list of author information is available at the end of the article



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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.

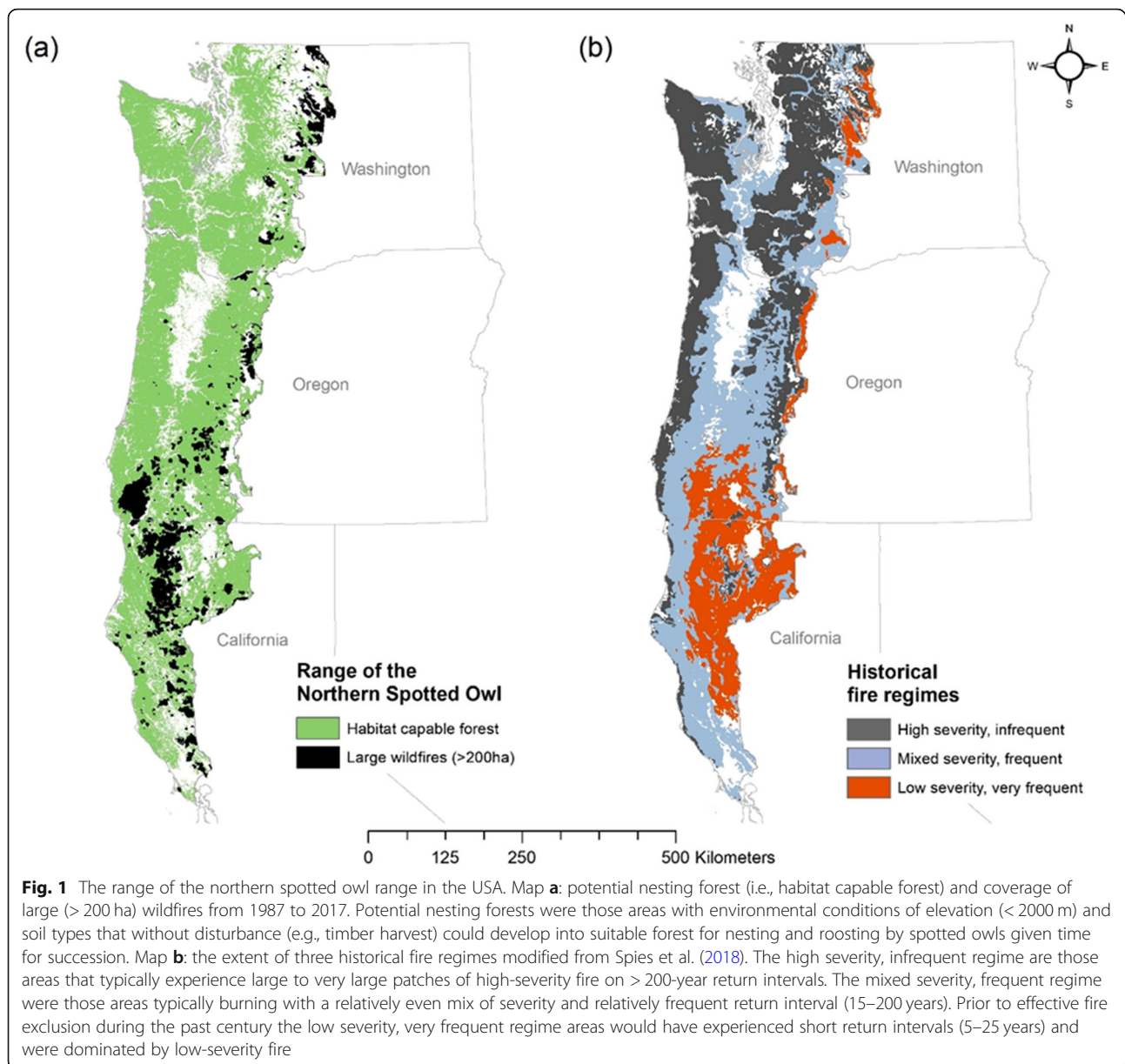
Fire refugia can be defined as landscape elements that remain unburned, burn less frequently, or burn at lower severity than the surrounding landscape (Meddens et al. 2018). We sought to determine if northern spotted owl nesting forest may be considered fire refugia by burning at lower severity than 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.



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 km² 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).

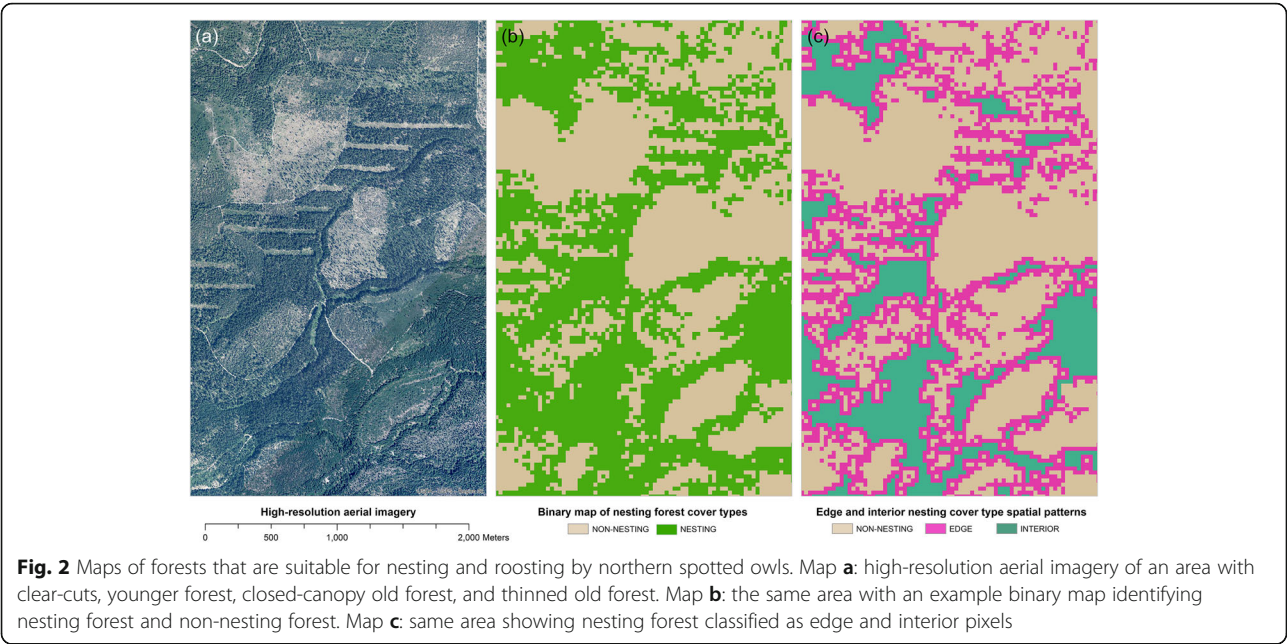
Information on pre-fire forest species composition and structure is critical for examining relationships between forest types and wildfire effects (Meigs and Krawchuk 2018; Lesmeister et al. 2019). We used newly developed maps of suitable nesting forests that were generated by the NWFP northern spotted 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 km², with 17,273 km² 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



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 km²) 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)

^aAverage stand age based on field-recorded ages of live dominant and codominant trees
^bPercent canopy cover of live conifer trees
^cDiameter (cm) at breast height of live conifer trees
^dIndex of structural diversity based on live conifer tree densities in different diameter classes (Davis et al. 2016)
^eAverage height (m) of live dominant and codominant trees
^fDensity (trees/ha) of large (> 75 cm d.b.h.) live conifer trees

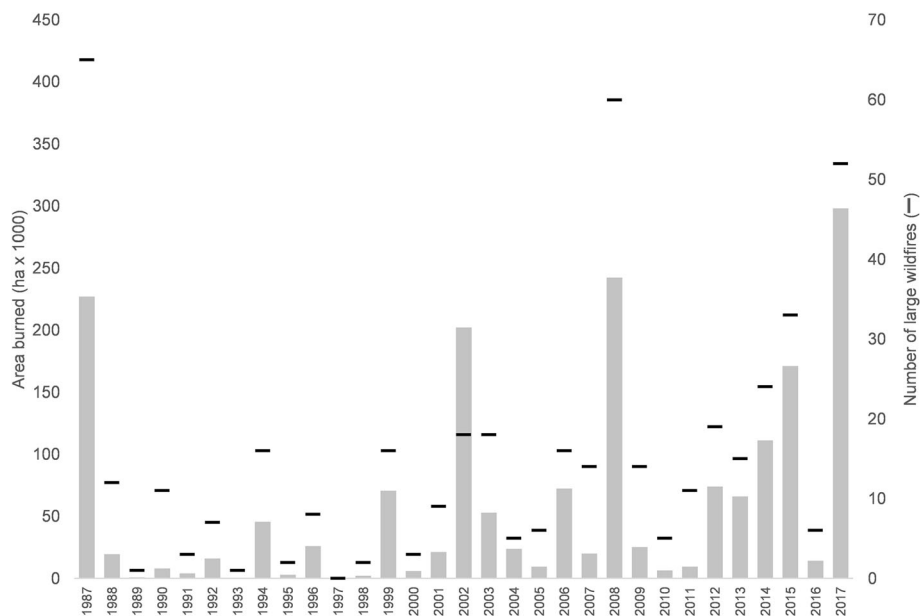


Fig. 3 Total area of potential nesting forest that burned each year during large wildfires (≥ 200 ha). Potential nesting forests were those areas with environmental conditions of elevation (below 2000 m) and soil types that without disturbance (e.g., timber harvest) could develop into suitable forest 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 ($B/A = 1.17$, $CI = 1.13\text{--}1.22$) and lower average odds of burning at moderate ($B/A = 0.84$, $CI = 0.79\text{--}0.90$) or high ($B/A = 0.89$, $95\% CI = 0.81\text{--}0.96$) fire severity (Fig. 4a). Conversely, NON-NESTING forest had lower average odds of burning at unburned-low severity ($B/A = 0.97$, $CI = 0.95\text{--}0.98$) and higher average odds of burning at moderate ($B/A = 1.04$, $CI = 1.03\text{--}1.06$) or high ($B/A = 1.05$, $CI = 1.02\text{--}1.07$) 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 ($B/A = 1.25$, $CI = 1.18\text{--}1.31$) and lower odds of burning at moderate ($B/A = 0.81$, $CI = 0.72\text{--}0.89$) or high severity ($B/A = 0.86$, $CI = 0.74\text{--}0.99$; Fig. 4b). EDGE forest had lower odds of burning at moderate severity ($B/A = 0.95$, $CI = 0.92\text{--}0.98$), but B/A ratios were near 1 for unburned-low ($B/A = 1.02$, $CI = 0.99\text{--}1.05$) and high severity ($B/A = 1.04$, $CI = 0.94\text{--}1.13$; Fig. 4b). The NON-NESTING forest had low odds of burning at unburned-low severity ($B/A = 0.95$, $CI = 0.93\text{--}0.96$) but was more likely to burn at moderate ($B/A = 1.06$, $CI =$

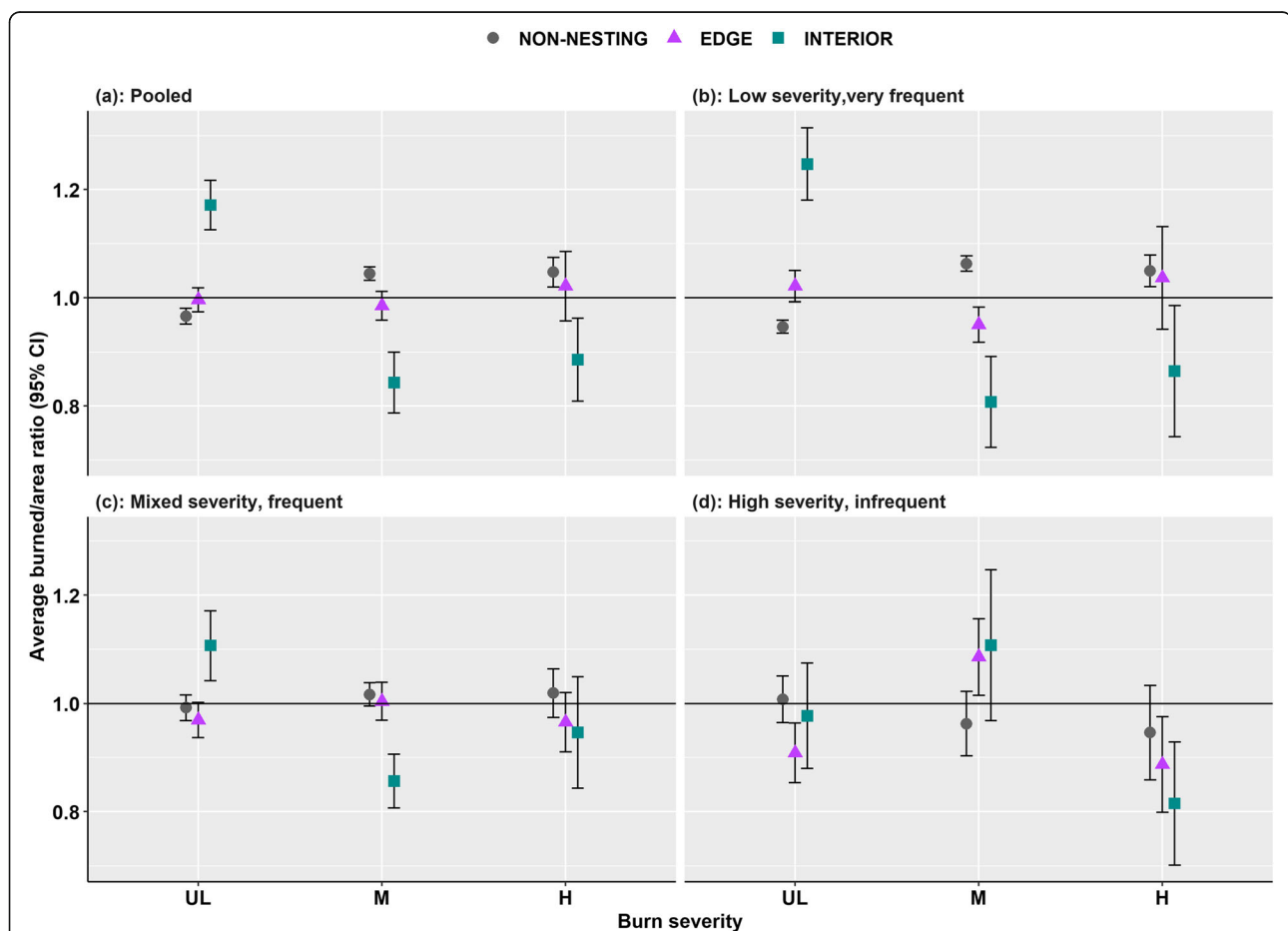


Fig. 4 Burned/area (B/A) ratios with 95% confidence intervals for forest types burned by severity class for 472 large (≥ 200 ha) wildfires in the range of the northern spotted owl, USA, 1987–2017. Forest types were INTERIOR nesting (cyan squares), EDGE nesting (orchid triangles), and NON-NESTING forest (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 CI s 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 CI s 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).

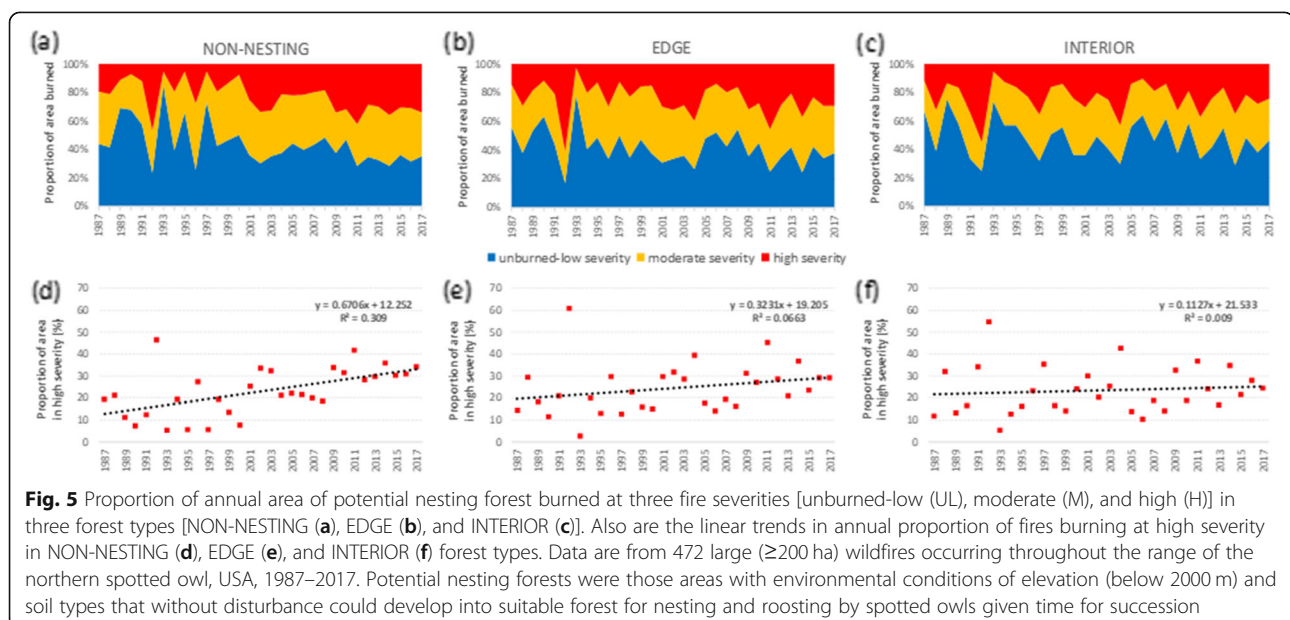
Fire severity patterns and trends

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





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 broad-scale 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

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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.

Author details

¹USDA Forest Service, Pacific Northwest Research Station, 3200 NW Jefferson Way, Corvallis, OR 97331, USA. ²Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, OR 97331, USA. ³USDA Forest Service, Pacific Northwest Region, 3200 NW Jefferson Way, Corvallis, OR 97331, USA. ⁴USDA Forest Service, Rocky Mountain Research Station, 507 25th Street, Ogden, UT 84401, USA.

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Salvage Logging, Ecosystem Processes, and Biodiversity Conservation

D.B. LINDENMAYER* AND R.F. NOSS†

*Centre for Resource and Environmental Studies, The Australian National University, Canberra, ACT 0200, Australia, email davidl@cres.anu.edu.au

†Department of Biology, University of Central Florida, Orlando, Florida 32816–2368, U.S.A.

Abstract: *We summarize the documented and potential impacts of salvage logging—a form of logging that removes trees and other biological material from sites after natural disturbance. Such operations may reduce or eliminate biological legacies, modify rare postdisturbance habitats, influence populations, alter community composition, impair natural vegetation recovery, facilitate the colonization of invasive species, alter soil properties and nutrient levels, increase erosion, modify hydrological regimes and aquatic ecosystems, and alter patterns of landscape heterogeneity. These impacts can be assigned to three broad and interrelated effects: (1) altered stand structural complexity; (2) altered ecosystem processes and functions; and (3) altered populations of species and community composition. Some impacts may be different from or additional to the effects of traditional logging that is not preceded by a large natural disturbance because the conditions before, during, and after salvage logging may differ from those that characterize traditional timber harvesting. The potential impacts of salvage logging often have been overlooked, partly because the processes of ecosystem recovery after natural disturbance are still poorly understood and partly because potential cumulative effects of natural and human disturbance have not been well documented. Ecologically informed policies regarding salvage logging are needed prior to major natural disturbances so that when they occur ad hoc and crisis-mode decision making can be avoided. These policies should lead to salvage-exemption zones and limits on the amounts of disturbance-derived biological legacies (e.g., burned trees, logs) that are removed where salvage logging takes place. Finally, we believe new terminology is needed. The word salvage implies that something is being saved or recovered, whereas from an ecological perspective this is rarely the case.*

Keywords: forest management, human disturbance, natural disturbance

Cosecha de Salvamento, Procesos Ecológicos y Conservación de la Biodiversidad

Resumen: *Resumimos los impactos documentados y potenciales de la cosecha de salvamento – una forma de cosecha de madera que remueve árboles y otros materiales biológicos después de una perturbación natural. Tales operaciones pueden reducir o eliminar legados biológicos, modificar hábitats post perturbación, influir en poblaciones, alterar la composición de comunidades, impedir la recuperación de la vegetación natural, facilitar la colonización de especies invasoras, alterar las propiedades del suelo y de niveles de nutrientes, incrementar la erosión, modificar regímenes hidrológicos y ecosistemas acuáticos, y alterar patrones de heterogeneidad del paisaje. Estos impactos se pueden asignar a tres efectos amplios e interrelacionados: (1) alteración de la complejidad estructural del bosque; (2) alteración de procesos y funciones ecológicas; y (3) alteración de poblaciones de especies y de la composición de la comunidad. Algunos impactos pueden ser diferentes a o adicionales a los efectos de la cosecha de madera tradicional que no es precedida de una perturbación natural severa porque las condiciones antes, durante y después de la cosecha de salvamento pueden diferir de las que caracterizan a la cosecha de madera tradicional. Los impactos potenciales de la cosecha de salvamento a menudo han sido pasados por alto, en parte porque los procesos de recuperación del ecosistema después de una perturbación natural son poco conocidos y en parte porque los efectos acumulativos potenciales de*

perturbaciones naturales y humanas no han sido bien documentados. Se requieren políticas ecológicamente informadas para la cosecha de salvamento para que cuando ocurran las perturbaciones naturales se evite la toma de decisiones en situaciones de crisis. Estas políticas deberán establecer zonas exentas de salvamento y límites a las cantidades de legados biológicos derivados de la perturbación (e. g., árboles quemados, troncos) que son removidos donde se lleva a cabo la cosecha de salvamento. Finalmente, creemos que se requiere una nueva terminología. La palabra salvamento implica que algo está siendo salvado o recuperado, y este raramente es el caso desde una perspectiva ecológica.

Palabras Clave: conservación de la biodiversidad, gestión forestal, procesos ecosistémicos

Introduction

Large-scale natural disturbances, including wildfires, floods, mudslides, volcanic eruptions, earthquakes, tsunamis, insect attacks, windstorms, and hurricanes occur at varying intervals in most ecosystems worldwide (Holling et al. 1995; Bryant 2001; Schoener et al. 2004). In many cases major efforts are mounted to “clean up” after natural disturbances (Robinson & Zappieri 1999; Beschta et al. 2004). This is particularly true in forest landscapes where salvage harvesting of disturbed stands is widely practiced for such reasons as recouping economic losses before serious deterioration of trees occurs (Ulbricht et al. 1999; Shore et al. 2003) and ostensibly assisting ecosystem recovery (e.g., by speeding the reestablishment of forest cover) (Sessions et al. 2004). Questionable assumptions used to justify salvage include the perception that naturally disturbed areas have limited value for biota (Morissette et al. 2002), that damaged trees will attract insects that will attack adjacent undisturbed stands (Amman & Ryan 1991), and that dead trees create abundant fuels and an increased fire risk and threat to public safety (Ne’eman et al. 1997; Shore et al. 2003).

The published literature is replete with studies of the impacts of traditional (nonsalvage) forms of logging on individual elements of the biota, the structure and composition of stands, landscape patterns and composition, and key ecosystem processes and functions (Hunter 1999; Lindenmayer & Franklin 2002; Burton et al. 2003). Considerably less work has been conducted on salvage logging (McIver & Starr 2001; Beschta et al. 2004; Karr et al. 2004), and much of that is in gray literature, which can be difficult to obtain. A key issue is whether the impacts of salvage logging are different from, and potentially more detrimental than, other forms of logging that are not preceded by a major natural disturbance. Conditions that precede logging, conditions under which logging occurs, type and characteristics of trees logged, and logging practices applied may all differ between salvage logging and conventional logging, and these differences may have important influences on the maintenance of ecosystem processes and biodiversity.

Special environmental conditions may precede major natural disturbance events. For example, extensive soil

wetting occurs before the high winds associated with hurricanes and cyclones (Elliott et al. 2002). Prolonged droughts and high temperatures are typical before wildfires in some forest types (Bradstock et al. 2002), and these can exert strong influences on many organisms (Rübsamen et al. 1984).

Salvage logging is conducted in disturbed ecosystems. In such ecosystems the organic component of soils may have been burned or mineral soil exposed, which can make soils vulnerable to additional impacts such as those associated with salvage logging (Shakesby et al. 1996; McIver & Starr 2000, 2001).

Salvage logging involves the removal of particular trees or stands that are often uncommon, such as charred standing stems, recently windblown trees, trees partially immersed in volcanic ash, or the largest trees that remain—because of their economic value (Morissette et al. 2002). Conditions following stand-replacing disturbances in many regions are among the most biologically diverse and most imperiled of all forest conditions (Franklin & Agee 2003).

Salvage logging sometimes takes place in ways that are more intensive or extensive than traditional forms of logging (McIver & Starr 2000; van Nieuwstadt et al. 2001) or in areas where traditional logging might not normally occur. For example, harvesting operations may affect soils that have been previously altered by fire, cutover sizes can be larger (Radeloff et al. 2000), and road networks more extensive.

Given these differences between traditional harvesting and salvage logging and that salvage logging is a combination of disturbances, a fundamental question is, does salvage logging have different and/or additional effects than either a natural disturbance alone or traditional logging alone? Answering this question is difficult because salvage logging has received relatively little attention from ecologists and conservation biologists (Morissette et al. 2002) and significant limitations plague many of the studies that have been completed (McIver & Starr 2000). Hence, salvage policies sympathetic to conservation concerns are not well developed in many jurisdictions (e.g., Quebec in Nappi et al. 2003; Lindenmayer et al. 2004).

The contributions to this special section of *Conservation Biology* attempt to redress some of the problems

created by the lack of knowledge and understanding of the impacts of salvage logging. As a prelude to the case studies, we provide a brief overview of the potential impacts of salvage logging on biota and ecosystem processes. Our review is based on a systematic search of the literature for published material on salvaging. We accessed biological databases and scanned citation lists of papers dedicated to the topic. We build on an earlier review by McIver and Starr (2000), which examines literature on postfire salvage logging up to mid-1998, primarily in western N. America, and add information from other parts of the world as well as make some important salvage-harvesting policy recommendations. Given limited space, our overview is indicative of the sorts of impacts that may accompany salvage logging rather than a comprehensive and exhaustive treatment of the literature. Most of our discussion relates to those forest ecosystems where salvaging is most prevalent.

Definitions and Background

We broadly define salvage logging as the harvesting of trees and other biological material from areas after natural, or sometimes human-caused, disturbance events. Salvage logging is practiced after floods (Gregory 1997), volcanic eruptions (Franklin & MacMahon 2000), wildfires (Stuart et al. 1993; McIver & Starr 2000; Nappi et al. 2004), insect attacks (Radeloff et al. 2000; Brooks 2001; Shore et al. 2003), and hurricanes, cyclones, and windstorms (Foster et al. 1997; Elliott et al. 2002; Greenberg 2002). Salvage harvesting is widespread and occurs in temperate (Morissette et al. 2002) and tropical forests (van Nieuwenstadt et al. 2001). It is most prevalent in ecosystems where natural disturbances, particularly wildfires and insect attacks, are stand-replacing or partial stand-replacing events (Nappi et al. 2004; reviewed by McIver & Starr 2000).

Salvage logging has been practiced for a long time. For example, extensive salvaging occurred after a major hurricane in northeastern United States in 1938 (Foster et al. 1997). Similarly, wet eucalypt forests in eastern Australia were salvage harvested following wildfires in 1926, 1932, and 1939 (Lindenmayer & Ough 2006 [this issue]). Forests in western Oregon (U.S.A.) damaged in the 1933 Tillamook burn were salvaged until at least 1959 (J. Franklin, personal communication).

Natural Disturbance Regimes and Ecosystem Dynamics

Prior to examining some of the potential impacts of salvaging logging, we provide context to our discussion by outlining some modern perspectives on the role of natural disturbance in ecosystem dynamics. Part of the

motivation for salvage logging is underpinned by common perceptions of events such as wildfires, hurricanes, or floods as disasters or catastrophes. The affected landscapes are widely referred to as “destroyed,” “damaged,” “consumed,” or “lost”—terms sometimes even used by ecologists (e.g., Ne’eman et al. 1997).

In contrast to past characterizations of disturbances as disasters that need cleaning up, it has become clear that natural disturbances are key processes in the majority of ecosystems (Pahl-Wostl 1995). Indeed, recent paradigms in ecology emphasize both the dynamic, nonequilibrium nature of ecological systems of which disturbance is a recurring feature (Pickett et al. 1992; Holling et al. 1995) and the interrelationships between natural disturbance regimes and the maintenance of biodiversity (Hansen & Rotella 1999; Bradstock et al. 2002; Shiel & Burslem 2003). An increasing body of evidence indicates that many species and ecosystems have evolved with, and are adapted to, various types of natural disturbance (Rülker et al. 1994; Bunnell 1995; Bradstock et al. 2002). Good empirical data also exist on natural recovery processes in intensively disturbed ecosystems, for instance the response of the Greater Yellowstone Ecosystem following the 1988 conflagration there (Turner et al. 2003) and the Mt. St. Helens ecosystem following the 1980 volcanic eruption (Franklin & MacMahon 2000).

Potential Impacts of Salvage Harvesting

As in the case of conventional logging, the impacts of salvage logging vary in response to a wide range of factors, including the ecosystem, ecological processes, and particular elements of the biota in question; the type, intensity, frequency, and spatial pattern of logging and the preceding natural disturbance; and the potential cumulative impacts of the type and intensity of a preceding natural disturbance coupled with logging pattern, intensity, and frequency. Generalizing from the limited research to date, the impacts of salvage logging can be classified into three broad categories: (1) impacts on the physical structure of forest stands and aquatic systems; (2) impacts on key ecosystem processes (e.g., hydrological cycles, nutrient cycling, and soil formation); and (3) impacts on particular elements of the biota and species assemblages. These impacts, considered below, are often interrelated and cumulative.

Salvage Harvesting, Stand Structural Complexity, and Biodiversity Responses

Patterns of ecosystem recovery and revitalization, together with the recovery of many elements of the biota within these ecosystems, are influenced by the types, numbers, and spatial arrangements of biological legacies remaining following natural disturbance (Lindenmayer & Franklin 2002). Biological legacies are organisms, organically derived structures, and organically produced

Table 1. Ecological roles of biological legacies* on patterns of ecosystem recovery and revitalization.

Role	Reference
Enriches recovering vegetation	Hansen et al. 1991; Lindenmayer & McCarthy 2002
Facilitates survival and population viability of various species in disturbed areas	Hutto 1995; Franklin & MacMahon 2000; Whelan 1995
Provides habitat for species that eventually recolonize a disturbed site	Lindenmayer et al. 1997; Nappi et al. 2003
Promotes plant and animal recolonization of disturbed areas	Whelan 1995
Provides a source of energy and nutrients for other organisms	Perry 1994; Hutto 1995
Modifies or stabilizes environmental conditions on disturbed sites	Perry 1994

*Biological legacies are organisms, organically derived structures, and organically produced patterns that survive from the predisturbance system (Franklin et al. 2000) (e.g., thickets of understory vegetation, logs, patches of undisturbed or partially disturbed forest).

patterns that survive from the predisturbance system (Franklin et al. 2000). In forests, biological legacies include intact thickets of understory vegetation (Ough 2002), large living and dead overstory trees (Gibbons & Lindenmayer 2002), logs (Harmon et al. 1986), and patches of undisturbed or partially disturbed forest (DeLong & Kessler 2000). Biological legacies can be critical for biodiversity and influence the rate and pathway of postdisturbance recovery (Franklin et al. 2000) in many ways (Table 1). Among the factors that make recently disturbed forests biologically diverse are a combination of surviving and pioneering species; diverse plant life forms and structures, which provide habitat for many organisms; high availability of light and moisture; and a variety of microclimates (Noss et al. 2006).

Salvage logging by definition removes some or all of the biological legacies created by natural disturbances and earlier mortality and patch dynamics, therefore potentially diminishing the effectiveness of some or all of the ecological roles listed in Table 1. Removal of biological legacies also simplifies the structure of forest stands (Hutto 1995; Franklin et al. 2000), homogenizes landscape pattern (Radeloff et al. 2000), and reduces connectivity between unburned areas (Morissette et al. 2002).

Dead and charred trees created by wildfires are key biological legacies lost or depleted through salvage operations (Murphy & Lehnhausen 1998; Nappi et al. 2003). Others include malformed trees (Cooper-Ellis et al. 1999), large logs and coarse woody debris (Minshall 2003), and tip-up mounds (Cooper-Ellis et al. 1999). The removal of large quantities of biological legacies can be followed by prolonged periods of time before new ones are created. For example, the removal of burned standing trees may preclude the recruitment of large pieces of coarse woody debris to the forest floor and associated stream environments for multiple decades (Minshall 2003).

The depletion or loss of biological legacies through salvage has implications for biota dependent on them (Hutto 1995, 2006 [this issue]; Saab & Dudley 1998; Haggard & Gaines 2001; Morissette et al. 2002). For example, areas regenerating after fire can be rare habitats in many landscapes as a consequence of long-term fire suppression and/or historical logging practices, as well as sal-

vage logging (Zackrisson 1977; Shinneman & Baker 1997; Noss et al. 2006). Many species of animals (some rare or threatened) are attracted to places that are burning and many plants germinate in recently burned areas (Murphy & Lehnhausen 1998; Imbeau et al. 2001; Smucker et al. 2005). Salvage logging removes key structural and other attributes from these habitats and may negatively influence species closely associated with them, thus substantially altering assemblages and communities (Morissette et al. 2002). These include taxa associated with charred standing trees and logs created by fires such as woodpeckers (Hutto 1995, 2006; Murphy & Lehnhausen 1998; Nappi et al. 2003), carnivorous mammals (Bull et al. 2001), highly specialized beetles (Buprestidae and Cerambycidae) (Buddle et al. 2000; Grove et al. 2002), and bryophytes (Scott 1985).

The impacts of salvage logging on biodiversity have been examined in several studies. The results are variable as would be expected from work conducted across a range of forest types subject to different intensities and frequencies of human and natural disturbance (e.g., Stuart et al. 1993; Greenberg et al. 1995) and across different taxa among and within forest types (e.g., Greenberg & McGrane 1996).

There appears to be a bias toward work on structural features of altered stands and biota associated with dead and charred trees (particularly birds and mammals), with many of these studies demonstrating or forecasting negative impacts of salvage logging (e.g., Morissette et al. 2002), although neutral or positive outcomes were reported in some investigations (Greenberg et al. 1995; Greenberg 2002) such as those of microbial assemblages (Khetmalas et al. 2002) and plants (Ne'eman et al. 1997; Elliott et al. 2002). Radeloff et al. (2000) suggest that area-sensitive species in the Pine Barrens of northwestern Wisconsin (U.S.A.), such as the Sharp-tailed Grouse (*Tympanuchus phasianellus*), benefit from the extensive open habitats created by salvage logging.

Several studies acknowledge problems of inference related to experimental design (see McIver & Starr 2000) such as a lack of disturbed but unsalvaged sites (Greenberg et al. 1995; Greenberg & McGrane 1996; Elliott et al. 2002; Khetmalas et al. 2002) and/or the absence of

predisturbance data (Greenberg et al. 1994). In addition, it is also unclear how prolonged the impacts of salvage logging may be. Work by Greenberg and Thomas (1995) shows no between-treatment differences in beetle assemblages 5–7 years after fire. In contrast, salvage logging after the 1939 Victorian wildfires has contributed to a pronounced shortage of cavity trees for more than 40 species of vertebrates—a major biodiversity conservation problem that will take more than 200 years to rectify (Lindenmayer et al. 1997).

Salvage harvesting may have impacts on biodiversity in ways other than through structural alteration of stands. For example, postdisturbance plant recovery can be changed (e.g., levels of resprouting; Cooper-Ellis et al. 1999; Lindenmayer & Ough 2006), leading to altered composition of plant species and abundance of plant life forms (Stuart et al. 1993). For example, seedlings that germinate following a wildfire may be damaged or killed by mechanical disturbance associated with subsequent salvage logging (van Nieuwstadt et al. 2001). Natural regeneration of conifers after high-severity fire in southwestern Oregon was generally abundant in unsalvaged stands, in contrast to salvaged areas where regeneration was significantly reduced and short-term fire risk increased (Donato et al. 2006). In addition, human intervention to speed the recovery of fire-damaged and salvaged vegetation through deliberate plantings to restore tree cover may actually impair natural regeneration processes, reduce or eliminate the distinctive biodiversity of slowly recovering forests, and even create weed problems when exotic grasses and other herbaceous species are established. This is considered to be the case in the Douglas-fir (*Pseudotsuga menziesii* [Mirb] Franco) forests of the Pacific northwest (U.S.A.), where large, naturally regenerating areas that have not been subject to salvage and replanting are extremely rare and valuable for many species (Noss et al. 2006; J. Franklin, personal communication).

Salvage Logging and Ecosystem Processes

Major disturbances can enhance ecological processes and aid ecosystem restoration by creating some of the structural complexity and landscape heterogeneity lost through past human management. For example, floods can reshape riparian areas through sediment erosion and deposition and debris movement (Bayley 1995) such that they revitalize human-modified aquatic ecosystems (Gregory 1997). Similarly, wildfires create dead wood (Angelstam 1996) and promote the development of cavities in trees (Inions et al. 1989)—structural attributes that are depleted by some forestry practices (Lindenmayer & Franklin 2002).

Conversely, salvage logging often impairs key ecosystem processes such as hydrological regimes (e.g., soil erosion and consequent in-stream sedimentation; Helvey 1980; Karr et al. 2004; Reeves et al. 2006 [this issue]),

cavity-tree formation, soil profile development, and nutrient cycling. In contrast to the natural recovery of a disturbed ecosystem, salvage harvesting has the potential to “convert a relatively intact system to a strongly modified site in which ecosystem control is reduced” (Cooper-Ellis et al. 1999:2693).

An example of the potential for salvage logging to impair ecosystem processes is the prolonged change in regional hydrological regimes that occurred after the massive “clean-up” operations that followed the 1938 hurricane in the northeastern United States (Foster et al. 1997). In a study in Portugal postfire salvage and subsequent site preparation for replanting led to sediment losses 100 times those of background levels (Shakesby et al. 1993). The horizon depth and organic content of soils under salvaged wind-blown forests in Maine were significantly more affected by subsequent fires than where salvage did not occur (Hansen 1983; M. Hunter, personal communication). Results of studies in Quebec show that salvage logging on sites subject to high-severity fires led to depleted soil calcium, magnesium, and phosphorus that will not return to prefire levels within the planned rotation time of 110 years (Brais et al. 2000). Additional road building associated with salvage logging and ground skidding of logs (which alters the properties of upper soil layers) increases both soil compaction and erosion in already fire-damaged watersheds (McIver & Starr 2000, 2001). The sediment-catching role played by logs is lost when they are removed, which in turn may lead to significant negative impacts on aquatic ecosystems and associated macroinvertebrates (Minshall 2003). Such effects are apparent in burned catchments in southeastern Australia, where extensive salvage logging of exotic radiata pine (*Pinus radiata* D. Don) plantations has taken place.

Salvage Harvesting and Cumulative Effects

Organisms are typically best adapted to the disturbance regimes under which they evolved (Bergeron et al. 1999; Spies & Turner 1999), as highlighted by examples of taxa closely associated with recently burned areas. Nevertheless, these and other species may be susceptible to novel forms and combinations of disturbances (Paine et al. 1998). For example, they may be maladapted to the interactive effects of two disturbance events in rapid succession (Paine et al. 1998), such as the compounding, cumulative, or magnified effects of following an intense natural disturbance event soon after with intensive (and often prolonged) salvage logging (van Nieuwstadt et al. 2001; Lindenmayer & Ough 2006).

Minshall (2003) found that fire had minor and short-term impacts on stream benthic invertebrates in the western United States. Nevertheless, in burned catchments that were subsequently salvaged, impacts were predicted to be significantly greater and more prolonged.

Another form of cumulative effect relates to postdisturbance recovery patterns. In southeastern Asia, salvage logging of burned rainforests led to significant forest deterioration, with major negative impacts on the regenerative potential of stands and a wide range of other undesirable effects such as facilitating the colonization of invasive grassland plants (van Nieuwstadt et al. 2001). Similar effects have been reported for forests in northwestern North America (Roy 1956, in McIver & Starr 2000). In addition, seed banks for many species may be activated following a wildfire but then exhausted if extensive mechanical harvesting follows soon after (van Nieuwstadt et al. 2001) and/or if a second fire occurs (Whelan 1995), as is the case when regeneration burns are used to promote germination of commercial-crop trees after salvage logging of fire-damaged stands in the wet forests of Victoria, southeastern Australia (Lindenmayer & Ough 2006).

Finally, in these same forests, anecdotal information suggests that salvage logging may have impacts on key elements of stand structure that are additive to those of traditional logging. For example, large trees killed in a wildfire can remain standing for over 50 years in an unsalvaged stand (Lindenmayer et al. 1997). Conversely, fire-killed trees are more likely to collapse when the surrounding stand is logged and the remaining slash is burned in a high-intensity fire applied to promote regeneration (Ball et al. 1999). In this case, two fires (a wildfire and a postharvest regeneration burn), in combination with harvesting impacts, create greater susceptibility to collapse than a single wildfire (Lindenmayer et al. 1990). Accelerated rates of tree loss create nesting-site shortages for an array of cavity-dependent vertebrates in wet eucalypt forests (Lindenmayer et al. 1997). Similar problems are likely to occur in forests in western North America where up to 150 species of vertebrates rely on dead trees for nesting and denning (Rose et al. 2001).

Discussion

Some of the impacts we have outlined may be different from or additional to the effects of traditional forms of logging that are not preceded by large, natural disturbance events. This is because the conditions preceding, during, and after salvage logging may differ from those in areas subject to traditional logging. Moreover, the ecological benefits derived from large-scale disturbances (such as the creation of charred trees and coarse woody debris) can be lost or severely diminished by salvage operations for decades and even centuries (Lindenmayer & Ough 2006). These problems have often been overlooked or poorly understood by conservation biologists, foresters, and other natural resource managers. In some cases salvage impacts may have been so substantial that past interpretations of ecosystem responses to natural disturbance may need to be reexamined. That is, ecosystem processes and biotic

responses may have been more influenced by salvage logging than by the initial natural disturbance event. This may be true for hydrological regimes in the northeastern United States following the 1938 hurricane (Foster et al. 1997), aquatic macroinvertebrates in the western United States (Minshall 2003), and arboreal marsupials in the forests of Victoria, Australia, after the 1939 and 1983 wildfires (Lindenmayer et al. 1997).

Whereas most documented effects of salvage logging are negative from an ecological standpoint, others can be neutral or positive, depending on the response variables measured. Effects are likely to vary over time and among and within vegetation types in response to the type, intensity, and periodicity of natural disturbance and disturbance by salvage logging. Therefore, there can be no generic recipes for salvage logging that can be uncritically applied in all landscapes.

Perhaps one of the problems associated with the lack of appreciation of the impacts of salvage logging lies in the terminology itself. Dictionary definitions of the term *salvage* associate it with "recover or save" or "saving of anything from loss or danger" (e.g., Delbridge & Bernard 1989). Although salvage logging removes wood from burned areas, such practices generally do not help regenerate or save ecosystems, communities, or species (but see Radeloff et al. 2000) and often have the opposite effect. Hence, in many respects, the term *salvage* is inappropriate and misleading from ecological and conservation perspectives. An alternative term might be *postdisturbance logging*.

Some Ways Forward

There needs to be broader recognition by conservation biologists and resource managers of the (1) ability of ecosystems to recover from natural disturbances (Noss et al. 2006); (2) essential role of natural disturbances in the maintenance of biodiversity and ecosystem processes (Hutto 1995; Cooper-Ellis et al. 1999; Schmiegelow et al. 2006 [this issue]); and (3) value of recently disturbed areas as rare but often critical habitats for particular elements of the biota (Murphy & Lehnhausen 1998; Morissette et al. 2002; Noss et al. 2006). Alongside this is a need for greater recognition that the effects of human disturbances, such as logging in an environment that has been naturally disturbed, can be quite different from those of natural disturbances in isolation (Lindenmayer & McCarthy 2002). This is clear from a commentary provided by Rackham (2001: 202) in reference to forests affected by a major windstorm in southeastern England in October 1987:

... there was an immediate sense of urgency, stoked up by the press. Action was a substitute for thought. All through that [following] very wet winter, machines galumphed through the woods, getting out timber which was sold at bottom prices ... Ecological damage done by clearing up and replanting exceeded that done by the storm itself.

Components of an ecologically defensible salvage policy include the following measures.

- (1) Exclude salvage logging entirely from some areas (Hutto 1995, 2006), such as nature reserves and water catchments (e.g., Land Conservation Council 1994), extensive areas of old-growth forest, and places with few or no roads (Trombulak & Frissell 2000). Sensitive sites such as steep slopes and fragile or highly erodible soils also should be exempt from salvage harvesting (Minshall 2003; Karr et al. 2004).
- (2) Ensure that unburned or partially burned patches within the perimeter of a disturbed area (e.g., see De Long & Kessler 2000) are either exempt from salvage or subject to low-intensity harvesting with high levels of legacy retention.
- (3) Ensure that certain biological legacies are retained in salvage-logged areas such as fire-damaged trees (Hutto 1995; Nappi et al. 2004) and large (damaged or undamaged) commercially valuable trees (Morissette et al. 2002). These often have either high habitat value (e.g., for foraging by woodpeckers; Nappi et al. 2003) or a high probability of remaining standing for a prolonged period (Gibbons & Lindenmayer 2002).
- (4) Modify salvage policies to limit the amounts of biological legacies that are removed from particular sorts of areas (Hobson & Schieck 1999)—such as from burned old-growth stands within wood-production zones as currently occurs in some parts of northwestern North America (e.g., Forest Ecosystem Management Team 1993).
- (5) Schedule salvage logging so that effects on natural recovery of vegetation are limited (e.g., Roy 1956 in McIver & Starr 2000; van Niuewstadt et al. 2001). This suggestion is related to a need to appraise the ability of disturbed stands to recover naturally (Cooper-Ellis et al. 1999) and, hence, the ecological desirability of programs to replant fire-damaged areas (Noss et al. 2006).
- (6) Related to the points above, ensure the future maintenance or creation of particular habitat elements for species of conservation concern within burned areas potentially subject to salvage logging, such as some woodpeckers (Hutto 1995; Smucker et al. 2005), rare forest carnivores (Bull et al. 2001), cavity-using mammals (Lindenmayer & Ough 2006), invertebrates (Hoyt & Hannon 2002), and plants (Scott 1985).
- (7) Ensure adequate riparian buffers are in place to protect aquatic ecosystems within areas where salvage-harvesting operations occur (Minshall 2003), and retain structures such as logs and logging slash on the ground to limit soil erosion (Shakesby et al. 1993).
- (8) The effects of ground-based logging on soil and water in postdisturbance environments can be great; thus, this type of harvesting should be limited and, when-

ever possible, replaced with cable or helicopter systems for removing fire-burned trees.

A key part of better management of salvage logging is the acquisition of new knowledge to inform policies and on-the-ground operations. Although extensive research has been undertaken on the impacts of many types of disturbances (fire, logging, windstorms), remarkably little work has been conducted on salvage operations that often follow them (McIver & Starr 2000; Morissette et al. 2002). This knowledge gap needs to be addressed urgently, particularly given (1) current plans for extensive salvage operations following major natural disturbances in North America, Australia, Asia, and Europe (Lindenmayer et al. 2004; Schmiegelow et al. 2006); (2) that wood salvaged from disturbed areas is an increasing proportion of harvest volume in some regions (e.g., western North America; McIver & Starr 2000); and (3) that climate change may increase the frequency of major disturbance events such as wildfires (e.g., see Lenihan et al. 2003 for predictions for California) and insect attacks (e.g., in Canada, Shore et al. 2003) and this in turn will result in increased demands for salvage logging (Spittlehouse & Stewart 2003).

Prescriptions for the retention of biological legacies in salvaged areas are poorly formulated in many jurisdictions (e.g., Quebec; Nappi et al. 2003, 2004). Until research can catch up with the needs of forest managers, guidelines for legacy retention should be based on knowledge and understanding generated by studies of natural disturbance regimes (Lindenmayer & McCarthy 2002; Noss et al. 2006), such as the quantities, types, and spatial arrangements of biological legacies (Franklin et al. 2000). Moreover, in cases where salvage logging is permitted, well-designed experiments, natural experiments, observational studies, and monitoring programs should be established so that impacts can be investigated and rigorously compared with both undisturbed parts of landscapes and disturbed areas exempt from harvesting.

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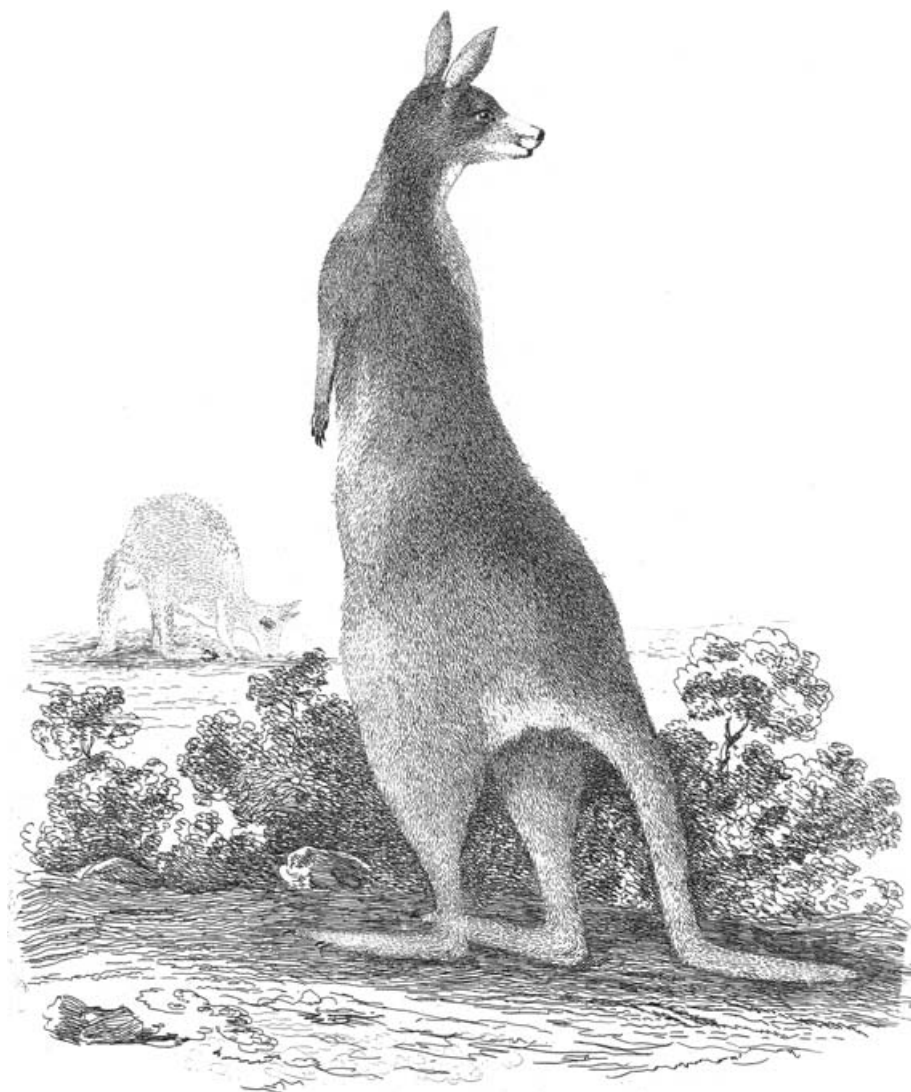
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Thinning of young Douglas-fir forests decreases density of northern flying squirrels in the Oregon Cascades

Tom Manning^{a,*}, Joan C. Hagar^b, Brenda C. McComb^a^a Department of Forest Ecosystems & Society, Oregon State University, Corvallis, OR 97331, USA^b Forest & Rangeland Ecosystem Science Center, US Geological Survey, Corvallis, OR 97331, USA

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ABSTRACT

Large-scale commercial thinning of young forests in the Pacific Northwest is currently promoted on public lands to accelerate the development of late-seral forest structure for the benefit of wildlife species such as northern spotted owls (*Strix occidentalis caurina*) and their prey, including the northern flying squirrel (*Glaucomys sabrinus*). Attempts to measure the impact of commercial thinning on northern flying squirrels have mostly addressed short-term effects (2–5 years post-thinning) and the few published studies of longer-term results have been contradictory. We measured densities of northern flying squirrels 11–13 years after thinning of young (55–65 years) Douglas-fir forest stands in the Cascade Range of Oregon, as part of the Young Stand Thinning & Diversity Study. The study includes four replicate blocks, each consisting of an unthinned control stand and one stand each of the following thinning treatments: Heavy Thin; Light Thin; and Light Thin with Gaps. Thinning decreased density of northern flying squirrels, and squirrel densities were significantly lower in heavily thinned stands than in more lightly thinned stands. Regression analysis revealed a strong positive relationship of flying squirrel density with density of large (>30 cm diameter) standing dead trees and a negative relationship with percent cover of low understory shrubs. Maintaining sufficient area and connectivity of dense, closed canopy forest is recommended as a strategy to assure that long-term goals of promoting late-seral structure do not conflict with short-term habitat requirements of this important species.

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1. Introduction

In the Pacific Northwest of North America, forest managers confronted with the legacy of decades of clearcut harvest and subsequent plantation establishment are increasingly employing a strategy of multiple commercial thinnings and long rotations to accelerate the development of late-seral structure and function from young homogeneous forests (Hayes et al., 1997; Tappeiner et al., 1997; Carey et al., 1999b; Sullivan et al., 2001). Whereas there may be economic and other objectives in pursuing this strategy (Busing and Garman, 2002), one goal is to provide more complex habitat for wildlife species with a wide range of needs (Hagar et al., 1996; Hayes et al., 1997, 2003; Humes et al., 1999).

The northern flying squirrel (*Glaucomys sabrinus*) has been considered a keystone species (Carey, 2002; Smith, 2007) in Pacific Northwest forests because it serves several important ecological functions. In much of the region, this squirrel is the primary prey of the threatened northern spotted owl (*Strix occidentalis caurina*)

(Carey et al., 1992; Forsman et al., 2001, 2004). In addition to this arboreal rodent's importance as prey for owls and other predators (Reynolds and Meslow, 1984; Wilson and Carey, 1996; Fryxell et al., 1999; Bull, 2000), its consumption of both hypogeous and epigeous fungi and dispersal of fungal spores aids in maintaining mycorrhizal communities (Maser et al., 1978; Li et al., 1986; Zabel and Waters, 1997; Gomez et al., 2005). Northern flying squirrels also are thought to be an important vector for dispersal of canopy lichens (Rosentreter et al., 1997; Zabel and Waters, 1997). Because of these relationships, this squirrel has been used as a forest-health indicator species in diverse regions of North America (McLaren et al., 1998; Betts and Forbes, 2005; Smith et al., 2005), and thus is of central concern in planning forest management and maintaining biological diversity in coniferous forests.

Considerable evidence exists that northern flying squirrels are relatively more abundant, and correlates of squirrel fitness are optimized, in forests with many large live trees (Smith et al., 2004; Gomez et al., 2005; Holloway and Malcolm, 2006; Lehmkühl et al., 2006), many large dead trees (Carey, 1995; Smith et al., 2004; Holloway and Malcolm, 2006; Meyer et al., 2007b), well-developed understories (Carey et al., 1999a; Pyare and Longland, 2002), and many large logs on the ground (Carey et al., 1999a; Gomez et al., 2005; Smith et al., 2005). Collectively, these structural elements

* Corresponding author. Tel.: +1 541 737 0946; fax: +1 541 737 1393.

E-mail addresses: tom.manning@oregonstate.edu (T. Manning), joan_hagar@usgs.gov (J.C. Hagar), brenda.mccomb@oregonstate.edu (B.C. McComb).

are typical of late-seral (mature and old-growth) forests. Some or all of these elements are largely lacking in most of the young forests now covering extensive areas of the Pacific Northwest (Spies and Cline, 1988; Halpern and Spies, 1995; Franklin et al., 2002).

As stated above, a goal of some public land managers is to use commercial thinning to accelerate the development of late-seral features within young forests, to provide high-quality habitat for late-seral species, including the northern flying squirrel. In the last two decades, experiments and retrospective studies have been attempting to test the effectiveness of this strategy, with varying results. Most found negative short-term (2–5 years) impacts of thinning (Carey, 2001; Herbers and Klenner, 2007; Meyer et al., 2007a) or similar partial harvest techniques (Waters and Zabel, 1995; Bull et al., 2004; Holloway and Malcolm, 2006) on northern flying squirrel populations, though 2 studies found no short-term effect of thinning (Ransome and Sullivan, 2002; Gomez et al., 2005).

Because thinning is expected to eventually improve habitat conditions for northern flying squirrels through acceleration of large tree growth rates, increasing mid-story complexity, and enriching understory diversity, and because these developments are relatively slow and may change trajectory over decades, studies of wildlife responses over the long term gain value in proportion to time since thinning. Only three studies have been published which describe mid-to-long-term effects of thinning on northern flying squirrels, and results are contradictory. In a retrospective study of 55–65-year-old stands in western Washington, Carey (2000) reported lower abundance of flying squirrels in twice-thinned stands than in unthinned stands with legacies of large live trees, snags, and logs. Wilson (2010), in a re-sampling of Carey's sites 12 years after half of the stands were treated with variable-density thinning, found that flying squirrel densities were very low in both thinned and unthinned stands. Ransome et al. (2004) found that pre-commercial thinning of young densely-stocked lodgepole pine (*Pinus contorta*) forests had a neutral or positive effect on flying squirrel density 12–14 years after treatment.

A recent meta-analysis of effects of silvicultural practices on northern flying squirrels (Holloway and Smith, 2011) attempted to resolve the inconsistencies of the work done so far, and found that studies asserting a benefit or no effect of harvesting on squirrel populations (Cote and Ferron, 2001; Ransome and Sullivan, 2002; Gomez et al., 2005) lacked statistical power needed to support those assertions. The implication of Holloway and Smith's meta-analysis is that forest management practices that are currently widespread in the Pacific Northwest (thinning and clearcutting) have negative short-term and long-term impacts on northern flying squirrels.

As with most of the studies cited above, the major impetus for the Young Stand Thinning & Diversity Study (YSTDS) was to investigate the effects of commercial thinning on habitat for late-seral species and to assess the potential for accelerating the development of late-successional features such as those associated with high abundance of northern flying squirrels. Similar work has taken place in British Columbia (Ransome and Sullivan, 2002; Ransome et al., 2004), Washington State (Carey, 2000; Wilson, 2010), northeastern Oregon (Bull et al., 2004), and the northern Oregon Coast Range (Gomez et al., 2005), but the YSTDS is the only experiment of this kind in the Oregon Cascades. The design of the YSTDS facilitates testing of a set of three orthogonal hypotheses about differences among treatments, minimizing the Type I error rate relative to multiple comparisons (Lehmann, 1986). With respect to the northern flying squirrel in particular, the three null hypotheses are: (1) that flying squirrel density does not differ between thinned and unthinned treatments; (2) that flying squirrel density does not differ among different thinning intensities; and (3) that flying squirrel

density does not differ between lightly thinned stands with and without small gaps.

Garman (2001) described responses of ground-dwelling small mammals and amphibians 2–5 years post-thinning for the YSTDS, but his protocol did not target tree squirrels and relatively few were captured, so data were insufficient to derive estimates of density. Nevertheless, Garman (2001) indicated that thinning had negative short-term impacts on flying squirrel densities, agreeing with most other studies that have more thoroughly investigated short-term responses of flying squirrels to thinning and similar silvicultural treatments. Here we describe patterns of density for northern flying squirrels 11–13 years after thinning in young Douglas-fir forests.

2. Methods

2.1. Study area description

The YSTDS comprises a randomized block design with 16 forest stands located on the Willamette National Forest on the west slope of the Cascade Range in Oregon (Fig. 1). The study is composed of four replicate blocks, each consisting of an unthinned control stand and 1 stand each of the following thinning treatments: (1) a Heavy Thin treatment leaving 125–137 trees per hectare (tph) and underplanted with native conifer seedlings; (2) a Light Thin treatment, approximating the timber industry standard, with 250–275 residual tph; and (3) a Light Thin with Gaps (hereafter simply “Gaps”) treatment, again with 250–275 tph but with an additional 20% of the stand harvested to create 0.2-ha gaps planted with native conifer seedlings. Thinnings were conducted by removing trees of relatively small diameter.

All stands are located within the western hemlock (*Tsuga heterophylla*) zone of Franklin and Dyrness (1988) and were established after clearcutting and planting 55–65 years before thinning was initiated in 1995. Slopes range from 0% to 24%, and elevation ranges from 430 to 920 m. Stand areas average 31 ha, ranging from 15 to 53 ha.

Stands within two blocks (Christy and Sidewalk) are directly contiguous with each other or separated only by narrow riparian corridors or roads; distances among stands within the other two blocks (Cougar and Mill Creek) average 1.6 km and no two stands within a block are more than 4 km apart. Thus, landscape context for the stands within each block is similar over the scales at which northern flying squirrels can travel. Distances between blocks range from 2.5 km to 21 km.

Before thinning, Douglas-fir (*Pseudotsuga menziesii*) was the dominant overstory tree species with varying amounts of western hemlock (*T. heterophylla*), western redcedar (*Thuja plicata*), and hardwoods including bigleaf maple (*Acer macrophyllum*), and golden chinquapin (*Chrysolepis chrysophylla*). The understory consisted primarily of vine maple (*Acer circinatum*), cascara buckthorn (*Rhamnus purshiana*), bitter cherry (*Prunus emarginata*), Oregon-grape (*Mahonia nervosa*), salal (*Gaultheria shallon*), and swordfern (*Polystichum munitum*).

Pre-thinning sampling of the vegetative structure within each stand in 1993 established that stands within each block were similar with respect to tree basal area (overall mean 34.8 m²/ha; average CV for 4 blocks = 8.7%) and tree density (overall mean density 718 trees per ha; average CV over 4 blocks = 10.1%; (Davis et al., 2007). Before treatment commenced, each stand was assigned randomly to one of the thinning treatments or as an unthinned control. Thinning began in late 1994, and was completed by February 1997. Most harvest activity occurred simultaneously on all blocks between February 1995 and September 1996 and with no particular pattern to order of treatments.

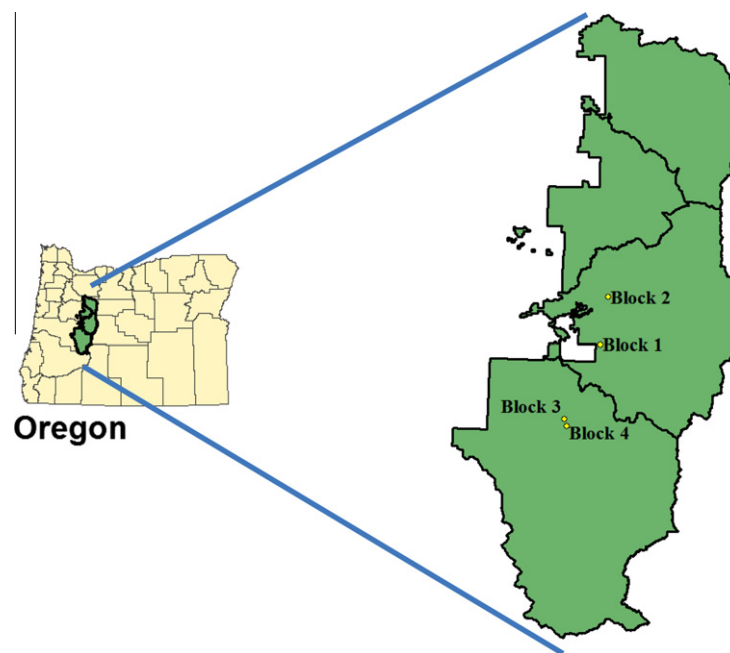


Fig. 1. Location of the Young Stand Thinning & Diversity Study within the Willamette National Forest, Oregon, USA.

Table 1

Treatment level means (and SE) of habitat variables in the Young Stand Thinning and Diversity Study, measured in 2006, 10 years after thinning and just prior to estimation of northern flying squirrel population density in 2007–2008. Superscript letters indicate significant differences at $\alpha = 0.05$, from single-classification ANOVA; tree density and basal area were log-transformed, and % cover variables were arc-sin-square-root transformed before comparison.

	Control	Heavy	Light	Gaps
Density of trees (≥ 8 cm dbh) per ha	686 (33) ^A	233 (39) ^B	307 (50) ^B	273 (41) ^B
Basal area (m^2/ha) of trees	52.7 (4.3) ^A	21.4 (1.6) ^C	31.0 (2.6) ^B	25.6 (2.3) ^{BC}
Large (>30 cm dbh) snags per ha	10.4 (3.8)	5.8 (3.4)	8.5 (3.0)	7.5 (2.5)
Mean tree diameter (cm dbh)	28.8 (1.4)	31.7 (3.7)	34.4 (2.3)	31.8 (2.9)
% Cover overstory canopy	81% (2%) ^A	47% (7%) ^C	67% (5%) ^B	60% (4%) ^B
% Cover herbs	23% (4%)	25% (1%)	29% (4%)	28% (4%)
% Cover low shrubs	19% (3%) ^A	44% (6%) ^B	41% (3%) ^B	43% (5%) ^B
% Cover tall shrubs	46% (5%)	37% (9%)	27% (5%)	28% (6%)

To increase the density of snags with diameter at breast height (dbh) ≥ 30 cm to at least 2.5 snags/ha in all treatment units, a small percentage of trees (ranging from 0.13% to 1.42%) distributed through each stand were killed by chainsaw topping to a height no less than 15 m in late 2001. Half of the topped trees were also inoculated with heart-rot fungus to accelerate decay. In 2009, these artificial snags were surveyed for cavity formation and use by birds and mammals, but the snags were still relatively sound and no evidence of use by flying squirrels was found.

Measurements of vegetation 5–7 years after treatment revealed that thinning created substantial differences in overstory cover, tree density, and tree basal area among the treatments (Davis et al., 2007; Davis and Puettmann, 2009). Percent cover of low shrubs (≤ 2 m high) was reduced about 40% ($P < 0.001$) by harvest damage in thinned stands; a corresponding reduction in tall shrubs (>2 m high) was also significant (55% reduction; $P = 0.002$), but by 2001 both low and tall shrub cover had recovered to levels indistinguishable from the Controls (Davis and Puettmann, 2009). In 2006, 10 years after thinning (Table 1), trees per ha, basal area, and percent overstory cover in all thinned treatments were still lower than in Control stands (all $P < 0.01$; A. Ares, unpublished results). Percent cover of low shrubs in 2006 was significantly lower in Control stands than in thinned stands ($P = 0.0004$). Though high variability among blocks masked statistical differences, there was weak evidence that percent cover of tall shrubs in 2006 was

greater ($P = 0.0702$) in Control stands than in thinned stands. We defined large snags as ≥ 30 cm dbh based on the minimum size likely to be used by flying squirrels (Mellen-McLean et al., 2009). Density of large snags was low and variable (mean 8.06 per ha, s.d. = 5.98), and in 2006 treatments and controls could not be distinguished by snag density ($P = 0.54$), though there was a large difference among blocks ($P = 0.0193$). Volume of coarse woody debris (CWD) > 10 cm diameter ranged from a mean of $107 \text{ m}^3/\text{ha}$ in Light Thin stands to a mean of $270 \text{ m}^3/\text{ha}$ in Heavy Thin stands (s.d. = 112.2), and though thinning increased CWD volume, high variability among replicates severely compromised our ability to detect statistical differences among treatments (B. McComb, unpublished results).

2.2. Mammal sampling

In 2007–2008 (11–13 years after thinning), all stands were sampled to estimate abundance of small mammals, especially northern flying squirrels. Trapping occurred for four consecutive nights in each stand from late September to late November. Two stands in each block were sampled simultaneously and the other two stands in the same block were sampled in the following week. The order for sampling stands within blocks was randomized, and blocks were sampled sequentially. Considerations for the order of

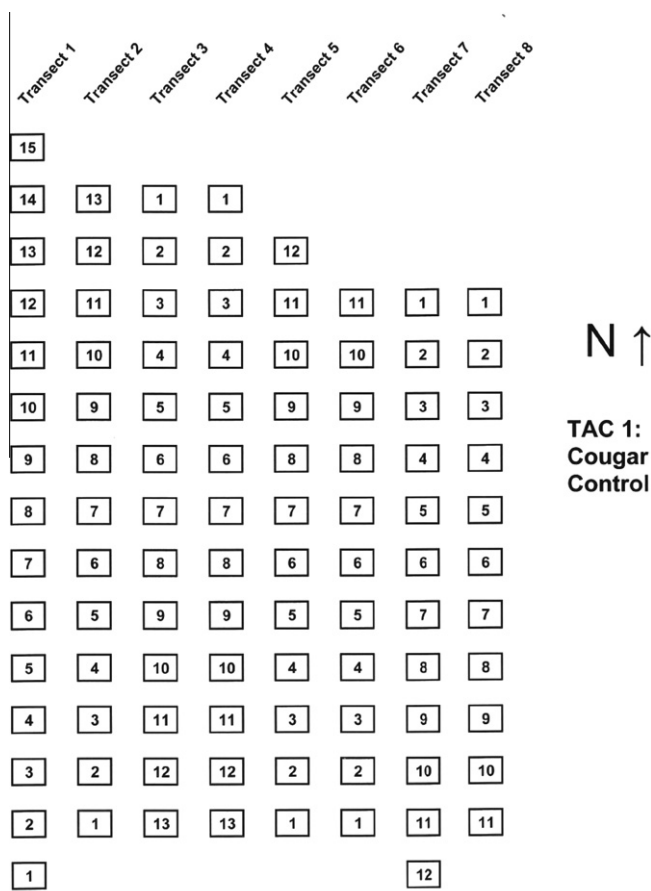


Fig. 2. Example of one of the trapping arrays based on variable-length transects. Numbered boxes indicate positions of trapping stations along transects. Inter-trap distance equals 30 m in both dimensions.

sampling among blocks included elevation, seasonal road closures due to snow or hunting, and proximity to other blocks.

We used variable-length transects, varying in number from 4 to 11 depending on stand shape, but each stand included a total of 100 trapping stations. This meant that most trapping arrays did not form rectangles but rather had more complex shapes (Fig. 2); nevertheless, distance between transects and between traps on each transect was 30 m, such that the trapping stations formed a grid network from which we were able to compute the total area of the trapping array, as well as distances moved by each flying squirrel between captures.

One trap was placed at each station. In each stand, Sherman traps (Model LFATDG) alternated with Tomahawk traps (Model 201) along each transect, so that 50 Sherman traps and 50 Tomahawk traps were distributed evenly throughout the 100 stations in each stand. Half (25) of the Tomahawk traps were attached to the boles of trees (approx. 1.5 m high), and the other 25 were placed on the ground; tree and ground placements of Tomahawk traps alternated along transects. Thus, effective spacing among Tomahawk traps was 60 m. Sherman traps were used to capture terrestrial rodents and insectivores, and so were placed on the ground; we include Sherman traps in this analysis because a substantial number of flying squirrels were captured in them. To increase capture rates, all traps were locked open and pre-baited once 10 days before the trap session began. During the trapping session, traps were checked twice daily to minimize mortality of trap-prone diurnal species, particularly chipmunks. Traps were set in the afternoon on the 1st day of each trap session, checked

twice each day for 3 days, then checked and closed on the morning of the 5th day; thus, each trap session included four nights. In both years, traps were baited with a mixture of peanut butter, oats, and sunflower seeds. Upholstery cotton was placed in each trap for insulation, and traps were placed within weather-resistant covers. Captured mammals were identified to species, weighed, sexed, marked with individually-numbered eartags, and immediately released at the point of capture. Trap mortalities were frozen for later necropsy to confirm species and sex. All procedures were conducted under protocols approved by the Institutional Animal Care and Use Committee at Oregon State University.

2.3. Analytical procedures

We calculated trap-nights (TN) as total Tomahawk and Sherman traps deployed multiplied by the number of nights deployed. We computed corrected trap-nights by subtracting 1 TN for each trap found to be inoperable and 0.5 TN for each trap found closed but empty.

We computed estimates of flying squirrel abundance using program MARK (White and Burnham, 1999). Within MARK, we used the Huggins full closed captures model with heterogeneity to derive estimates of population size within each stand for each year separately. The Huggins model assumes population closure and allows for capture probabilities to vary by individual, by behavioral response to trapping, and through time, and is thus relatively robust to the low and heterogeneous capture probabilities typical of northern flying squirrels. We assumed that our populations were demographically closed for the brief period of our trapping regime (4 days), and employed tests for closure (Stanley and Burnham, 1999) to confirm that any violations of this assumption were negligible.

Because we trapped for fewer nights (4) than many previous studies, and because population estimators are sensitive to low capture probabilities, we employed an additional check on our results by also computing densities based on total number of individuals captured without estimating additional uncaptured animals.

We computed the effective area trapped in each stand (Table 2) by adding a buffer around the perimeter of each trapping array. Buffer width was one-half of the mean maximum distance moved (MMDM) by flying squirrels in that stand. Because we could detect no statistical difference in MMDM between years or sexes (ANOVA, $P = 0.70$ and 0.46 , respectively), we used the average MMDM for the 2 years for each stand without regard to sex. Because northern flying squirrels are known to have larger home ranges in low density populations (Carey, 1995, 2000), we used different computations for MMDM depending on estimated abundance of each particular stand: for each stand with estimated abundance ≥ 10 for either year, MMDM was computed from data specific to that stand; for stands with estimated abundance < 10 animals, and thus having few data to compute MMDM, we used mean MMDM for all animals in all low-abundance stands to compute the array buffer. Mean MMDM for six high-density stands was 75.2 m, ranging from 59 to 102 m, and MMDM for all low-density stands was 101 m. Effective area trapped was computed as 0.5 MMDM multiplied by array perimeter, added to the area of the trapping array. We then computed density of flying squirrels in each stand as the number of animals estimated with MARK, divided by the effective area of trapping (Table 2).

We compared the effects of thinning on northern flying squirrel density, MMDM, sex ratio, and sex-specific body mass using a randomized block one-way ANOVA design with repeated measures. Treatment and year were fixed effects; block and the block by treatment factors were random effects. Density estimates and sex-specific body mass were square-root-transformed to correct for unequal variances, and sex ratios were logit transformed. We

Table 2

Effective trapping areas, total individuals captured, estimated abundances^a, and densities^b of northern flying squirrels (*Glaucomys sabrinus*) on the Young Stand Thinning & Diversity Study, September–November of 2007 and 2008.

Treatment	Block	Effective trapped area (ha)	Total individual flying squirrels captured		Flying squirrel abundance ^a (individuals)		Flying squirrel density ^b (individuals/ha)	
			2007	2008	2007	2008	2007	2008
Control	Cougar	12.16	23	17	43	18	3.54	1.48
Control	Mill Creek	12.32	15	34	28	36	2.27	2.92
Control	Christy	11.54	18	27	33	30	2.86	2.60
Control	Sidewalk	17.48	4	2	7	2	0.40	0.11
Heavy Thin	Cougar	15.80	4	6	4	7	0.25	0.44
Heavy Thin	Mill Creek	14.63	1	1	1	1	0.07	0.07
Heavy Thin	Christy	16.24	0	0	0	0	0.00	0.00
Heavy Thin	Sidewalk	14.32	1	5	1	6	0.07	0.42
Light Thin	Cougar	13.39	14	21	12	21	0.90	1.57
Light Thin	Mill Creek	17.88	5	8	5	8	0.28	0.45
Light Thin	Christy	13.19	0	3	0	3	0.00	0.23
Light Thin	Sidewalk	15.59	1	1	1	1	0.06	0.06
Gaps	Cougar	15.46	5	7	6	14	0.39	0.91
Gaps	Mill Creek	11.72	11	6	14	12	1.19	1.02
Gaps	Christy	14.51	0	3	0	6	0.00	0.41
Gaps	Sidewalk	15.54	1	3	1	6	0.06	0.39

^a Abundance estimated with Program MARK closed population estimators.

^b Density estimates based on abundance estimated with Program MARK.

used a set of orthogonal contrasts to minimize Type I error rate (Lehmann, 1986). The set consisted of three comparisons: Control stands vs. all thinning treatments; Heavy Thin vs. Light Thin and Gaps; and Light Thin vs. Gaps. These comparisons test three corresponding hypotheses: (1) that flying squirrel density, MMDM, sex ratio, and body mass did not differ between thinned and unthinned treatments; (2) did not differ between heavy and light thinning intensities; and (3) did not differ between lightly thinned stands with and without small gaps. Our comparison-wise criterion for statistical significance was $\alpha < 0.05$.

We explored relationships between stand-level flying squirrel densities and habitat characteristics by developing *a priori* a set of mixed-effect linear regression models with block held as a random effect. Habitat variables available to us were tree density, tree basal area, density of large snags, tree diameter, overstory canopy cover, herbaceous plant cover, low shrub cover, and tall shrub cover (A. Ares, unpublished data). One year before sampling of flying squirrels commenced, these habitat components were measured on permanent 0.1-ha circular plots, placed systematically throughout each stand, and covering approximately 7.5% of the area of each stand. To ensure adequate sampling effort of gap interiors and gap edges in Gaps stands, plots were placed in the center of 10 randomly-chosen 0.2-ha gaps, and 10 more plots on the edges of 10 other randomly-chosen gaps; in addition, 10 plots were placed randomly in the matrix surrounding the gaps. Percent overstory cover was measured at the center of each circular plot and at four points 10.25 m distant from center in each cardinal direction. Overstory cover included live foliage and tree boles, limbs, and snags. Diameter at breast height (dbh) was also measured for all trees >5 cm dbh in each plot. All understory species present in the plot were recorded. Within each plot, eight subplots (each 0.1 m²) were evenly spaced along each of two parallel 14.5-m transects, providing a total of 16 subplots per plot. In each subplot, percent cover of all understory plant species was visually estimated, as was percent cover of ground surface features including exposed mineral soil, coarse litter, and fine litter. Graminoids and bryophytes were not identified below family level. Along each 14.5-m transect, line intercept methods were employed to estimate understory tall shrub cover and cover of trees with dbh <5 cm. Low shrubs were distinguished from tall shrubs by potential stature of plant at maturity of less or more than 1 m, respectively. More details about this measurement protocol may be found in Davis et al. (2007) and Davis and Puettmann (2009).

Our explorations of northern flying squirrel habitat associations were primarily driven by *a priori* hypotheses about effects of thinning on squirrel densities. Specifically, we reasoned that variables representing the overstory (percent overstory cover, tree density, basal area) would be profoundly reduced by thinning, would be reduced more in Heavy Thin stands than in Light Thin stands, and would have important implications for flying squirrel locomotion and avoidance of predators (Wilson, 2010). All three of those variables were still significantly higher in Control stands than in thinned stands in 2006 (A. Ares, unpublished data), so we reasoned that one or more was likely related to flying squirrel densities; because all were highly collinear with each other, we chose one variable (tree basal area) which had the highest correlation with our measured flying squirrel densities for inclusion in our models. Large snags are generally considered an important habitat component for flying squirrels (Carey, 1995; Carey et al., 1999a; Smith et al., 2004; Holloway and Malcolm, 2006), so we included density of snags with dbh ≥ 30 cm in our modeling. In 2006, percent cover of low shrubs (species whose maximum height generally does not exceed 1 m) was the only understory variable that was significantly different between control stands and thinned stands; while there seemed little compelling reason to expect *a priori* that this stratum would influence flying squirrel abundance, the pattern seemed compelling enough to include in exploratory analyses. A set of eight models were fitted, residuals were examined for departures from normality and/or homoscedasticity, and variables were transformed where necessary to meet statistical assumptions. All ANOVA and regression analyses were performed in SAS version 9.2 (SAS, 2003). Regression models were ranked based on Akaike's Information Criterion, corrected for small sample size (AICc).

3. Results

In 2007–2008, a total of 11,873 corrected trap-nights were deployed, approximately equally distributed between the 2 years. A total of 103 individual flying squirrels were captured 134 times in 2007; 144 individuals were captured 213 times in 2008 (Table 2). Approximately 12% of all flying squirrel captures were in Sherman traps. All other flying squirrel captures were in Tomahawk traps; approximately 59% of those were in traps set on tree boles, and the rest were in traps set on the ground. Capture prob-

Table 3

ANOVA table for repeated-measures orthogonal comparisons of northern flying squirrel (*Glaucomys sabrinus*) densities, mean maximum distance moved (MMDM), sex ratios, and sex-specific body mass among thinning treatments of the Young Stand Thinning & Diversity Study, 2007–2008.

Dependent variable	Factor	df	F	P
Density (individual squirrels/ha)	Treatment	3	45.14	<0.0001
	Block	3	21.05	<0.0001
	Block * Treatment	9	7.88	0.0003
	Year	1	2.88	0.1106
Mean maximum distance moved (MMDM)	Treatment	3	0.43	0.7347
	Sex	1	1.93	0.1705
	Block	3	0.74	0.5334
	Block * Treatment	4	1.12	0.3570
	Block * Sex	3	1.18	0.3270
	Year	1	0.25	0.6178
	Treatment	3	0.14	0.9360
Sex ratio (Male individuals: female individuals)	Block	3	3.78	0.0336
	Block * Treatment	9	2.12	0.0954
	Year	1	7.16	0.0173
	Treatment	3	0.51	0.6756
Female body mass	Block	3	2.73	0.0473
	Block * Treatment	9	0.50	0.8513
	Year	1	1.23	0.2703
	Treatment	3	1.46	0.2299
Male body mass	Block	3	1.50	0.2192
	Block * Treatment	9	0.95	0.4828
	Year	1	1.26	0.2638
	Treatment	3	0.95	0.4828

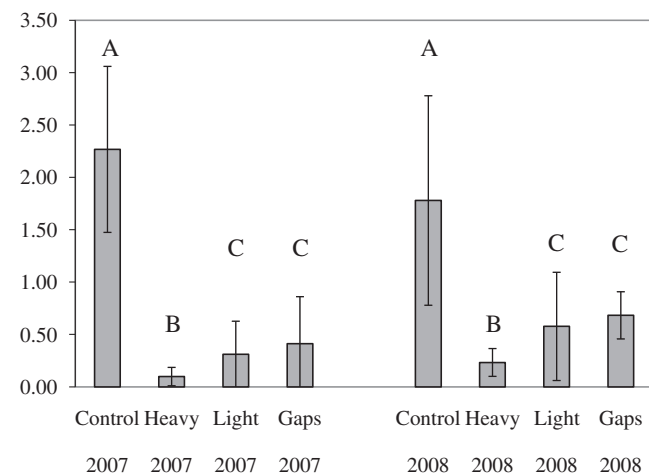


Fig. 3. Mean density (individuals per ha) of northern flying squirrels (*Glaucomys sabrinus*) in treatment stands of the Young Stand Thinning and Diversity Study, 2007 and 2008. Each treatment was replicated four times. Error bars represent ± 1 SE.

ability (P) within stands ranged from 0.18 to 1.00, and averaged 0.48.

Flying squirrel density (Table 3 and Fig. 3) was significantly greater ($P < 0.0001$) in unthinned Control stands (mean 2.02 squirrels/ha, SE = 0.78) than in thinned stands (0.39/ha, SE = 0.31), and significantly greater ($P = 0.0034$) in the Light Thin and Gaps treatments (0.50/ha, SE = 0.35) than in Heavy Thin (0.17/ha, SE = 0.10). Differences between Light Thin (0.44/ha, SE = 0.38) and Gaps (0.55/ha, SE = 0.31) treatments were not significant ($P = 0.36$). Differences in densities between years also did not reach the level of statistical significance ($P = 0.11$), but were higher in 2008 than in 2007 in all thinned treatments and correspondingly lower in Control stands (Fig. 3).

Table 4

Results of mixed-effects regression modeling of northern flying squirrel (*Glaucomys sabrinus*) habitat relationships on the Young Stand Thinning & Diversity Study, 2007–2008. Post-thinning basal area was log-transformed. Flying squirrel density and snag density were log+1-transformed because there were values of zero. Percent cover of low shrubs was arc-sin-square-root transformed. AICc is Akaike's Information Criterion, corrected for small sample size.

Model	AICc	Δ AIC	AIC (wt)
Null model	47.6	35.8	0.000
Log(GLSA) = log (basal area)	18.9	7.1	0.015
Log(GLSA) = log (snag density)	40.4	28.6	0.000
Log(GLSA) = arcsin-sqrt (% cover low shrubs)	21.9	10.1	0.003
Log(GLSA) = log (basal area) log (snag density)	17.2	5.4	0.034
Log(GLSA) = log (basal area) arcsin-sqrt (% cover low shrubs)	16.9	5.1	0.040
Log(GLSA) = log (snag density) arcsin-sqrt (% cover low shrubs)	11.8	0	0.510
Full model (all three regressors)	12.3	0.5	0.398

Using the more conservative approach of simple enumeration of individuals (i.e., computing densities without estimation of additional uncaptured animals) resulted in lower densities overall, of course, and more so for Controls than for thinned stands, but did not change significance of differences appreciably, nor our overall conclusions. Flying squirrel density using this approach was significantly greater ($P < 0.0001$) in unthinned Control stands (mean 1.43 squirrels/ha, SE = 0.54) than in thinned stands (0.33/ha, SE = 0.22), and greater ($P = 0.0298$) in the Light Thin and Gaps treatments (0.40/ha, SE = 0.25) than in the Heavy Thin treatment (0.18/ha, SE = 0.09). Light Thin (0.46/ha, SE = 0.32) and Gaps (0.35/ha, SE = 0.17) treatments were not significantly different ($P = 0.51$). Density differences between years were more pronounced using this enumeration approach ($P = 0.05$). Carrying out this alternative test increased our confidence that our population estimates are reliable, but doing so also ignores the certainty that naïve counts of individuals captured are inherently negatively biased. For this reason, we refer hereafter to our results using statistically estimated population densities only.

Thinning treatments did not affect maximum distance moved by individual flying squirrels (Table 3, $P = 0.73$) and distances moved were similar for males and females ($P = 0.17$). Neither sex ratio ($P = 0.94$) nor sex-specific body mass ($P = 0.68$ for females and 0.23 for males) differed among treatments.

The mixed-effects linear regression model best supported by our data included snag density and percent cover of low shrubs (Table 4). Flying squirrel density was positively related with snag density, and negatively related with low shrub cover. Each of these two relationships was highly statistically significant ($P < 0.001$). The full model including all three regressors was included for completeness. The fit of the full model (AIC wt = 0.398) was slightly poorer than that of the best model (AIC wt = 0.510). Thus, the two models are nearly equivalent in explaining densities of northern flying squirrels in these young stands.

4. Discussion

Most previous studies of northern flying squirrel response to thinning and similar silvicultural treatments have been short-term, and most have indicated negative effects on squirrel densities (Waters and Zabel, 1995; Carey, 2001; Bull et al., 2004; Holloway and Malcolm, 2006; Herbers and Klenner, 2007; Meyer et al., 2007a; Holloway and Smith, 2011). However, some of these short-term studies were unable to detect differences in northern flying squirrel densities between thinned stands and control stands (Ransome and Sullivan, 2002; Gomez et al., 2005), most likely due to lack of statistical power (Holloway and Smith, 2011). Our long-

er-term study provides evidence that the negative impacts of commercial thinning on northern flying squirrel can persist even after 11–13 years. This finding of persistent negative impacts of commercial thinning on flying squirrel density is supported by a large negative effect size (Hedges' $d = -1.53$ for Control vs. all thinned treatments), the result of large differences between means and relatively low variability among replicates.

In addition, we found that intensity of thinning (Heavy vs. Light Thin) also significantly affected northern flying squirrel densities. Densities on average were twice as high in Light Thin and Gaps stands as in Heavy Thin stands, and this difference was consistent for the 2 years of our study. The only habitat variable we measured which exhibits the same pattern is percent cover of overstory canopy, which is clearly higher in Light Thin and Gaps stands (overall mean 64%, SE 5%) than in Heavy Thin stands (mean 47%, SE 7%). Other variables representing forest density (trees/ha, basal area) were generally higher in Light Thin and Gaps stands than in Heavy Thin stands, but differences may be obscured by high variability (Table 1). Only two other studies have investigated the effects of thinning intensity on northern flying squirrels. Gomez et al. (2005), working in forests thinned to two levels very similar to ours, found no effect of thinning on flying squirrel densities regardless of intensity. Herbers and Klenner (2007) found that thinning decreased densities of northern flying squirrels in south central British Columbia from 0.64 to 0.26 squirrels/ha, but that the decrease did not vary over three levels of thinning intensity, nor with harvest pattern (uniform vs. patch cuts).

It is interesting to note that, in both years of this study, squirrel densities in Gaps stands were slightly higher than in Light Thin stands. Variability among replicates is so high in relation to the small differences between Light Thin stands and Gaps stands that the significance of such a difference is highly doubtful. Although Gaps stands were designed to have 20% fewer trees and less dense canopies than Light Thin stands, by 2006 differences in trees/ha, basal area, and percent overstory cover were not significant between these two treatments (Table 1), so there seems little reason to think that any apparent difference in squirrel density relates directly to thinning, even if the differences had been large enough to qualify as statistically significant, which they were not. Such a conclusion would certainly be contrary to previous findings (ours and others') that thinning decreases flying squirrel densities, and would be unique in implying that forest openings were in some way beneficial to the squirrels. Longer and more frequent monitoring of flying squirrel abundance in the YSTDS treatment stands may resolve this apparent anomaly.

More time and monitoring are also needed to estimate when impacted flying squirrel populations might recover to levels comparable with those in unthinned stands, and to compare the influence of various habitat features on that recovery. Future sampling efforts should include measurements specifically designed to test hypotheses regarding the influence of particular habitat features (e.g., mid-story occlusion as protection from predators; see Wilson, 2010) on northern flying squirrel population ecology, rather than relying opportunistically on data collected for analysis of vegetative responses to thinning.

The densities of flying squirrels we report here (0–3.54 squirrels per ha, mean = 0.79; Table 2) are consistent with the range (0–4 squirrels per ha) reported by other authors and reviewed by Smith (2007). Mean density for our Control stands (2.02/ha) was quite high compared to nine previous studies (mean 1.06/ha) of northern flying squirrels in young forests (Carey et al., 1992; Rosenberg and Anthony, 1992; Witt, 1992; Carey, 1995; Waters and Zabel, 1995; Ransome and Sullivan, 2002, 2003; Gomez et al., 2005; Lehmkuhl et al., 2006), and is higher or comparable to the high densities (mean 1.44/ha) reported by several authors for mature and old-growth forests in the Pacific Northwest (Carey et al., 1992; Rosen-

berg and Anthony, 1992; Witt, 1992; Carey, 1995; Waters and Zabel, 1995; Ransome and Sullivan, 2003; Lehmkuhl et al., 2006; Herbers and Klenner, 2007). While the high densities we measured may suggest that these young stands represent unusually good habitat for flying squirrels, we do not have the measures of reproductive fitness or survival necessary to refute the possibility that these areas could be operating as demographic sinks, occupied by subdominant animals from areas of higher quality habitat (Van Horne, 1983; Wheatley et al., 2002). Other authors (Smith and Nichols, 2003; Lehmkuhl et al., 2006) have reported dense populations of flying squirrels that exhibited negative growth rates, suggesting they might be operating as demographic sinks. We recommend that future work on the Young Stand Thinning & Diversity Study sample flying squirrel populations for at least three consecutive years, and make more effort to quantify reproductive success, so that reproductive fitness and rates of survival and population growth can be compared among treatments. Until then, inferences about the negative effects of thinning on flying squirrels are incomplete.

We know of only two other experimental studies that have measured northern flying squirrel densities more than 5 years after thinning. Wilson (2010) found that flying squirrel densities were low (<0.2 squirrels/ha) 12 years after variable-density thinning on the Forest Ecosystem Study (FES) in the Puget Trough of western Washington. Wilson's conclusion was that variable-density thinning had not yet promoted the development of high-quality habitat for flying squirrels in that time frame, primarily due to lack of sufficient midstory development (e.g., recruitment and growth of shade-tolerant trees under the existing canopy) and loss of overstory trees from various causes (wind, suppression mortality, and laminated root rot) unrelated to the thinning treatments, resulting in limited development of greater complexity in forest structure. Wilson's work, like ours reported here, found no support for the hypothesis that thinning for increased forest complexity results in habitat that supports high densities of northern flying squirrels, at least in short- or mid-term time frames. Forest structural processes (accelerated tree growth, development of mid-story occlusion, recruitment and decay of snags) that are presumably critical to high densities of northern flying squirrels will apparently take longer than 12 years to develop after thinning of young forests. Thus, it will be important to continue to monitor critical habitat components and flying squirrel densities over the long term in manipulative stand-level studies designed to accelerate late-seral forest conditions.

Ransome et al. (2004), working 12–14 years after pre-commercial thinning of young lodgepole pine forests in British Columbia, found densities of 0.14, 0.37, and 0.51 northern flying squirrels/ha in stands thinned to low, medium, and high tree densities, respectively, and 0.20 flying squirrels/ha in unthinned control stands. Medium- and high-density thinning treatments had significantly higher flying squirrel densities than control stands ($P = 0.05$). Remarkably, high-density thinned stands had 70% higher flying squirrel densities than in old-growth stands (0.31 squirrels/ha). This is an unexpected finding, and the authors point out that the observed density differences do not necessarily reflect differences in habitat quality, which should be assessed on the basis of relative reproductive fitness of the squirrels. Unfortunately, as in our own study, Ransome et al. (2004) lacked direct information concerning reproductive fitness of flying squirrels, but they found no effects of thinning on recruitment, movement, or survival of flying squirrels. Adult male body mass, an indirect indicator of fitness, was significantly greater for animals in old-growth stands than in high-density thinned stands, indicating that the thinned stands may not have provided habitat quality comparable to that in old-growth. Additionally, the densities reported by Ransome et al. (2004) were relatively low, and squirrel densities were not mea-

sured before thinning, so conclusions that pre-commercial thinning can produce high-quality habitat for northern flying squirrels are not well supported.

Northern flying squirrels are primarily mycophagous, feeding largely on the fruiting bodies of hypogeous fungi (truffles), and several authors have stressed the importance of truffle abundance (Waters and Zabel, 1995; Gomez et al., 2005; Lehmkuhl et al., 2006) and habitat features that have been correlated with abundance of truffles, such as coarse woody debris, particularly large logs (Carey et al., 1999a; Smith et al., 2004). Attempting to explain their unique finding that squirrel densities were higher in thinned stands than in old-growth, Ransome et al. (2004) speculated that post-thinning increases in squirrel densities might be the result of concomitant increases in food resources, particularly hypogeous fungi, epigeous fungi, and understory vegetation. Unfortunately, understory vegetation was not measured before thinning, and fungal biota were not measured at any stage, so it was not possible to test these speculations. Our study also lacks data to directly address the relationship between squirrel density and abundance of food resources, though response to thinning by one genus of epigeous mushroom (*Cantharellus* sp.) was measured on our sites (Pilz et al., 2006). Thinning had strong short-term negative impacts on abundance and mass of *Cantharellus* sporocarps, but those impacts had almost entirely disappeared by 6 years after thinning. *Cantharellus* are not generally considered to be forage species for northern flying squirrels, and we cannot say whether fungal taxa more important to flying squirrels (i.e., truffles) showed similar patterns of changes in abundance.

In our work, the strong negative effect of thinning on northern flying squirrel densities was associated with decreased live tree basal area, and to differences in density of large snags. This association with canopy variables (live trees and snags) supports the conclusion of others that forest canopy structure, particularly abundance of large live trees (Smith et al., 2004, 2005; Gomez et al., 2005; Lehmkuhl et al., 2006) and large snags (Carey, 1995; Carey et al., 1999a; Smith et al., 2004; Holloway and Malcolm, 2006), is the most important determinant of habitat quality for northern flying squirrels. Smith et al. (2005) stressed that response of northern flying squirrels to any particular habitat feature might depend on the relative abundance of such features within a local landscape, so that features in low abundance may be limiting. This may be the case for our sites, where trees were relatively small (mean dbh = 27.2 cm), and large snags were scarce and variable (Table 1). Holloway and Smith (2011) recently presented meta-regression results that indicate studies showing the greatest negative effects of harvest practices on northern flying squirrels tended to have the lowest rates of retention of large snags (>40 cm dbh), most having fewer than 8 snags/ha. The importance of large snags as nesting sites for northern flying squirrels has been extensively documented (Carey et al., 1997; Cotton and Parker, 2000; Bakker and Hastings, 2002; Meyer et al., 2005, 2007b).

Our modeling of northern flying squirrel habitat relationships also indicates a negative association with the percent cover of low shrubs. We see this as an indirect effect of the decrease in tree basal area (and consequently percent overstory cover). We cannot explain why the model including cover of low shrubs fits the squirrel density data slightly better than the full model which includes basal area, but we point out that the difference in ΔAIC is 0.5, indicating that the models are nearly equivalent.

Wilson (2010) argued that flying squirrels in the Pacific Northwest are largely limited by the amount of protective cover from predators, primarily owls and weasels, and that four factors could be used collectively to measure protective cover and predict squirrel abundance (large live trees, area of canopy and bole intercept at 10 m above ground, and percent area of stand without gaps >100 m²) or distinguish between stands supporting high or low

abundances (variance in live tree dbh, area of canopy and bole intercept at 10 m above ground, and percent of stand without gaps >100 m²). Our data roughly agree with Wilson's findings, though there are some important differences. Overstory cover in our Light Thin stands had recovered in the first 5 years after thinning and was no longer statistically distinguishable from Control stands (Davis et al., 2007), yet densities of flying squirrels 12 years after thinning were still much lower in Light Thin stands; thus, overstory cover alone does not appear to provide the habitat quality needed for flying squirrels to occupy stands in high densities. Vertical structural complexity on our YSTDS stands was estimated from 3-year post-thinning data with two metrics (live crown ratio and foliage height diversity; Davis et al., 2007), and no differences were found among the treatments, but it is not clear that these structural metrics are appropriate for measuring the sort of occlusion that Wilson (2010) hypothesized was vital for flying squirrels to avoid predators, nor that conditions have remained unchanged in the intervening 9 years. We have not mapped or measured the canopy gaps in the YSTDS stands, but it seems likely that the large gaps (ca. 2000 m²) created in our Gaps treatment stands would be formidable barriers to the gliding locomotion of flying squirrels, and certainly our finding of much lower densities of flying squirrels in Gaps stands than in Controls does not contradict those of Wilson (2010).

The question of whether flying squirrels are more limited by availability of large trees and snags or by mid-story structural complexity may ultimately be answered by continued long-term monitoring of the YSTDS stands. Simulation studies by Garman et al. (2003), for which initial pre-treatment conditions and thinning prescriptions on the YSTDS stands were projected through harvest and many years of subsequent recovery, predict that the Heavy Thin treatment will develop large live trees and large snags most quickly. This prescription allows for maximal growth of large trees in minimal time, and while diameter growth of trees in Heavy Thin stands has already increased significantly over other thinning treatments and controls (Davis et al., 2007), several decades seem likely to pass before this growth benefits northern flying squirrel densities. Development of large snags and large volumes of coarse woody debris in these Heavy Thin stands will require either intentional killing of large trees or restraint from subsequent thinning to enable large tree mortality through competition. Simulations by Garman et al. (2003) also predict that the YSTDS treatment likely to develop overstory and mid-story complexity most slowly will be the Light Thin stands. Therefore, dense stands like the YSTDS Control treatment are likely to provide the most mid-story cover from predation in mid-successional conifer stands. This is supported by our data, where 12 years after thinning, flying squirrel density was greater in the Control than the thinned stands. However, cover provided by conifer stems is expected to diminish as suppression mortality reduces stand density in the Control stands. Development of shade-tolerant tree species such as hemlock and cedar would likely then lag behind that in thinned stands, where such development started soon after thinning, with the possible result that the Control stands could become less suitable than thinned stands as habitat for flying squirrels some decades later. Thus, management of these young forests represents a tradeoff between providing short-term, ephemeral habitat in dense unthinned stands and thinning to promote the development of more complex habitat in the longer term.

5. Conclusions

Currently, forest managers of public lands in the Pacific Northwest are treating many thousands of hectares of young forests by thinning and other partial cutting methods, with major objectives

being to accelerate the development of larger trees and promote the sort of structural complexity more typical of late-seral forests. Regardless of the motivations for this strategy, our research makes it clear that densities of northern flying squirrels are particularly sensitive to thinning in young Douglas-fir forests, for at least 12 years after treatment. Whether observed decreases in density also mean decreases in population viability has not been adequately addressed, and will require comparison of flying squirrel reproductive fitness and survival rates between thinned and unthinned young stands. Until this question of fitness is answered, a conservative strategy would strive to maintain adequate area and connectivity of dense, closed-canopy forests within managed landscapes to maintain northern flying squirrel populations, by leaving areas of young forest unthinned.

The question of how much closed-canopy forest is “adequate” calls for a landscape-level assessment of northern flying squirrel habitat associations in the Pacific Northwest, something not yet accomplished in the region. Northern flying squirrels in New Brunswick (Ritchie et al., 2009) responded more to the total amount of habitat available on a landscape scale than they did to its configuration within the landscape, and thus manipulation of landscape configuration (i.e., connectivity) is unlikely to be useful in maintaining metapopulation viability in the face of habitat loss. This would seem to argue for caution in carrying out commercial thinning across large portions of the Pacific Northwest landscape, especially if one eventual goal is to sustain the primary prey of the northern spotted owl. Continued monitoring of northern flying squirrels and habitat features in the Young Stand Thinning & Diversity Study should eventually tell us when flying squirrel populations begin to recover in thinned stands, in which treatment levels this recovery occurs most quickly, and which habitat features are most important in that recovery.

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PERSPECTIVE

Protect large trees for climate mitigation, biodiversity, and forest resilience

David J. Mildrexler¹  | Logan T. Berner² | Beverly E. Law³ |
Richard A. Birdsey⁴ | William R. Moomaw^{4,5}

¹Eastern Oregon Legacy Lands, Joseph, Oregon, USA

²EcoSpatial Services L.L.C, Juneau, Alaska, USA

³Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA

⁴Woodwell Climate Research Center, Falmouth, Massachusetts, USA

⁵Center for International Environment and Resource Policy, Fletcher School, Tufts University, Medford, Massachusetts, USA

Correspondence

David J. Mildrexler, Eastern Oregon Legacy Lands, PO Box 666, Joseph, OR 97846, USA.

Email: davidm@eoregacylands.org

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Abstract

Protecting the climate system requires urgently reducing carbon emissions to the atmosphere and increasing cumulative carbon stocks in natural systems. Recent studies confirm that large trees accumulate and store a disproportionate share of aboveground forest carbon. In the temperate forests of the western United States, a century of intensive logging drastically reduced large-trees and older forest, but some large trees remain. However, recent changes to large tree management policy on National Forest lands east of the Cascade Mountains crest in Oregon and southeastern Washington allows increased harvesting of large-diameter trees (≥ 53 cm or 21 inches) that account for just 3% of all stems, but hold 42% of total aboveground carbon. In this article, we describe synergies with protecting large trees for climate mitigation, biodiversity, and forest resilience goals to shift species composition, reduce fuel loads and stem density, and adapt to climatically driven increases in fire activity in eastern Oregon.

KEYWORDS

aboveground forest carbon, biodiversity, climate change, eastern Oregon, large trees

1 | INTRODUCTION

Society has a narrow window of opportunity left to avert catastrophic consequences from the intertwined climate and biodiversity crises (IPCC, 2022), and forests offer major solutions at the intersection of these urgent imperatives. Forests account for 92% of all terrestrial biomass globally (Pan et al., 2013), store about 45% of the total organic carbon on land in their biomass and soils (Bonan, 2008), and removed the equivalent of about 30% of fossil fuel emissions annually from 2009 to 2018, of which 44% was by temperate forests (Friedlingstein et al., 2019). Moreover, forests provide critical habitats to

more than half of all known plant and animal species on Earth (Gibson et al., 2011; Vié et al., 2009). As climate change increases and accelerates amplifying feedbacks, preserving species- and carbon-rich forests becomes ever more important, alongside a rapid transition to net-zero fossil fuel CO₂ emissions (Matthews et al., 2022).

Forests of the western US contain large stocks of carbon and remove significant quantities of CO₂ from the atmosphere to help protect climate, biodiversity, and water security (Buotte et al., 2020; Law et al., 2021). But how we manage these forests will play a large role in determining future outcomes (Fargione et al., 2018; Hudiburg et al., 2009; Law et al., 2018). Oregon stands

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out with the most forested area in the western USA, yet the lowest proportion of its forests protected (Law et al., 2021), and significant opportunities to create strategic forest reserves (Law, Berner, et al., 2022). About 80% of tree mortality in Oregon and Washington is attributed to harvest (Berner et al., 2017). In this article we provide insights from a recent study that quantified large tree carbon stocks in diverse forests of eastern Oregon (Mildrexler et al., 2020), and describe synergies with protecting disproportionately valuable large trees for biodiversity and climate mitigation, and forest resilience goals.

2 | LARGE TREES DOMINATE ABOVEGROUND CARBON STORAGE

Trees capture and store massive amounts of carbon, thus forests are an essential component of limiting global warming to 1.5–2°C (IPCC, 2018). However, trees are not all equal in their capacity to slow climate change in the coming critical decades. Large trees play an inordinately large role in removing carbon from the atmosphere and storing it in long-lived tissues (Figure 1; Lutz et al., 2012; Leverett et al., 2021). Globally, studies have found that about half the aboveground carbon is concentrated in a small proportion of large trees (1%–5% of total stems) (Lutz et al., 2018; McNicol et al., 2018). Because most global forests are well below their potential carbon stocks due to past and current land management practices, they could store twice the carbon than now (Erb et al., 2018). As large trees grow larger, small increases in diameter add a relatively large amount of volume and biomass (Mildrexler et al., 2020; Stephenson et al., 2014). Protecting existing forests with large trees and letting more forests mature and develop additional large trees is crucial for preventing carbon emissions and for continued

accumulation of carbon from the atmosphere in the coming decades (Birdsey et al., 2023; Law, Moomaw, et al., 2022; Moomaw et al., 2019).

2.1 | The 21-inch rule and carbon stocks

Forests in eastern Oregon and southeastern Washington are recovering from a century of intensive logging that eliminated much of the region's large trees by selective harvest of the largest, most robust trees including clear-cutting older forests. Nevertheless, the United States Forest Service (USFS) recently weakened protection for trees 21 inches diameter at breast height (DBH) and larger ("21-inch rule") across six national forests in this region. The 21-inch rule specifically applied to large-diameter trees on millions of acres of federal public lands. To assess the consequences of the loss of these trees it is essential to quantify large tree carbon stocks prior to changes in management actions. Mildrexler et al. (2020) evaluated carbon storage in large-diameter trees across the six national forests located east of the Cascade Crest in Oregon and Washington ("eastside forests") (Figure 2). Specifically, we quantified the relative contribution of large trees (≥ 21 inches DBH) to aboveground carbon (AGC) storage based on analysis of 636,520 trees on 3335 USFS Forest Inventory & Analysis (FIA) plots, and also assessed the carbon implications of relaxing the 21-inch rule. In these forests, large trees compose a small fraction of total stems (2.0% to 3.7% of all stems among five dominant tree species) yet hold 33% to 46% of total AGC stored by each species (Figure 3). The very largest trees, >30 inches DBH, held an even greater proportion of carbon (16.6%) relative to their small numbers (0.6%) demonstrating the importance of letting large trees grow larger and accumulate more carbon. Our research contributes to growing recognition that forests with large trees play a



FIGURE 1 Large-diameter grand fir (*Abies grandis*) in a mesic, mixed-conifer forest of northeast Oregon. These carbon-rich forests have a large cooling effect on maximum temperatures, provide thermal refugia for biodiversity including sensitive species, and are a high priority for protection. Large grand fir form the best hollow trees for wildlife (Rose et al., 2001).

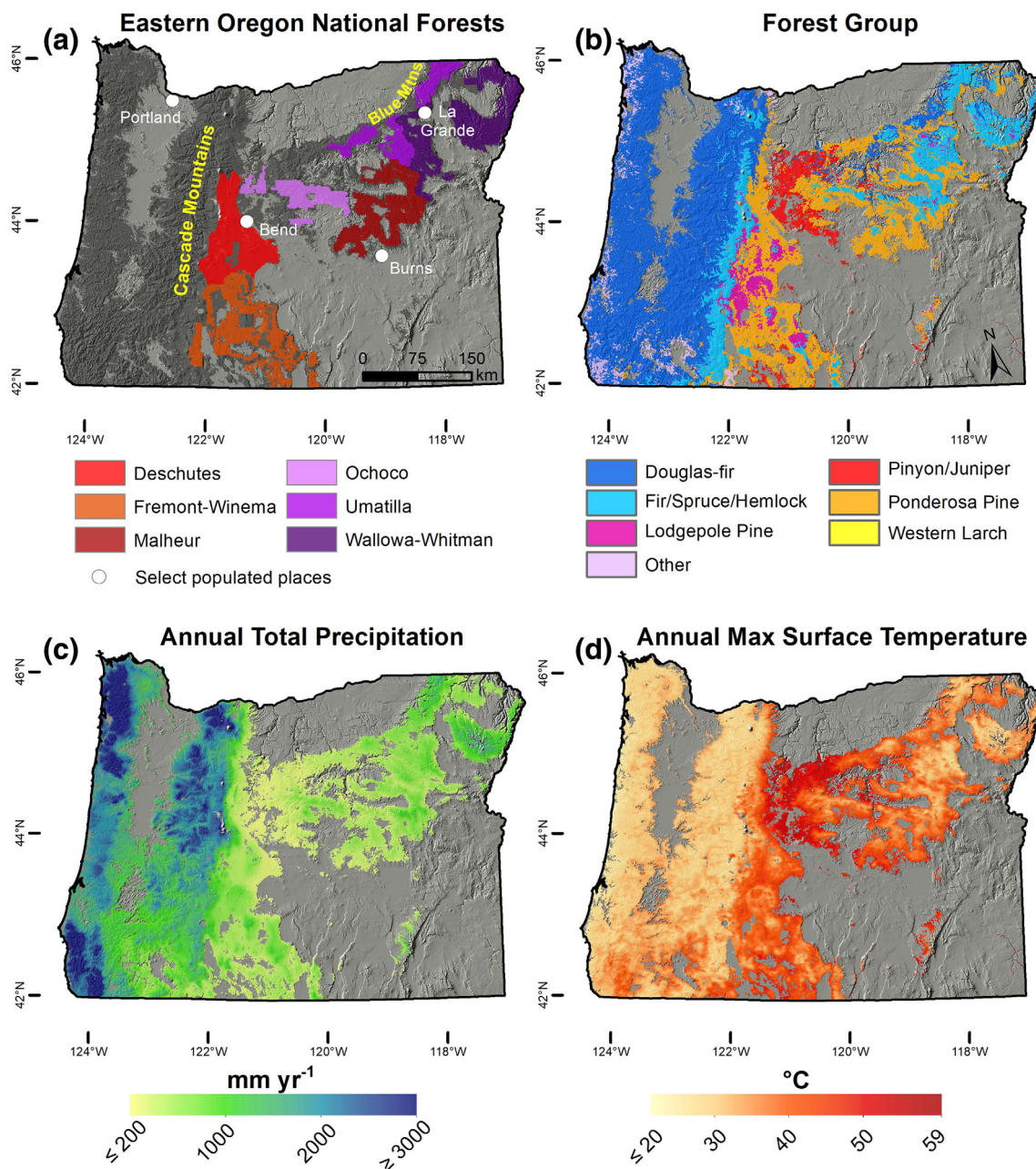


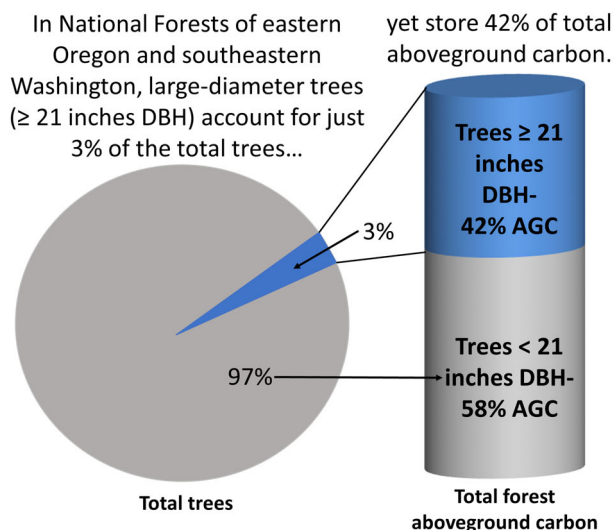
FIGURE 2 Forest and climatic diversity across the state of Oregon. (a) Extent of National Forests in Eastern Oregon. (Note a small portion of southeastern Washington included in our original study is not shown in this figure). (b) Distribution of forest groups. (c) Mean annual total precipitation from 1981 to 2010. (d) Mean annual maximum land surface temperature [LSTmax] from 2003 to 2020. Data sources include forest groups from Ruefenacht et al. (2008), precipitation climatology from Daly et al. (2008), and annual LSTmax derived using MODIS Aqua satellite data from Wan (2014).

very important role in climate mitigation now and in the near future (Lutz et al., 2018; Stephenson et al., 2014).

2.2 | A wildlife protection measure with a crucial carbon co-benefit

The 21-inch rule was implemented in the early 1990s as a habitat and species protection measure to recover large

tree structure and to protect remaining late successional and old-growth forest and associated species (e.g., American Marten, Northern Goshawk) (Bull et al., 2005; Bull & Hohmann, 1994; Henjum et al., 1994), similar to the Northwest Forest Plan (NWFP) that was implemented to ensure persistence of old-growth forest species and their habitat in the western portion of the region (FEMAT, 1993). The NWFP resulted in a strong carbon benefit for climate mitigation, in addition to protecting sensitive species and riparian



Species common name	% of total species trees ≥ 21 inches	% of total species AGC in trees ≥ 21 inches
Douglas-fir	3.7	37.5
Engelmann spruce	2.4	34.7
Grand fir	2.0	38.4
Ponderosa pine	3.7	45.8
Western larch	2.8	33.3
Overall	3.1	42.2

FIGURE 3 Percentage of all tree stems above and below the 21-inch DBH threshold and their total aboveground carbon (AGC) stores overall, and for five dominant tree species, evaluated based on measurements from USFS inventory plots located in the six eastside national forests.

systems (Turner et al., 2011). Mildrexler et al. (2020) showed that carbon storage associated with the 21-inch rule on the six eastside national forests is a significant co-benefit of this protective measure (Pörtner et al., 2021).

Detailed analysis of stand structure and carbon impacts is essential for science-based decision-making about large-tree forest management policies because such policies affect many different values and services provided by forests (Davis et al., 2019; Teich et al., 2022), including consequences on greenhouse gas emissions and for increasing atmospheric carbon removal and accumulation in forests (Fargione et al., 2018; Griscom et al., 2017). Moreover, large live trees eventually create large-diameter snags and downed wood that continue to store carbon for decades and contribute directly to biodiversity by providing unique specialized habitats such as hollow trees and logs, and micro-environments (Lutz et al., 2021; Rose et al., 2001). However, the USFS General Technical Report on the 21-inch rule did not assess large tree carbon stocks (Hessburg et al., 2020), even though storage and accumulation of carbon in forests is an increasing priority in National Forests (Depro et al., 2008; Dilling et al., 2013; Dugan et al., 2017). Consequently, quantitative assessments of management effects on both forest carbon and biodiversity are important, including assessment of the effects of long-standing rules before they are eliminated or weakened (Mildrexler et al., 2020).

The 21-inch rule has since been amended. Grand fir (DBH ≥ 53 cm and < 150 years) has lost protections in stands not designated as Late and Old Structure, and protections for all tree species have been significantly weakened from a standard to a guideline (USDA, 2021). This represents a major shift in management of large trees across the region, highlighting escalating tradeoffs between goals for carbon sequestration to mitigate climate change, and efforts to increase the pace, scale, and intensity of cutting across national forest lands. The potential impacts of removal of large grand fir on wildfire

are unclear, although a trait-based approach to assess fire resistance found that the grand fir forest type had the second highest fire resistance score, and one of the lowest fire severity values among forest types of the Inland Northwest USA (Moris et al., 2022).

3 | ARE LARGE GRAND FIR OUTCOMPETING LARGE PONDEROSA PINE AND LARCH?

The key rationale for amending the 21-inch rule is that increased cutting of large-diameter fir trees (≥ 53 cm DBH and < 150 years) is needed to facilitate the conservation and recruitment of early-seral, shade-intolerant old ponderosa pine (*Pinus ponderosa*) and western larch (*Larix occidentalis*) by reducing competition from shade-tolerant large grand fir (*Abies grandis*) (USDA, 2021). Previous studies have looked at tree age-size relationships (Merschel et al., 2019; Perry et al., 2004), large tree numbers, and changes in basal area (Hessburg et al., 2022), but there has been no spatial analysis of close-range comingling of large-diameter tree species across the six national forests covered by the 21-inch rule. This is an important consideration because the competitive interaction among large-diameter trees, and their protection under the 21-inch rule, should not be conflated with small tree dynamics and common dry forest restoration strategies to reduce small tree density and favor retention of early-seral species.

We therefore examined how often large trees (≥ 53 cm DBH) of these species co-mingle on USFS FIA plots (~ 1 acre) across the same six eastside national forests where we previously examined carbon storage by large trees (Mildrexler et al., 2020). Drawing on the same USFS FIA measurements as our prior study, we found that large ponderosa pine, grand fir, and western larch were present

TABLE 1 Coverage, mean annual precipitation from 1981 to 2010, and mean annual maximum land surface temperature from 2003 to 2020 for the major FTG's within the six national forests, standard deviations in parenthesis (excludes lands in Washington and Idaho).

Forest type group	Area (km ²)	Mean annual precipitation		Mean annual maximum LST	
		mm	in	°C	°F
Douglas-fir	2372	679.9 (187.3)	26.8 (7.4)	37.8 (3.5)	100.1 (6.3)
Fir/Spruce/Hemlock	12,224	974.3 (369.5)	38.4 (14.5)	33.2 (2.8)	91.8 (5.0)
Lodgepole pine	3573	822.0 (274.6)	32.4 (10.8)	37.2 (3.8)	99.0 (6.8)
Pinyon/Juniper	634	329.5 (96.0)	13.0 (3.8)	50.4 (3.7)	122.7 (6.6)
Ponderosa pine	18,514	548.3 (139.2)	21.6 (5.5)	39.8 (3.5)	103.6 (6.3)
Western larch	47	746.9 (78.9)	29.4 (3.1)	31.5 (2.4)	88.7 (4.3)

on 56%, 18%, and 7% of all plots ($n = 3335$). Large ponderosa pine co-mingle with large grand fir about 14% of the time (259 plots), leaving 86% of plots with large ponderosa pine without large grand fir (1616 plots). Similarly, large western larch co-mingle with large grand fir about 56% of the time. Large ponderosa pine and grand fir are found together on only 8% of all plots in the region, while large larch and grand fir are found together on only 4% of all plots in the region. In other words, large ponderosa pine are by far the most common tree species found in these six National Forests and infrequently co-mingle with large grand fir at the FIA plot scale, whereas large western larch are far less common and co-mingle with large grand fir about half the time, which is expected since these species occupy similar environmental settings that receive more moisture (Table 1, Johnson & Clausnitzer, 1992).

The relative prevalence of large ponderosa pine in eastside forests is good for climate resilience given that large-diameter pines are exceptionally drought and fire-resistant trees (Irvine et al., 2004; Irvine et al., 2007). In the drought-prone region of central Oregon, mature and old ponderosa pine forests had 60% to 85% higher seasonal gross photosynthesis than a young forest (Irvine et al., 2004). Large ponderosa pine trees experienced only 34% mortality in moderate severity fire, and accounted for 91% of post-fire stemwood production, while small trees experienced 82% mortality (Irvine et al., 2007).

Across the entirety of all six national forests large grand fir represent 2% of the total species population, a proportion slightly lower, but roughly on par with other dominant species (Figure 3, Mildrexler et al., 2020). It is not uncommon for grand fir to reach 250 to 300 years of age (Howard & Aleksoff, 2000). Thus, large grand fir ≥ 53 cm DBH and <150 years of age can continue growing and play an important role in storing and accumulating carbon from the atmosphere to help abate the climate crisis.

Synergy: Enhancing forest resilience does not necessitate widespread cutting of any large-diameter tree species. Favoring early-seral species can be achieved with a

focus on smaller trees and restoring surface fire, while retaining the existing large tree population.

4 | LARGE TREES, VULNERABILITY, STAND DYNAMICS, AND THE CARBON COST OF THINNING

As eastside forests recover from a century of intensive logging, it is important to distinguish between the shift of AGC stocks into small-diameter, fire-sensitive trees and the retention of a small fraction of the largest more fire-resistant trees that store disproportionately massive amounts of carbon. Small tree carbon stores are relatively unstable and at risk of loss to fire and drought, whereas large tree carbon stores are relatively stable and resistant (Hurteau et al., 2019). Physiological-based studies in ponderosa pine forests of Oregon have found that small trees are most vulnerable during drought relative to mature trees that have reached full root, bark and canopy development and respond to climate variability better than smaller trees (Domec et al., 2004; Irvine et al., 2004; Vickers et al., 2012). Buotte et al. (2019, 2020) identified forests in the western U.S. with high potential carbon accumulation and low vulnerability to future drought and fire using the Community Land Model and two climate models with high CO₂ emissions (RCP8.5), and species-specific traits capturing sensitivity of different species to water limitations and to drought and fire. The Eastern Cascades and Blue Mountains contain substantial area with opportunity to enhance forest carbon in large trees (Buotte et al., 2020; Law et al., 2018).

In dry forests historically maintained by a frequent, low-severity fire regime, the priority ought to be restoring the process of periodic surface fire. Prescribed fires create landscape heterogeneity, reduce surface and ladder fuels, lower stand density, and confer drought resistance to surviving trees (Knapp & Keeley, 2006; van Mantgem et al., 2016). In

these forests prescribed fire can modulate future fire activity (Schoennagel et al., 2017), and favor early-seral species such as ponderosa pine, western larch and Douglas-fir. Large trees of these species and grand fir are resilient to prescribed fire because they have attained the thick bark that provides resistance to low- and moderate-severity fire (Howard & Aleksoff, 2000; Pellegrini et al., 2017).

Thinning also has an inherent carbon cost that increases as larger trees are harvested, thereby putting thinning of larger trees in conflict with carbon goals because it takes so long to replace the harvested biomass (James et al., 2018; Law & Harmon, 2011). The underlying principle for these losses is the negative relationship between harvest intensity and forest carbon stocks whereby as harvest intensity increases, forest carbon stocks decrease and emissions increase (Hudiburg et al., 2009; Mitchell et al., 2009; Simard et al., 2020). Claims that carbon stores will be “stabilized” by increasing harvest of large-diameter trees that store and accumulate the most carbon (Johnston et al., 2021) are inconsistent with basic science on thinning (Zhou et al., 2013) and the carbon cycle (Campbell et al., 2012; Law et al., 2018). These claims ignore the large amounts of CO₂ rapidly released to the atmosphere following harvest (Hudiburg et al., 2019), and that large trees cannot be replaced in short timeframes. It can take centuries to reaccumulate forest carbon stocks reduced by harvest of large trees (Birdsey et al., 2006).

Even thinning smaller trees involves substantial carbon tradeoffs in the short term, a 30%–40% reduction in live tree carbon stores in some forests (Krofcheck et al., 2017; North et al., 2009). To minimize reductions in carbon stocks and emissions, focus on removing smaller-sized trees, restoring surface fire, and managed wildfire in favorable weather conditions (Mitchell et al., 2009; Stenzel et al., 2021).

Synergy: Small trees are more relevant to drought and fire vulnerability and store less carbon, whereas large trees are more resilient to fire and drought and are the highest priority for keeping carbon in the forest.

5 | DIVERSE CLIMATE REGIMES AND FOREST TYPES REDUCE CLIMATIC EXTREMES

It is critical to accurately represent the diversity of climatic regimes and forest types in decisions affecting large tree management because large trees play unique roles in ecosystem water and energy cycles, and these biophysical effects can promote local climate stability by reducing extreme temperatures in all seasons and times of day (Lawrence et al., 2022). Forest modulation of summer maximum temperature is especially powerful (Mildrexler et al., 2018) and can partly offset the projected increases in temperature due

to anthropogenic climate change (de Frenne et al., 2019). With heatwave frequency and severity projected to increase, the capacity of forests to buffer against temperature extremes and provide refugia is increasingly recognized as important to sustaining biodiversity in a warming world (Davis et al., 2019; de Frenne et al., 2019).

The six eastside national forests affected by the 21-inch rule cover a region of pronounced geographic and climatic variation and associated forest types (Figure 2; Johnson & Clausnitzer, 1992; Wyatt, 2017). Mean annual precipitation varied from 484 to 571 mm per year on the Ochoco and Malheur National Forests, to ~800 mm per year on the Deschutes, Umatilla and Wallowa Whitman National Forests (Mildrexler et al., 2020). We further examined the climatic regimes of the major forest types across the six national forests using satellite-based annual maximum land surface temperature (LST_{max}) and mean annual precipitation datasets (Figure 2D, Table 1). Our analysis shows that ponderosa pine and fir/spruce/hemlock types cover the largest area on the six national forests. The fir/spruce/hemlock type received the most total precipitation (~974 mm yr⁻¹) and had the second lowest annual LST_{max} (33.2°C). Average LST_{max} for the fir/spruce/hemlock type was 6.6°C (~12 °F) cooler than ponderosa pine (39.8°C), and 4.6°C (~8 °F) cooler than Douglas-fir (37.8°C). The pinyon juniper type had the lowest total precipitation (329 mm yr⁻¹) and highest annual LST_{max} (50.4°C) due to low canopy cover and heating of the dry surface during summer. These results show the region's pronounced variability in hydrologic and forest thermal regimes and highlight the thermal offsetting capacity of closed-canopied mesic forest systems. These valuable ecosystem services can be severely degraded by industrial logging (Lindenmayer et al., 2009).

Synergy: Mature and old mesic forests are a high priority for protection, provide crucial biophysical benefits on climate, including a large cooling effect on maximum temperatures regulating climate extremes and protecting biodiversity. Large grand fir is essential to this ecology.

6 | CONCLUSIONS

The 21-inch rule is an excellent example of a policy initiated for wildlife and habitat protection that has also provided significant climate mitigation values across extensive forests of the PNW Region. The rule resulted in a valuable resource of large-diameter trees in a landscape that remains below historical levels for large live trees and large snags due to historical logging (Bell et al., 2021). We have described synergies between protecting these disproportionately valuable large trees and forest resilience goals, providing common potential solutions for these urgent challenges.

Inland PNW forests can make a significant contribution to climate mitigation goals by protecting and enhancing carbon stores in large trees that accumulate and store the most carbon and are much more resistant to fire and drought than small trees, even when the current status of ecosystems has changed from historical baselines. Climate science makes clear that we do not have time to wait for regrowth after logging to accomplish these important ecosystem services (IPCC, 2022).

AUTHOR CONTRIBUTIONS

David J. Mildrexler led the writing. David J. Mildrexler and Logan T. Berner performed data analysis, investigation, and visualization. All authors commented on drafts, and assisted with writing, review and editing. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

This study relied on data from prior studies that are publicly available: Forest Inventory Data from the United States Forest Service (<https://apps.fs.usda.gov/fia/datamart/datamart.html>), MODIS Land Surface Temperature data from the Land Processes Distributed Active Archive Center accessed through Google Earth Engine, and gridded precipitation climatologies from Oregon State University PRISM Climate Group (<https://prism.oregonstate.edu/normals/>).

ORCID

David J. Mildrexler  <https://orcid.org/0000-0001-8370-8714>

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Intact Forests in the United States: Proforestation Mitigates Climate Change and Serves the Greatest Good

William R. Moomaw^{1*}, Susan A. Masino^{2,3} and Edward K. Faison⁴

¹ Emeritus Professor, The Fletcher School and Co-director Global Development and Environment Institute, Tufts University, Medford, MA, United States, ² Vernon Roosa Professor of Applied Science, Trinity College, Hartford, CT, United States, ³ Charles Bullard Fellow in Forest Research, Harvard Forest, Petersham, MA, United States, ⁴ Senior Ecologist, Highstead Foundation, Redding, CT, United States

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*Correspondence:

William R. Moomaw
william.moomaw@tufts.edu

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Climate change and loss of biodiversity are widely recognized as the foremost environmental challenges of our time. Forests annually sequester large quantities of atmospheric carbon dioxide (CO₂), and store carbon above and below ground for long periods of time. Intact forests—largely free from human intervention except primarily for trails and hazard removals—are the most carbon-dense and biodiverse terrestrial ecosystems, with additional benefits to society and the economy. Internationally, focus has been on preventing loss of tropical forests, yet U.S. temperate and boreal forests remove sufficient atmospheric CO₂ to reduce national annual *net* emissions by 11%. U.S. forests have the potential for much more rapid atmospheric CO₂ removal rates and biological carbon sequestration by intact and/or older forests. The recent *1.5 Degree Warming Report* by the Intergovernmental Panel on Climate Change identifies *reforestation* and *afforestation* as important strategies to increase negative emissions, but they face significant challenges: afforestation requires an enormous amount of additional land, and neither strategy can remove sufficient carbon by growing young trees during the critical next decade(s). In contrast, growing existing forests intact to their ecological potential—termed *proforestation*—is a more effective, immediate, and low-cost approach that could be mobilized across suitable forests of all types. Proforestation serves the greatest public good by maximizing co-benefits such as nature-based biological carbon sequestration and unparalleled ecosystem services such as biodiversity enhancement, water and air quality, flood and erosion control, public health benefits, low impact recreation, and scenic beauty.

Keywords: biodiversity crisis, Pinchot, afforestation, reforestation, forest ecosystem, biological carbon sequestration, old-growth forest, second-growth forest

INTRODUCTION

Life on Earth as we know it faces unprecedented, intensifying, and urgent imperatives. The two most urgent challenges are (1) mitigating and adapting to climate change (Intergovernmental Panel on Climate Change, 2013, 2014, 2018), and (2) preventing the loss of biodiversity (Wilson, 2016; IPBES, 2019). These are three of the Sustainable Development Goals, Climate, Life on Land and Life under Water (Division for Sustainable Development Goals, 2015), and significant international resources are being expended to address these crises and limit

negative impacts on economies, societies and biodiverse natural communities. The recent *1.5 Degree Warming Report* of the Intergovernmental Panel on Climate Change (2018) was dire and direct, stating the need for “rapid, far-reaching and unprecedented changes in all aspects of society.” We find that growing additional existing forests as intact ecosystems, termed *proforestation*, is a low-cost approach for immediately increasing atmospheric carbon sequestration to achieve a stable atmospheric carbon dioxide concentration that reduces climate risk. Proforestation also provides long-term benefits for biodiversity, scientific inquiry, climate resilience, and human benefits. This approach could be mobilized across all forest types.

Forests are essential for carbon dioxide removal (CDR), and the CDR rate needs to increase rapidly to remain within the 1.5 or 2.0°C range (Intergovernmental Panel on Climate Change, 2018) specified by the Paris Climate Agreement (2015). Growing existing forests to their biological carbon sequestration potential optimizes CDR while limiting climate change and protecting biodiversity, air, land, and water. Natural forests are by far the most effective (Lewis et al., 2019). Technologies for direct CDR from the atmosphere, and bioenergy with carbon capture and storage (BECCS), are far from being technologically ready or economically viable (Anderson and Peters, 2016). Furthermore, the land area required to supply BECCS power plants with tree plantations is 7.7 million km², or approximately the size of Australia (Intergovernmental Panel on Climate Change, 2018). Managed plantations that are harvested periodically store far less carbon because trees are maintained at a young age and size (Harmon et al., 1990; Sterman et al., 2018). Furthermore, plantations are often monocultures, and sequester less carbon more slowly than intact forests with greater tree species diversity and higher rates of biological carbon sequestration (Liu et al., 2018). Recent research in the tropics shows that natural forests hold 40 times more carbon than plantations (Lewis et al., 2019).

Alternative forest-based CDR methods include *afforestation* (planting new forests) and *reforestation* (replacing forests on deforested or recently harvested lands). Afforestation and reforestation can contribute to CDR, but newly planted forests require many decades to a century before they sequester carbon dioxide in substantial quantities. A recent National Academy study titled *Negative Emissions Technologies and Reliable Sequestration: A Research Agenda* discusses afforestation and reforestation and finds their contribution to be modest (National Academies of Sciences, 2019). The study also examines changes in conventional forest management, but neglects proforestation as a strategy for increasing carbon sequestration. Furthermore, afforestation to meet climate goals requires an estimated 10 million km²—an area slightly larger than Canada (Intergovernmental Panel on Climate Change, 2018). The massive land areas required for afforestation and BECCS (noted above) compete with food production, urban space and other uses (Searchinger et al., 2009; Sterman et al., 2018). More importantly, neither of these two practices is as effective quantitatively as proforestation in the next several decades when it is needed most. For example, Law et al. (2018) reported that extending harvest cycles and reducing cutting on public lands had a larger effect than either afforestation

or reforestation on increasing carbon stored in forests in the Northwest United States. In other regions such as New England (discussed below), longer harvest cycles and proforestation are likely to be even more effective. Our assessment on the climate and biodiversity value of natural forests and proforestation aligns directly with a recent report that pinpointed “stable forests” – those not already significantly disturbed or at significant risk – as playing an outsized role as a climate solution due to their carbon sequestration and storage capabilities (Funk et al., 2019).

Globally, terrestrial ecosystems currently remove an amount of atmospheric carbon equal to one-third of what humans emit from burning fossil fuels, which is about 9.4 GtC/y (10⁹ metric tons carbon per year). Forests are responsible for the largest share of the removal. Land use changes, i.e., conversion of forest to agriculture, urban centers and transportation corridors, emit ~1.3 GtC/y (Le Quéré et al., 2018). However, forests’ potential carbon sequestration and additional ecosystem services, such as high biodiversity unique to intact older forests, are also being degraded significantly by current management practices (Foley et al., 2005; Watson et al., 2018). Houghton and Nassikas (2018) estimated that the “current gross carbon sink in forests recovering from harvests and abandoned agriculture to be –4.4 GtC/y, globally.” This is approximately the current gap between anthropogenic emissions and biological carbon and ocean sequestration rates by natural systems. If deforestation were halted, and secondary forests were allowed to continue growing, they would sequester –120 GtC between 2016 and 2100 or ~12 years of current global fossil carbon emissions (Houghton and Nassikas, 2018). Northeast secondary forests have the potential to increase biological carbon sequestration between 2.3 and 4.2-fold (Keeton et al., 2011).

Existing proposals for “Natural Climate Solutions” do not consider explicitly the potential of proforestation (Griscom et al., 2017; Fargione et al., 2018). However, based on a growing body of scientific research, we conclude that protecting and stewarding intact diverse forests and practicing proforestation as a purposeful public policy on a large scale is a highly effective strategy for mitigating the dual crises in climate and biodiversity and ultimately serving the “greatest good” in the United States and the rest of the world. **Table 1** summarizes some of the key literature supporting this point.

A SMALL FRACTION OF U.S. FORESTS IS MANAGED TO REMAIN INTACT

Today, <20% of the world’s forests remain intact (i.e., largely free from logging and other forms of extraction and development). Intact forests are largely tropical forests or boreal forests in Canada and Russia (Watson et al., 2018). In the U.S.—a global pioneer in national parks and wildlife preserves—the percentage of intact forest in the contiguous 48 states is only an estimated 6–7% of total forest area (Oswalt et al., 2014), with a higher proportion in the West and a lower proportion in the East. Setting aside a large portion of U.S. forest in Inventoried Roadless Areas (IRAs) was groundbreaking yet only represents 7% of total forest area in the lower 48 states—and, ironically,

TABLE 1 | Comparison of climate and biodiversity benefits of *intact* (either old-growth forest or younger forest managed as Gap 1 or Gap 2, and thus protected from logging and other resource extraction) and traditionally *managed* forests for multiple forest types in the United States.

	Location	Forest type	Forest condition with greater value	References
ECOSYSTEM CHARACTERISTICS				
Density of large trees (>60 cm DBH)	Eastern US	mid-Atlantic oak-hickory forests, northern hemlock-hardwood forests, and boreal spruce-fir forests	Intact (81% greater)	Miller et al., 2016
Proportion of old forest	Eastern US	Same as above	Intact	Miller et al., 2016
Basal area of dead standing trees	Eastern US	Same as above	Intact	Miller et al., 2016
Coarse woody debris volume	Eastern US	Same as above	Intact (135% greater)	Miller et al., 2016
Carbon storage	Pacific Northwest US	Douglas fir and western hemlock;	Intact (75–138% greater)	Harmon et al., 1990
Carbon storage	Northeastern US	Northern hardwood conifer	Intact (39–118% greater)	Nunery and Keeton, 2010
Forest fire burn severity	Western US	Pine and mixed conifer forests	Managed (two SEs greater)	Bradley et al., 2016
BIODIVERSITY				
Tree species richness	Eastern US	mid-Atlantic oak-hickory forests, northern hemlock-hardwood forests, and boreal spruce-fir forests	Intact	Miller et al., 2018
Proportion rare tree species	Eastern US	Same as above	Intact	Miller et al., 2018
Bird species richness and abundance	Northeastern Minnesota	Hemi-boreal	Intact (12–20% greater)	Zlonis and Niemi, 2014
Trunk bryophyte and lichen species richness	Northwestern Montana	Grand-fir	Intact (33% greater)	Lesica et al., 1991
Salamander density	Ozark Mountains, Missouri	Oak-hickory	Intact (395–9,500% greater)	Herbeck and Larsen, 1999
Probability of occurrence of invasive plant species	Eastern US	Deciduous and mixed forest	managed	Riitters et al., 2018

Intact forests range in size and previous disturbance history but they are not under active management and have been allowed to continue growing according to the procedures described for proforestation.

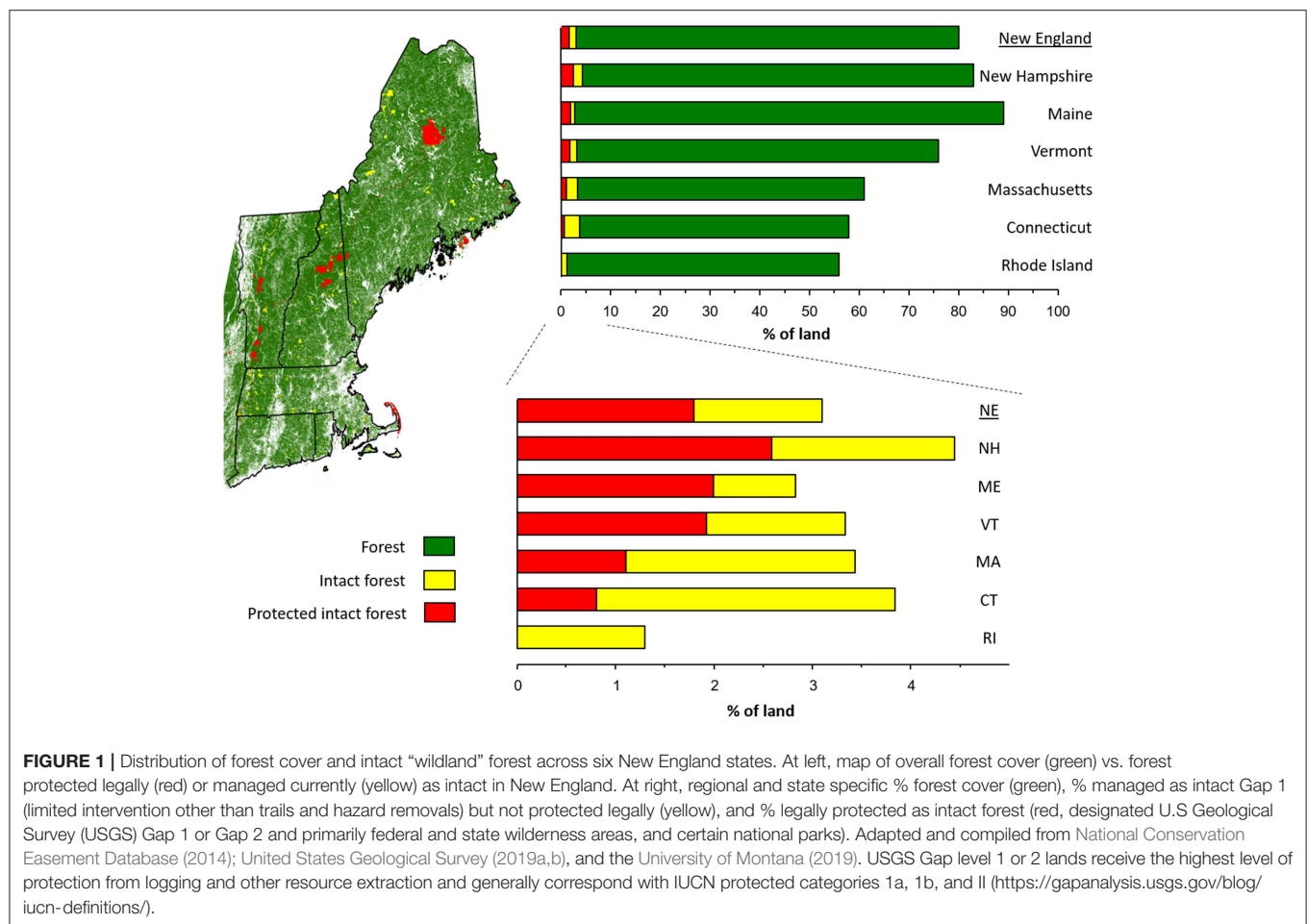
management of some IRAs allows timber harvest and road building (Williams, 2000), a scenario happening currently in the Tongass National Forest in Alaska (Koberstein and Applegate, 2018). These scant percentages worldwide and particularly in the U.S. are insufficient to address pressing national and global issues such as rising CO₂ levels, flooding, and biodiversity loss, as well as provide suitable locations for recreation and associated public health benefits (Cordell, 2012; Watson et al., 2018). In heavily populated and heavily forested sub-regions in the Eastern U.S., such as New England, the total area dedicated as intact (i.e., primary management is for trails and hazard removals) is even more scarce, comprising only ~3% of land area. Just 2% of the region is legally protected from logging and other resource extraction (Figure 1). A large portion of forest managed currently as intact or “reserved forest” – and thus functioning as “stable forest” (Funk et al., 2019) – is designated solely by administrative regulations that can be altered at any time.

Intact forests in the U.S. include federal wilderness areas and national parks, some state parks, and some privately-owned holdings and conservation trust lands. Recent studies reveal that intact forests in national parks tend to be older and have larger trees than nearby forests that are not protected from logging (Miller et al., 2016; Table 1). Scaling up protection of intact forests and designating and significantly expanding reserved forest areas are public policy imperatives that are compatible with public access and with the country’s use

of forest products. Identifying suitable forest as intact (for carbon sequestration, native biodiversity, ecosystem function, etc.) can spawn new jobs and industries in forest monitoring, tourism and recreation, as well as create more viable local economies based on wood reuse and recycling. Public lands with significant biodiversity and proforestation potential also provide wildlife corridors for climate migration and resilience for many species.

PROFORESTATION INCREASES BIOLOGICAL CARBON SEQUESTRATION AND LONG-TERM STORAGE IN U.S. FORESTS

Net forest carbon reflects the dynamic between gains and losses. Carbon is lost from forests in several ways: damage from natural disturbances including insects and pathogens (“pests”), fire, drought and wind; forest conversion to development or other non-forest land; and forest harvest/management. Together, fires, drought, wind, and pests account for ~12% of the carbon lost in the U.S.; forest conversion accounts for ~3% of carbon loss; and forest harvesting accounts for 85% of the carbon lost from forests each year (Harris et al., 2016). Forests in the Southern US have the highest percentage of carbon lost to timber harvest (92%) whereas the Western US is notably lower (66%) because of the



greater contribution of fires to carbon removal. The Northern U.S. is roughly equivalent to the national average at 86% (Harris et al., 2016).

Proforestation produces natural forests as maximal carbon sinks of diverse species (while supporting and accruing additional benefits of intact forests) and can reduce significantly and immediately the amount of forest carbon lost to non-essential management. Because existing trees are already growing, storing carbon, and sequestering more carbon more rapidly than newly planted and young trees (Harmon et al., 1990; Stephenson et al., 2014; Law et al., 2018; Leverett and Moomaw, in preparation), proforestation is a near-term approach to sequestering additional atmospheric carbon: a significant increase in “negative emissions” is urgently needed to meet temperature limitation goals.

The carbon significance of proforestation is demonstrated in multiple ways in larger trees and older forests. For example, a study of 48 undisturbed primary or mature secondary forest plots worldwide found, on average, that the largest 1% of trees [considering all stems ≥ 1 cm in diameter at breast height (DBH)] accounted for half of above ground living biomass (The largest 1% accounted for $\sim 30\%$ of the biomass in U.S. forests due to larger average size and fewer stems compared to the tropics) (Lutz

et al., 2018). Each year a single tree that is 100 cm in diameter adds the equivalent biomass of an entire 10–20 cm diameter tree, further underscoring the role of large trees (Stephenson et al., 2014). Intact forests also may sequester half or more of their carbon as organic soil carbon or in standing and fallen trees that eventually decay and add to soil carbon (Keith et al., 2009). Some older forests continue to sequester additional soil organic carbon (Zhou et al., 2006) and older forests bind soil organic matter more tightly than younger ones (Lacroix et al., 2016).

If current management practices continue, the world’s forests will only achieve half of their biological carbon sequestration potential (Erb et al., 2018); intensifying current management practices will only decrease living biomass carbon and increase soil carbon loss. Forests in temperate zones such as in the Eastern U.S. have a particularly high untapped capacity for carbon storage and sequestration because of high growth and low decay rates (Keith et al., 2009) and because of recent recovery from an extensive history of timber harvesting and land conversion for agriculture in the 18th, 19th, and early 20th centuries (Pan et al., 2011; Duveneck and Thompson, 2019). In New England, median forest age is about 75 years of age (United States Forest Service, 2019), which is only about 25–35% of the lifespan of many of the common tree species in these

forests (Thompson et al., 2011). Much of Maine's forests have been harvested continuously for 200 years and have a carbon density less than one-third of the forests of Southern Vermont and New Hampshire, Northwestern Connecticut and Western Massachusetts—a region that has not been significantly harvested over the past 75–150 years (National Council for Air Stream Improvement, 2019). Western Massachusetts in particular has a significant portion classified as Tier 1 matrix forest, defined as “large contiguous areas whose size and natural condition allow for the maintenance of ecological processes” (Databasin, 2019). However, forests managed as intact do not need to be large or old in absolute terms to have ecological value: disturbances create gaps and young habitats, and the official policy of the Commonwealth of Massachusetts Department of Environmental Management (now Department of Conservation and Recreation) considers an old-growth forest of at least 2 hectares ecologically significant (Department of Environmental Management, 1999).

As shown in **Table 1**, ecosystem services accrue as forests age for centuries. Far from plateauing in terms of carbon sequestration (or added wood) at a relatively young age as was long believed, older forests (e.g., >200 years of age without intervention) contain a variety of habitats, typically continue to sequester additional carbon for many decades or even centuries, and sequester significantly more carbon than younger and managed stands (Luyssaert et al., 2008; Askins, 2014; McGarvey et al., 2015; Keeton, 2018). A recent paper affirmed that letting forests grow is an effective way to sequester carbon—but unlike previous studies it suggested that sequestration is highest in “young” forests (Pugh et al., 2019). This conclusion is problematic for several reasons. One confounding factor is that older forests in the tropics were compared to young forests in temperate and boreal areas; temperate forests in particular have the highest CO₂ removal rates and overall biological carbon sequestration (Keith et al., 2009) but this high rate is not limited to young temperate and boreal forests. The age when sequestration rates decrease is not known, and Pugh et al. defined “young” as up to 140 years. As noted above, Keeton et al. (2011) estimate that secondary forests in the Northeast have the potential to increase their biological carbon sequestration several-fold. More field work is needed across age ranges, species and within biomes, but the inescapable conclusion is that growing forests is beneficial to the climate and maintaining intact forest has additional benefits (**Table 1**). We conclude that proforestation has the potential to provide rapid, additional carbon sequestration to reduce *net* emissions in the U.S. by much more than the 11% that forests provide currently (United States Environmental Protection Agency, 2019). A recent report on natural climate solutions determined that negative emissions could be increased from 11 to 21% even without including proforestation (Fargione et al., 2018). Quantified estimates of increased forest sequestration and ecosystem services were based on re-establishing forests where possible and lengthening rotation times on private land; they explicitly did not account for proforestation potential on public land.

Although biological carbon storage in managed stands, regardless of the silvicultural prescription, is generally lower than in unmanaged intact forests (Harmon et al., 1990; Ford and

Keeton, 2017)—even after the carbon stored in wood products is included in the calculation—stands managed with reduced harvest frequency and increased structural retention sequester more carbon than more intensively managed stands (Nunery and Keeton, 2010; Law et al., 2018). Such an approach for production forests, or “working” forests—balancing resource extraction with biological carbon sequestration—is often termed “managing for net carbon” or “managing for climate change” and an approach that should be promoted alongside dedicating significant areas to intact ecosystems. Oliver et al. (2014) acknowledge a balance between intact and managed forest and suggest that long term storage in “efficient” wood products like wood building materials (with the potential for less carbon emissions compared to steel or concrete, termed the “avoidance pathway”) can offer a significant carbon benefit. To achieve this, some questionable assumptions are that 70% of the harvested wood is merchantable and stored in a lasting product, all unmerchantable wood is removed and used, harvesting occurs at optimum intervals (100 years) and carbon sequestration tapers off significantly after 100 years. Forestry models underestimate the carbon content of older, larger trees, and it is increasingly clear that trees can continue to remove atmospheric carbon at increasing rates for many decades beyond 100 years (Robert T. Leverett, pers. comm. Stephenson et al., 2014; Lutz et al., 2018; Leverett et al., under review). Because inefficient logging practices result in substantial instant carbon release to the atmosphere, and only a small fraction of wood becomes a lasting product, increasing market forces and investments toward wood buildings that have relatively short lifetimes could increase forest extraction rates significantly and become unsustainable (Oliver et al., 2014).

HABITAT PROTECTION, BIODIVERSITY AND SCIENTIFIC VALUE OF PROFORESTATION

Large trees and intact, older forests are not only effective and cost-effective natural reservoirs of carbon storage, they also provide essential habitat that is often missing from younger, managed forests (Askins, 2014). For example, intact forests in Eastern U.S. national parks have greater tree diversity, live and dead standing basal area, and coarse woody debris, than forests that are managed for timber (Miller et al., 2016, 2018; **Table 1**). The density of cavities in older trees and the spatial and structural heterogeneity of the forest increases with stand age (Ranius et al., 2009; Larson et al., 2014), and large canopy gaps develop as a result of mortality of large trees, which result in dense patches of regeneration (Askins, 2014). These complex structures and habitat features support a greater diversity of lichens and bryophytes (Lesica et al., 1991), a greater density and diversity of salamanders (Petranka et al., 1993; Herbeck and Larsen, 1999), and a greater diversity and abundance of birds in old, intact forests than in nearby managed forests (Askins, 2014; Zlonis and Niemi, 2014; **Table 1**). Forest bird guilds also benefit from small intact forests in urban landscapes relative to unprotected matrix forests (Goodwin and Shriver, 2014). Several bird species

in the U.S. that are globally threatened—including the wood thrush, cerulean warbler, marbled murrelet, and spotted owl are, in part, dependent on intact, older forests with large trees (International Union for Conservation of Nature, 2019). Two species that are extinct today—Bachman's warbler and Ivory-billed woodpecker—likely suffered from a loss of habitat features associated with old forests (Askins, 2014).

Today, forest managers often justify management to maintain heterogeneity of age structures to enhance wildlife habitat and maintain “forest health” (Alverson et al., 1994). However, early successional forest species (e.g., chestnut-sided warbler and New England cottontail) that are common targets for forest management may be less dependent on forest management than is commonly believed (cf. Zlonis and Niemi, 2014; Buffum et al., 2015). Management also results in undesirable consequences such as soil erosion, introduction of invasive and non-native species (McDonald et al., 2008; Riitters et al., 2018), loss of carbon—including soil carbon (Lacroix et al., 2016), increased densities of forest ungulates such as white-tailed deer (Whitney, 1990)—a species that can limit forest regeneration (Waller, 2014)—and a loss of a sense of wildness (e.g., Thoreau, 1862).

Forest health is a term often defined by a particular set of forestry values (e.g., tree regeneration levels, stocking, tree growth rates, commercial value of specific species) and a goal of eliminating forest pests. Although appropriate in a commercial forestry context, these values should not be conflated with the ability of intact natural forests to continue to function and even thrive indefinitely and provide a diversity of habitats on their own (e.g., Zlonis and Niemi, 2014). Natural forests, regardless of their initial state, naturally develop diverse structures as they age and require from us only the time and space to self-organize (e.g., Larson et al., 2014; Miller et al., 2016).

Intact forests provide irreplaceable scientific value. In addition to a biodiverse habitat an intact forest provides an area governed by natural ecological processes that serve as important scientific controls against which to compare the effects of human activities and management practices (Boyce, 1998). Areas without resource extraction (i.e., timber harvesting, hunting), pest removal, or fire suppression allow for a full range of natural ecological processes (fire, herbivory, natural forest development) to be expressed (Boyce, 1998). Only if we have sufficient natural areas can we hope to understand the effects of human activities on the rest of our forests. Additional research and monitoring projects that compare ecological attributes between intact and managed forests at a range of spatial scales will also help determine how effective protected intact forests can be at conserving a range of biota, and where additional protected areas may need to be established (e.g., Goodwin and Shriver, 2014; Jenkins et al., 2015).

PROFORESTATION AND FOREST FIRES

Given the increase in forest area burned in the United States over the past 30 years (National Interagency Fire Center, 2019), it is important to address the relationship between forest management and forest fires. There is a widely held perception

that the severity and size of recent fires are directly related to the fuels that have accumulated in the understory due to a lack of forest management to reduce these fuels (i.e., pulping, masticating, thinning, raking, and prescribed burning; Reinhardt et al., 2008; Bradley et al., 2016). However, some evidence suggests that proforestation should actually *reduce* fire risk and there are at least three important factors to consider: first, fire is an integral part of forest dynamics in the Western U.S.; second, wildfire occurrence, size, and area burned are generally not preventable even with fuel removal treatments (Reinhardt et al., 2008); and third, the area burned is actually far less today than in the first half of the twentieth century when timber harvesting was more intensive and fires were not actively suppressed (Williams, 1989; National Interagency Fire Center, 2019). Interestingly, in the past 30 years, intact forests in the Western U.S. burned at significantly *lower* intensities than did managed forests (Thompson et al., 2007; Bradley et al., 2016; **Table 1**). Increased potential fuel in intact forests appear to be offset by drier conditions, increased windspeeds, smaller trees, and residual and more combustible fuels inherent in managed areas (Reinhardt et al., 2008; Bradley et al., 2016). Rather than fighting wildfires wherever they occur, the most effective strategy is limiting development in fire-prone areas, creating and defending zones around existing development (the wildland-urban interface), and establishing codes for fire-resistant construction (Cohen, 1999; Reinhardt et al., 2008).

PROFORESTATION AND ECOSYSTEM SERVICES: SERVING THE GREATEST GOOD

In 1905 Gifford Pinchot, Chief of the U.S. Forest Service, summarized his approach to the nation's forests when he wrote “...where conflicting interests must be reconciled, the question will always be decided from the standpoint of the greatest good of the greatest number in the long run.” This ethos continues to define the management approach of the U.S. Forest Service from its inception to the present day. Remarkably, however, even in 2018 the five major priorities of the Forest Service do not mention biodiversity, carbon storage, or climate change as major aspects of its work (United States Forest Service, 2018).

Today, the needs of the nation have changed: emerging forest science and the carbon and biodiversity benefits of proforestation demand a focus on growing intact natural public and private forests, including local parks and forest reserves (Jenkins et al., 2015). There is also a growing need across the country, and particularly within reach of highly populated areas, for additional local parks and protected forest reserves that serve and provide the public with solitude, respite, and wild experiences (e.g., Thoreau, 1862). Detailed analysis of over one thousand public comments regarding management of Hoosier National Forest, a public forest near population centers in several states, revealed a strong belief that wilderness contributes to a sense of well-being. Responses with the highest frequency reflected an interest in preservation and protection of forests and wildlife, a recognition of the benefits to human physical and mental health, a sense

of ethical responsibility, opposition to damage and destruction, monetary concerns, and a preponderance of sadness, fear and distress over forest loss (Vining and Tyler, 1999).

Quantifiable public health benefits of forests and green spaces continue to emerge, and benefits are highest in populations with chronic and difficult-to-treat conditions like anxiety, depression, pain and post-traumatic stress disorder (Karjalainen et al., 2010; Frumkin et al., 2017; Hansen et al., 2017; Oh et al., 2017). In the United Kingdom “growing forests for health” is the motto of the National Health Service Forest (2019) and there is a recognized need for evidence-based analysis of human health co-benefits alongside nature-based ecosystem services (Frumkin et al., 2017).

POLICY RECOMMENDATIONS

To date, the simplicity of the idea of proforestation has perhaps been stymied by inaccurate or non-existent terminology to describe it. Despite a number of non-binding international forest agreements (United Nations Conference on Environment Development, 1992; United Nations Forum on Forests, 2008; Forest Declaration, 2014) and responsibilities by a major UN organization [Food and Agriculture Organization (FAO)], current climate policies lack science-based definitions that distinguish forest condition—including the major differences between young and old forests across a range of ecosystem services. Lewis et al. (2019) further note that broad definitions and confused terminology have an unfortunate result that policymakers and their advisers mislead the public (Lewis et al., 2019). Most discussions concerning forest loss and forest protection are in terms of percentage of land area that has tree canopy cover (Food and Agriculture Organization, 2019). This lack of specificity significantly hampers efforts to evaluate and protect intact forests, to quantify their value, and to dedicate existing forests as intact forests for the future. For example, the UN Framework Convention on Climate Change and the FAO consider and group tree plantations, production forests, and mature intact forests equally under the general term “forest” (Mackey et al., 2015). In addition, “forest conservation” simply means maintaining “forest cover” and does not address age, species richness or distribution—or the degree that a forest ecosystem is intact and functioning (Mackey et al., 2015). The erroneous assumption is that all forests are equivalently beneficial for a range of ecosystem services—a conclusion that is quantitatively inaccurate in terms of biological carbon sequestration and biodiversity as well as many other ecosystem services.

Practicing proforestation should be emphasized on suitable public lands as is now done in U.S. National Parks and Monuments. Private forest land owners might be compensated to practice proforestation, for sequestering carbon and providing associated co-benefits by letting their forests continue to grow. At this time, we lack national policies that quantify and truly maximize benefits across the landscape. At a regional scale, however, some conservation visions do explicitly recognize and

promote the multiple values and services associated with forest reserves or wildlands (e.g., Foster et al., 2010) and climate offset programs can be used explicitly to support proforestation. For example, a recent project by the Nature Conservancy protected 2,185 hectares (5,400 acres) in Vermont as wildland and is expected to yield ~\$2 M over 10 years for assuring long-term biological carbon storage (Nature Conservancy, 2019). Burnt Mountain is now protected by a “forever wild” easement and part of a 4,452 hectare (11,000 acre) preserve. More public education and similar incentives are needed.

CONCLUSIONS

To meet any proposed climate goals of the Paris Climate Agreement (1.5, 2.0° C, targets for reduced emissions) it is essential to simultaneously *reduce greenhouse gas emissions from all sources* including fossil fuels, bioenergy, and land use change, and *increase CDR* by forests, wetlands and soils. Concentrations of these gases are now so high that reducing emissions alone is insufficient to meet these goals. Speculation that untested technologies such as BECCS can achieve the goal while allowing us to continue to emit more carbon has been described as a “moral hazard” (Anderson and Peters, 2016). Furthermore, BECCS is not feasible within the needed timeframe and CDR is urgent. Globally, existing forests only store approximately half of their potential due to past and present management (Erb et al., 2018), and many existing forests are capable of immediate and even more extensive growth for many decades (Lutz et al., 2018). During the timeframe while seedlings planted for afforestation and reforestation are growing (yet will never achieve the carbon density of an intact forest), proforestation is a safe, highly effective, immediate natural solution that does not rely on uncertain discounted future benefits inherent in other options.

Taken together, proforestation is a rapid and essential strategy for achieving climate and biodiversity goals and for serving the greatest good. Stakeholders and policy makers need to recognize that the way to maximize carbon storage and sequestration is to grow intact forest ecosystems where possible. Certainly, all forests have beneficial attributes, and the management focus of some forests is providing wood products that we all use. But until we acknowledge and quantify differences in forest status (Foster et al., 2010), we will be unable to develop policies (and educate landowners, donors, and the public) to support urgent forest-based benefits in the most effective, locally appropriate and cost-effective manner. A differentiation between production forests and natural forest ecosystems would garner public support for a forest industry with higher value products and a renewed focus on reducing natural resource use—and for recycling paper and wood. It could also spur long-overdue local partnerships between farms and forests—responsible regional composting keeps jobs and resources within local communities while improving soil health and increasing soil carbon (Brown and Cotton, 2011). The forest industry as a whole can benefit from proforestation-based jobs that focus on scientific data collection, public education, public health and a full range of ecosystem services.

In sum, proforestation provides the most effective solution to dual global crises—climate change and biodiversity loss. It is the only practical, rapid, economical, and effective means for atmospheric CDR among the multiple options that have been proposed because it removes more atmospheric carbon dioxide in the immediate future and continues to sequester it long-term. Proforestation will increase the diversity of many groups of organisms and provide numerous additional and important ecosystem services (Lutz et al., 2018). While multiple strategies will be needed to address global environmental crises, proforestation is a very low-cost option for increasing carbon sequestration that does not require additional land beyond what is already forested and provides new forest related jobs and opportunities along with a wide array of quantifiable ecosystem services, including human health.

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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, engulfing 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 biodiversity¹, 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 CO₂ to the atmosphere each year between 2010 and 2050. This estimate approaches the increase in emissions expected

“Converting mature forests to young forests results in a considerable loss of carbon stocks.”

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 mills⁵.

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 stocks⁶. 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 carbon¹⁰.

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 harvest⁸.

Wood harvests are increasingly used as a



Figure 1 | The felling of giant ancient cedars in the Cayuse region in western Canada.

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 CO₂, 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 calculated¹³. 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 CO₂ emissions¹⁵.

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 CO₂ 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 CO₂ 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 emissions¹⁷. 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.

William R. Moomaw is in the Fletcher School, Tufts University, Medford, Massachusetts 02155, USA. **Beverly E. Law** is in the Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331, USA.
e-mail: william.moomaw@tufts.edu

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Introduction

Modern industrial societies are built on models of efficiency and neatness. Waste and messiness are seen as bad. And so it is with the industrial model of forestry, which appears to be widely accepted by many societies as an appropriate way to manage natural resources. Wildfires (especially those that are stand replacing), hurricanes, and other major disturbances are seen not as natural events and processes that generate biodiversity, but as catastrophes that destroy forests. They create messes that need to be cleaned up. If by cleaning up dead and dying trees after a disturbance, some money can be made from the timber, so much the better. This is the fundamental justification for postdisturbance ("salvage") logging. Indeed, the word *salvage* implies saving something, in this case saving money that otherwise would be lost if burned wood is left to decay. Many people who oppose large-scale logging of natural forests voice no objection to salvage logging of these same forests after a fire. Somehow, these "damaged" forests are no longer natural, or at least no longer as pretty in the eyes of many people. This seems to be the general perception around much of the world, as the internationality of the papers in this special section makes clear.

Natural resources agencies take advantage of the public's lack of esthetic appreciation for disturbed vegetation and its limited understanding of the ecological role of natural disturbance. As conservation scientists, we know that natural disturbances at various spatial and temporal scales and intensities are fundamental to the generation and maintenance of biodiversity in ecosystems across the world (Connell 1978; Pickett & White 1985; Platt & Connell 2003). Beyond that, and less appreciated by the public and even many environmentalists, naturally disturbed, unsalvaged, early successional forests are often the most biologically diverse of all forest conditions and are both more rare and more imperiled than old-growth forest in many regions (Noss et al. 2006).

In the first paper of the special section, we review the literature on impacts of postdisturbance logging worldwide. We point out that natural disturbances enhance ecological processes and biodiversity and can re-create some of the structural complexity and landscape heterogeneity of forests that were lost through past human management. Three general impacts of salvage logging are the alteration of stand structural complexity, changes in ecosystem pro-

cesses, and changes in the composition and abundance of species. Importantly, the effects of salvage logging are generally different from the effects of logging in forests not affected by a major disturbance. In many cases, forest ecosystems are more strongly affected by postdisturbance logging than by the initial disturbance, yet the cumulative effects of combined natural and human disturbances have been poorly studied. Ecologically informed policies for postdisturbance management of forests need to be in place before major disturbances inevitably take place in order to avoid the ad hoc decision making that often leads to poorly planned and ecologically damaging salvage operations.

Foster and Orwig contrast the ecological effects of windstorms and invasive pests and pathogens in New England (U.S.A.) with the impacts of preemptive and salvage logging in that region. Their case study includes the largest salvage-logging operation in U.S. history—after the 1938 hurricane—and reviews a manipulative experiment that simulated the local effects of that hurricane. They also evaluate the controversial "protection forest" approach, in which silviculture is applied prior to major disturbance in an effort to reduce the susceptibility of forests to disturbance and stress. In keeping with the conclusion reached by Lindenmayer and Noss, they note that logging after natural disturbance often has more profound impacts on the ecosystem than the original disturbance. The natural disturbances they studied resulted in little disruption of biogeochemical processes and other ecosystem functions, whereas salvage logging exacerbated ecological change, resulting in pronounced effects on ecosystem composition, structure, and function. There was no indication that active or preemptive management can improve the resistance or resilience of forests; in fact, many forests seem to be more vulnerable to exogenous impacts after management. Foster and Orwig conclude that although there are often valid reasons to conduct salvage or preemptive logging (for instance, economic and safety concerns), from an ecological standpoint substantial benefits accrue from leaving forests alone when they are threatened or affected by natural disturbance.

The boreal forest of Canada is the largest and most intact forest on Earth, and amazingly enough it is still shaped largely by natural processes. In Canada, forest managers have embraced the "natural-disturbance model" as a

guide to managing forests. Nevertheless, Schmiegelow and coauthors find a fundamental mismatch between the general acceptance of a natural-disturbance model and what actually happens in forest management. The most egregious mismatch concerns policies that encourage postfire salvage logging. The boreal forests of Canada are at risk of vastly increased logging of this sort. With heightened demands for obtaining revenue from boreal forests, fire now competes with logging for timber. Although standards exist for structural retention (i.e., leaving live and dead trees and other plant material on site) during timber harvesting, the conventional standards are limited to those implemented at a stand level and disregard the legitimate biological need to maintain postfire forests on a landscape scale. The proportion and size of live residual trees in burned boreal forests can be quite high and can increase with fire size, although the abundance of these residual trees is typically underestimated by forest managers. Many fires are inaccurately described as "severe" or "stand replacing," when in fact they contain substantial areas that are unburned or that burned at low or moderate severity. Burned areas typically contain many bird species associated with late-successional forests. Salvaged sites, on the other hand, take decades to recover their habitat value for forest songbirds and other species.

Hutto expands on the observation that burned forests are hotspots of biodiversity. He points out that snag-retention guidelines developed for green-tree forests are not properly applied to burned forests because the birds and other species closely associated with severely burned forests require vastly higher densities of snags than do most species found in unburned forests. For example, some 60% or more of bird species that nest in severely burned conifer forests of the western United States use snags as nest sites, and large snags are disproportionately valuable. Many woodpeckers also feed from snags. The life cycle of most wood-boring beetles is 2–3 years, so the window of opportunity for birds that feed on these beetles in postfire habitats is exceptionally narrow. Meeting the needs of these specialized species essentially precludes salvage logging over vast areas of burned forest. Recent legislation in the United States and Canada generally encourages salvage logging and fails to provide adequate snag-retention standards for burned forests. Recognizing that public opinion will not shift immediately to an appreciation of the ecological values of burned forests, Hutto recommends several measures to reduce the impacts of salvage logging. Nevertheless, he concludes that he is "hard pressed to find any other example in wildlife biology where the effect of a particular land-use activity is as close to 100% negative" as typical salvage logging.

Reeves and coauthors examine the salvage logging issue from an aquatic perspective, focusing on postfire logging in riparian areas of the western United States. Riparian areas are of high ecological and biodiversity value

in these and other forests. Despite short-term impacts, aquatic and riparian organisms are generally well adapted to rapid recovery following fire, with fish populations, for instance, rebounding usually within a decade. The erosion that naturally follows wildfire contributes wood and coarse sediments to streams, which are vitally important for the long-term productivity of these systems. Logging or other human intervention appears unnecessary to sustain the biodiversity and productivity of naturally resilient aquatic networks after fire. Rather, post-fire logging in riparian areas poses a number of potential (but poorly documented) threats, including the spread of invasive species and increased vulnerability of adjacent forests to insects and disease; it also has uncertain effects on the frequency and behavior of future fires. Reeves et al. recommend that in the face of uncertainty about the consequences of salvage logging for riparian areas, the prudent course is to increase monitoring efforts and to provide riparian areas the same protections, such as adequate streamside buffers, that they receive before fire. Non-fish-bearing streams may require the same level of protection as fish-bearing streams.

In the final paper, Lindenmayer and Ough take us to the montane eucalypt forests of southeastern Australia, where wildfire and clearcut logging are the major forms of disturbance. Intensive and extensive salvage logging after wildfire has been the normal course of events in these forests since the 1930s, yet the effects of such logging have been poorly studied (i.e., a common theme among all papers in this special section, highlighting the need for a precautionary approach). Nevertheless, among the well-documented impacts of such logging is the loss of large trees with hollows, which has significant implications for a variety of cavity-using vertebrates, including endangered marsupials. Based on information on life histories, Lindenmayer and Ough predict declines of a number of other plant and animal species, for example resprouting tree ferns and seed regenerators that respond positively to fire. In this region, policies are needed that exempt some areas, especially old-growth forests and sites that experienced partial damage from fire, from salvage logging. Also needed are ecologically sensible guidelines for retention of large living and dead trees and other biological legacies after fire, a recommendation that echoes those of Schmiegelow et al. and Hutto. In those areas that will be salvaged, careful efforts should be made to reduce the level of physical disturbance to sites.

The papers in this special section provide a strong argument for increased research and monitoring on the effects of natural disturbances and postdisturbance logging on forests. A call for more research is not a call for business as usual and certainly not a call for increased levels of salvage logging. To the contrary, available evidence points to often severe and long-lasting negative effects of postdisturbance logging on a wide variety of ecosystems and their biota. To log what is often the

most biologically diverse and threatened forest condition in the landscape is fundamentally irrational. Legislation in several countries—most notably the United States, where bills before Congress would greatly expand salvage logging on public lands—should therefore be of great concern to foresters, ecologists, conservationist biologists, and any citizen who cares about the biological values of forests and the ecological services they provide. We hope this special section will help inform the debate.

Acknowledgments

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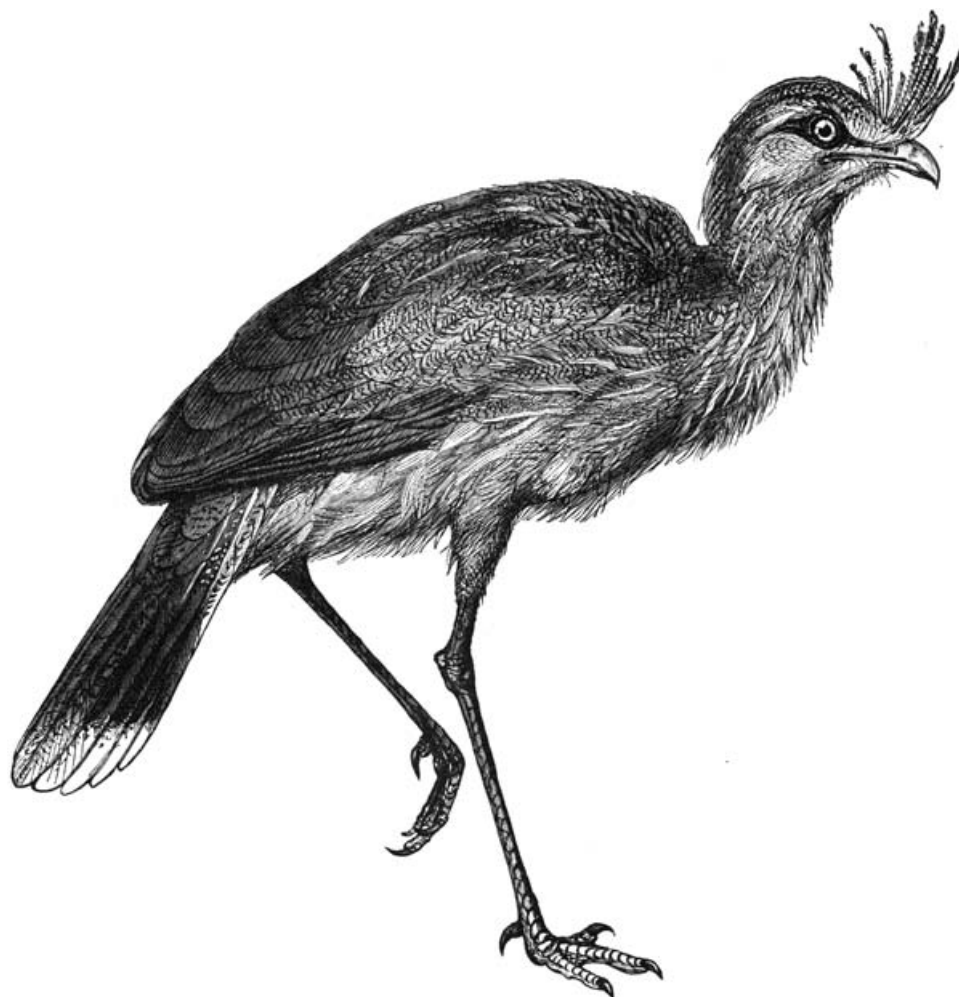
Reed F. Noss* and David B. Lindenmayer,† Guest Editors

*Department of Biology, University of Central Florida, Orlando, FL 32816-2368, U.S.A., email rnoss@mail.ucf.edu

†Centre for Resource and Environmental Studies, The Australian National University, Canberra, ACT 0200, Australia

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Effects of Fire and Commercial Thinning on Future Habitat of the Northern Spotted Owl

Dennis C. Odion^{1,*}, Chad T. Hanson², Dominick A. DellaSala³, William L. Baker⁴ and Monica L. Bond⁵

¹Earth Research Institute, University of California, Santa Barbara, California. 93106. Environmental Studies Department, Southern Oregon University, Ashland, Oregon, 97520

²Earth Island Institute, 2150 Allston Way, Suite #460, Berkeley, California, 94704

³Geos Institute, Ashland, Oregon, 97520

⁴Program in Ecology and Department of Geography, University of Wyoming, Laramie, WY, 80271

⁵Wild Nature Institute, PO Box 165, Hanover, NH 03755

Abstract: The Northern Spotted Owl (*Strix occidentalis caurina*) is an emblematic, threatened raptor associated with dense, late-successional forests in the Pacific Northwest, USA. Concerns over high-severity fire and reduced timber harvesting have led to programs to commercially thin forests, and this may occur within habitat designated as “critical” for spotted owls. However, thinning is only allowed under the U.S. Government spotted owl guidelines if the long-term benefits clearly outweigh adverse impacts. This possibility remains uncertain. Adverse impacts from commercial thinning may be caused by removal of key habitat elements and creation of forests that are more open than those likely to be occupied by spotted owls. Benefits of thinning may accrue through reduction in high-severity fire, yet whether the fire-reduction benefits accrue faster than the adverse impacts of reduced late-successional habitat from thinning remains an untested hypothesis. We found that rotations of severe fire (the time required for high-severity fire to burn an area equal to the area of interest once) in spotted owl habitat since 1996, the earliest date we could use, were 362 and 913 years for the two regions of interest: the Klamath and dry Cascades. Using empirical data, we calculated the future amount of spotted owl habitat that may be maintained with these rates of high-severity fire and ongoing forest regrowth rates with and without commercial thinning. Over 40 years, habitat loss would be far greater than with no thinning because, under a “best case” scenario, thinning reduced 3.4 and 6.0 times more dense, late-successional forest than it prevented from burning in high-severity fire in the Klamath and dry Cascades, respectively. Even if rates of fire increase substantially, the requirement that the long-term benefits of commercial thinning clearly outweigh adverse impacts is not attainable with commercial thinning in spotted owl habitat. It is also becoming increasingly recognized that exclusion of high-severity fire may not benefit spotted owls in areas where owls evolved with reoccurring fires in the landscape.

Keywords: Fire rotation, forest regrowth rate, forest thinning, future habitat, habitat loss, late-successional forest, policy implications, severe fire, spotted owl.

INTRODUCTION

Conservation of the emblematic Northern Spotted Owl (*Strix occidentalis* ssp. *caurina*) in the Pacific Northwest of North America has become a global example of balancing conflicting land management goals (DellaSala and Williams 2006). Concern over degradation of the owl’s dense, late-successional forest habitat led to the 1994 Northwest Forest Plan (NWFP). The NWFP shifted management on ~100,000 km² of federal USA forestlands from an emphasis on resource extraction to embrace ecosystem management and

biodiversity conservation goals. Under the NWFP, ~30% of federal lands traditionally managed for timber production were placed in late-successional reserves that emphasized conservation goals and limited timber harvesting (USFS/USDI 1994).

Over the last decade, managers and policy makers have become increasingly concerned about high-severity fire and reduced timber harvesting in NWFP dry forests (e.g., Spies *et al.* 2006, Power 2006, Thomas *et al.* 2006, Ager *et al.* 2007, USFWS 2011). Forest thinning has been viewed as a solution for controlling fires in dry forests throughout western North America (Agee and Skinner 2005, Stephens and Ruth 2005) and commercial criteria have been included to pursue timber harvest goals (Johnson and Franklin 2009, Franklin and Johnson 2012). Commercial thinning prescriptions currently being implemented under these

*Address correspondence to this author at the Earth Research Institute, University of California, Santa Barbara, California. 93106. Environmental Studies Department, Southern Oregon University, Ashland, Oregon, 97520; Tel/Fax: 541 821-0738; E-mail: dennis@odion.name

criteria may remove up to one-half of forest basal area, and may also include patch cutting or small clear cuts (USDI 2011). Commercial thinning is now proceeding rapidly without a full understanding of the long-term risks.

For spotted owls, thinning and associated activities often remove or reduce key habitat features in direct proportion to the intensity of the commercial prescription. Key spotted owl habitat features that may be reduced or removed directly or indirectly include high tree density and canopy cover (King 1993, Pidgeon 1995), recently killed pines (*Pinus* spp.) and abundant snags (Pidgeon 1995), multiple tree layers, with abundant medium and small white fir (*Abies concolor*) or Douglas-fir (*Pseudotsuga menziesii*) (King 1993, Pidgeon 1995, Everett *et al.* 1997, Irwin *et al.* 2012), large volume of mature-sized down logs (Pidgeon 1995), shrubs (King 1993, Pidgeon 1995, Irwin *et al.* 2012) and trees with heavy mistletoe infections (Hessburg *et al.* 2008), which are essential for spotted owl nesting (USFWS 2011). Thinning or contemporary harvest near the nest or activity center has been shown to displace Northern Spotted Owls (Forsman *et al.* 1984, King 1993, Hicks *et al.* 1999, Meiman *et al.* 2003). Telemetry studies on California Spotted Owls (*Strix occidentalis* ssp. *occidentalis*) in the Sierra Nevada found that owls avoided Defensible Fuel Profile Zones (an intensive thinning treatment) (USFS 2010). Unoccupied California Spotted Owl territories had a lower probability of re-occupancy after timber harvest, even when habitat alterations comprised <5% of a territory (Seamans and Gutiérrez 2007). In addition, Barred Owls (*S. varia*), which out-compete spotted owls (Dugger *et al.* 2011), use younger and more open forests compared to Northern Spotted Owls (Wiens 2012).

Studies also have found negative impacts of thinning to northern flying squirrels (*Glaucomys sabrinus*), the primary prey of Northern Spotted Owls in most of its range (Waters and Zabel 1995, Waters *et al.* 2000, Carey 2001, Ransome and Sullivan 2002, Gomez *et al.* 2005, Ransome *et al.* 2004, Bull *et al.* 2004, Meyer *et al.* 2007, Wilson 2008, Holloway and Smith 2011, Manning *et al.* 2012). Negative effects may persist for 15 years or longer (Wilson 2008). In addition, openings between trees from thinning may create barriers, due to predator avoidance, for flying squirrels to cross using its gliding locomotion (Manning *et al.* 2012). Thinning has also been found to have negative effects on the abundance of other main prey species for Northern Spotted Owls such as red-backed voles (*Myodes californicus*) (Suzuki and Hayes 2003) and woodrats (*Neotoma cinerea*, *N. fuscipes*) (Lehmkuhl *et al.* 2006).

Because of the many conflicts between thinning and spotted owl conservation, some authors have recommended that treatments aimed at controlling fire avoid spotted owl habitat and instead treat vegetation elsewhere that is the most flammable and strategic for accomplishing fuel treatment goals (Gaines *et al.* 2010). The 2011 Recovery Plan for the Northern Spotted Owl, the blueprint for management of this species on federal lands in the region (USFWS 2011), contains the proviso that long-term benefits to spotted owls of forest thinning treatments must clearly outweigh adverse impacts (USFWS 2011). The U.S. Fish and Wildlife agency that developed the plan suggested that benefits over time might accrue from a net increase in habitat because fire

disturbances would be reduced (USFWS 2011). But whether the benefits would outweigh the impacts remains uncertain due to limitations of previous assessments.

Previous assessments of the efficacy of thinning treatments in reducing fire disturbances in spotted owl habitat (Wilson and Baker 1998, Lee and Irwin 2005, Roloff *et al.* 2005, 2012, Calkin *et al.* 2005, Hummel and Calkin 2005, Ager *et al.* 2007, Lehmkuhl *et al.* 2007) have not incorporated the probability of high-severity fires occurring during the treatment lifespan. The effect of this is to overestimate treatment efficacy in potentially controlling fire or fire behavior (Rhodes and Baker 2008). Nor have the effects of recruitment of dense, late-successional forest that act to offset loss from fire been included in prior assessments. In addition, impacts of the kind of commercial thinning treatments being implemented to address dry forest concerns have not been fully considered for the owl or its prey (e.g., Ager *et al.* 2007, Lehmkuhl *et al.* 2007, Roloff *et al.* 2012). Current commercial thinning prescriptions being implemented in dry forests specifically identify desired future conditions to be maintained (e.g. Johnson and Franklin 2009) that have basal area and other structural targets mostly well below the minimum levels that have been found in spotted owl nesting, roosting and foraging habitat (NRF) in dry forests. For example, basal area targets in a project in southwest Oregon designed to demonstrate the thinning prescriptions in dry forest spotted owl habitat were 13.75-27.5 m²/ha (USDI 2011), while stands < 23 m²/ha very rarely support spotted owl nesting territories (Buchanan and Irwin 1995). In addition, the Recovery Plan (USFWS 2011) permits thinning in core areas, but emphasizes treating areas outside of core areas, so there is a need for assessment of impacts outside core areas as well. Areas outside cores may be essential for foraging and be part of the breeding season home range. Furthermore, owls often move outside core areas (USFWS 2011). Lastly, available habitat outside existing cores may become important to owl recovery, particularly if spotted owls are displaced from higher quality habitat by Barred Owls (Dugger *et al.* 2011).

To assess whether benefits of commercial thinning outweigh adverse impacts to spotted owls in dry forests (USFWS 2011), quantitative assessments are needed that allow for direct assessment of the amounts of any dense, mature or late-successional habitat that would be reduced by both commercial prescriptions and severe fire. Accordingly, we calculated these amounts by projecting them over 40 years and incorporated into our calculations the effects of forest regrowth. For our calculations, we used empirical data on fire and forest regrowth from the potential habitat within the two dry forest regions where spotted owls occur, the Klamath and dry Cascades of California, Oregon, and Washington, that are subject to thinning. We analyzed each region separately using region-wide data. Conservation planning for spotted owls commonly occurs at the scale of these regions. For our thinning treatment, we chose a "best" scenario for minimizing the amount of dense, late-successional forest to be treated (Lehmkuhl *et al.* 2007); while we used an optimistic scenario for treatment efficacy, assuming that a 50% reduction in high-severity fire would occur (Ager *et al.* 2007). We also illustrate the effects of varying treatment amount and efficacy. To calculate

rotations of severe fire in the forests of the study area, we used available fire data from a time period, 1996-2011, which includes exceptionally large, rare fire events. Our approach may be useful to managers interested in maintaining habitat for other species that rely on dense forests in fire-prone regions (Odion and Hanson 2013).

METHODS

Study Area

We analyzed fire and forest recruitment trends in 19,000 km² of dry forests in the Klamath and 18,400 km² in the Cascades provinces. As in Hanson *et al.* (2009), we analyzed only late-successional, or “older” forests present in 1995, as mapped by Moeur *et al.* (2005). This is a small fraction of the dry forest regions. Our analysis was further restricted to federal lands. Mapping by Moeur *et al.* (2005) corresponds to mid-montane forest zones where Northern Spotted Owls occur. These montane forest zones include forests dominated mainly by true firs (*A. grandis*, *A. concolor*), Douglas-fir (*Pseudotsuga menziesii*), and Ponderosa pine (*P. ponderosa*). Other conifers found in the central and northern Cascades in dry forests frequented by spotted owls are western hemlock (*Tsuga heterophylla*), western larch (*Larix occidentalis*), and limited amounts of western red cedar (*Thuja plicata*) and Engelmann spruce (*Picea engelmannii*). Forests in the Klamath are noted for high conifer diversity, with species such as incense cedar (*Calocedrus decurrens*) commonly found in the range of spotted owls. A variety of broad-leaved evergreen trees, such as madrone (*Arbutus menziesii*) and tanoak (*Lithocarpus densiflorus*) are also characteristic of these forests (Whittaker 1960).

Quantifying Future Habitat

We determined existing rates of dry-forest redevelopment following stand initiation in the forests of the study regions as delineated by Moeur *et al.* (2005) using the extensive U.S. Forest Service Forest Inventory and Analysis (FIA) forest monitoring data (<http://www.fia.fs.fed.us/tools-data/>). FIA is a monitoring system based on one permanent, random plot per ~2400 ha across forested lands. We excluded plots from forests not used by spotted owls (e.g. lodgepole pine, oak forest) and from non-conifer vegetation and non-federal lands. Most of these plots were already excluded by the mapping by Moeur *et al.* (2005) that delineated the study area.

An FIA plot consists of a 1-ha area. For tree measurements, this area is sub-sampled with four circular subplots that are 0.1 ha for large-tree sampling and 0.017 ha for smaller-tree sampling (defined by region). The diameter-at breast-height (dbh) and crown position of each tree and the ring count from two cores from dominant/codominant trees are measured in each subplot (USFS 2010). Stand age for an FIA plot is determined from the average of all ring counts from sub-plot samples, weighted by cover of sampled trees, and 8 years are added for estimated time to grow to breast height (1.4 m). We used live-tree dbh data to prepare regressions with stand age.

FIA data were available from 2001-2009, comprising 90% of the plots available within our study area. A total of 581 plots from the Klamath and 441 from the dry Cascades were considered, representing 13,944 and 10,680 km² in each region, respectively. The number would be higher, but we eliminated 139 plots in the Klamath and 141 in the Cascades that had different stand-initiation dates from different subplots of the main FIA plot. This situation occurs throughout the study area due to the patchy nature of mixed-severity fire. Including all the subplots as individual plots creates a larger sample size, but we chose not to do this because some individual locations would be overrepresented. Most importantly, both approaches lead to the same results.

We analyzed fire severity from 1996-2011 in late-successional, or “older” forests mapped by Moeur *et al.* (2005). For 1996-2008, we used the Monitoring Trends in Burn Severity (MTBS) (<http://www.mtbs.gov/>) data. We used the ordinal classification from MTBS, as MTBS analysts determine for each fire where significant thresholds exist in digital prefire and postfire images, supplemented with plot data and analyst experience with fire effects. In plot data, a composite burn index that sums mortality by vegetation stratum is used to identify high fire severity (see <http://www.mtbs.gov/>). For 2009-2011, we obtained U.S. Forest Service digital data (<http://www.fs.fed.us/postfire-vegcondition>) and classified these data following Miller and Thode (2007). We could not use pre-1996 MTBS fire severity data because the pre-burn map of spotted owl forest habitat is from 1995 (Moeur *et al.* 2005). From severity data we calculated high-severity fire rotation (FR^{hs}), the expected time to severely burn an area equivalent to the area of interest once, or the landscape mean interval for severe fire (Baker 2009).

We calculated annual high-severity fire and forest regrowth rates to future proportions for early-, mid- and mature or late-successional forests, denoted herein by “E,” “M,” and “L,” respectively, using annual time steps. We defined late-successional forests by selecting a value, 27.5 m²/ha. This amount corresponds with the maximum basal area that would be left according to currently implemented thinning prescriptions (USDI 2011). This is somewhat higher than the minimum basal area where spotted owls have been found to nest in dry forests. For example, the mean value minus one standard deviation in all the dry forest stands studied by Buchanan *et al.* (1995) was 23 m²/ha. However, we did not want to identify the rate of regrowth to the very minimum basal area that constitutes habitat, but regrowth to a basal area more likely to function as habitat. Mid- and early-successional forests were defined as 13.5-27.5 and <13.5 m²/ha tree basal area, respectively. We separated mid-successional from early-successional forest because, mid-successional forests may be included in thinning treatments, but early-successional forests may not. Thinned forest (“T”) was our fourth vegetation state. The forest states are diagrammed in Fig. (1). The proportion of each state in the landscape at time *t*, defined a vector (p_t^E , p_t^M , p_t^T , p_t^L). Transition probabilities ϕ_t^{rs} equaled the probability that any portion of state *r* at time *t* transitions to

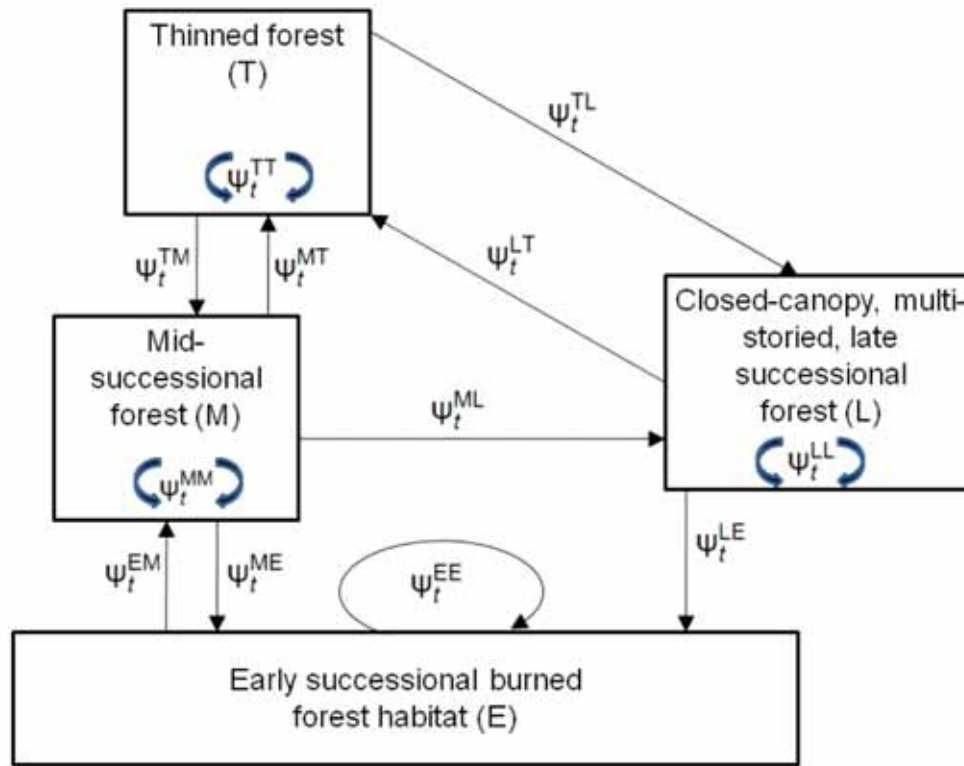


Fig. (1). State (boxes) and transition (arrows) model for dry Pacific Northwest Forest vegetation with fire disturbances and thinning. Variables are the transition rates between states indicated by the associated arrow.

state s at time $t + 1$, allowing calculation of future amounts of each forest type using the following equation:

$$\begin{bmatrix} \phi_t^{EE} & \phi_t^{ME} & \phi_t^{TE} & \phi_t^{LE} \\ \phi_t^{EM} & \phi_t^{MM} & \phi_t^{TM} & \phi_t^{LM} \\ \phi_t^{ET} & \phi_t^{MT} & \phi_t^{TT} & \phi_t^{LT} \\ \phi_t^{EL} & \phi_t^{ML} & \phi_t^{TL} & \phi_t^{LL} \end{bmatrix} \begin{bmatrix} P_t^E \\ P_t^M \\ P_t^T \\ P_t^L \end{bmatrix} = \begin{bmatrix} P_{t+1}^E \\ P_{t+1}^M \\ P_{t+1}^T \\ P_{t+1}^L \end{bmatrix} \quad (1)$$

The initial proportions, $P_{t=0}^{E-L}$ of the three natural-forest states were from the FIA basal-area analyses, with thinned forests considered zero for simplicity and because of lack of data. The annual transition from mid- and late- to early-successional forest from high-severity fire (ϕ_t^{LE} , ϕ_t^{ME}) was $1/\text{FR}^{\text{hs}}$. Early-successional forests also burned at this rate (ϕ_t^{EE}). Annual rates of forest redevelopment were from the inverse of the growth period ($1/G^{\text{EM}}$) to reach $13.5 \text{ m}^2/\text{ha}$ live-tree basal area, or to grow from 13.5 to $27.5 \text{ m}^2/\text{ha}$ live-tree basal area ($1/G^{\text{ML}}$), calculated from the regression of live basal area on age (see results). Lower-severity fire can reduce basal area from $>27.5 \text{ m}^2/\text{ha}$ basal area to $<27.5 \text{ m}^2/\text{ha}$. However, this transition is already considered in the regrowth rate, which also incorporates the effects of lower-severity fires that have occurred on rates of forest redevelopment. Because natural disturbances that may temporarily lower basal area are captured in the transitions from early- to late-successional forest, the transition from late to mid-successional forest was set to zero. Transition rates to thinned forest were based on treatment within 20

years, beginning in year $t + 1$, of the mid- and late-successional forests present at $t = 0$ (see Table 1 for annual rate). Based upon the empirical FIA and MTBS data described above, we used these transitions (Table 1) and Eq. 1 to project forward 40 years (see sample calculation in the Supplementary Materials). We chose this time interval because it represents one cycle of thinning and forest recovery.

Next, we calculated the effects of varying levels of thinning, and treatment efficacy (in terms of the effect on high-severity fire rotation intervals), over the study period. According to an analysis of a spotted owl landscape by Lehmkuhl *et al.* (2007), a “best” scenario for minimizing the short-term adverse impacts of thinning while reducing fire frequency and severity was one that treated only 22% of the landscape, and limited thinning in nesting, roosting, and foraging habitat to 21% of the area of this habitat. We used this prescription in our calculations to illustrate the effects under a best-case scenario. In our calculations, the amount of mid-successional forest thinning differed between the two regions because amounts of both mid- and late-successional forests were not the same. We also considered the effects of treating from 0 to 45% of forests, holding constant the proportions of treatments that were in late-successional vs. mid-successional forests.

We assumed that there would be no high-severity fire in treated forests over the treatment lifespan. We additionally assumed that thinning 22% of the landscape would lower the amount of high-severity fire in the unthinned landscape by half. This is based on the findings of Ager *et al.* (2007) who simulated the effects of wildfire ignitions following strategic

Table 1. Annual transition probabilities used in transition matrices for each scenario analyzed for dry provinces within the range of the Northern Spotted Owl. FR^{hs} is the high-severity fire rotation. G is the time required for stands to grow from early to mid- (EM) or mid- to late-successional (ML) forest (see Table 2). K = Klamath, C = Cascades. R is the amount that high severity fire is reduced by thinning (50% reduction at 22 percent of late-successional forest thinned).

Transition Probabilities	No Treat	Treat 22% Maintain	Treat 22% Recover
ϕ_t^{LE}	$1/FR^{hs}$	$(1/FR^{hs}-R)$	$(1/FR^{hs}-R)$
ϕ_t^{EM}	$1/G^{EM}$	$1/G^{EM}$	$1/G^{EM}$
ϕ_t^{ET}	0	0	0
ϕ_t^{EL}	0	0	0
ϕ_t^{ME}	$2/FR^{hs}$	$2/FR^{hs}$	$2/FR^{hs}$
ϕ_t^{ML}	$1/G^{ML}$	$1/G^{ML}$	$1/G^{ML}$
ϕ_t^{EE}	$1-1/G^{EM}$	$1-1/G^{EM}$	$1-1/G^{EM}$
ϕ_t^{MM}	$1-1/G^{ML}-(1/FR^{hs})$	$1-1/G^{ML}-(1/FR^{hs}-R)-\phi_t^{MT*}$	$1-1/G^{ML}-(1/FR^{hs}-R)-\phi_t^{MT*}$
ϕ_t^{MT*}	0	K = 0.033 C = 0.018	K = 0.033 C = 0.018
$\phi_t^{TM\dagger}$	0	0	K = 0.033 C = 0.018
ϕ_t^{TE}	0	0	0
$\phi_t^{TT\dagger}$	0	0	$1-\phi_t^{TL}-\phi_t^{TM\dagger}$
$\phi_t^{TL\dagger}$	0	0	K = 0.0114 C = 0.0105
ϕ_t^{LM}	0	0	0
ϕ_t^{LT*}	0	K = 0.0114 C = 0.0105	K = 0.0114 C = 0.0105
ϕ_t^{LL}	$1-1/FR^{hs}$	$1-1/FR^{hs}-R-\phi_t^{LT}$	$1-1/FR^{hs}-R-\phi_t^{LT}$

*Only in effect for the first 20 years.

†Does not take effect until after 20 years.

thinning treatments in a spotted owl landscape. When <22% of the landscape was affected at any given time (such as any time prior to year 20 when the full treatment would be incomplete, or after one-time treatments began to recover, or for scenarios with <22% of the landscape treated) the same ratio of area treated to reduction in high-severity fire (22% treat: 50% reduction in fire) was used to reduce the area burned at high severity (see Supplementary Material for an illustration). Thus, the amount that fire was reduced by thinning increased with each year as a function of the total area thinned (all other variables were constant). Ager *et al.* (2007) found little additional effect of treatments in reducing

wildfires as treatment level increased beyond 20%, so we did not calculate greater reductions in fire as treatment levels went from 22-45%. However, we additionally calculated future habitat amounts as a function of fire rotation to evaluate the effects of varying treatment efficacy, in which case we did calculate the reduced amount of habitat burned severely. This amount is the dependent variable in our summary figures. Treatment lifespan was assumed to be 20 years (Rhodes and Baker 2008) for “one-time thinning,” or maintained in perpetuity over the 40 years for “maintained.” A sample calculation using the model (equation 1) is presented in the Supplementary Material.

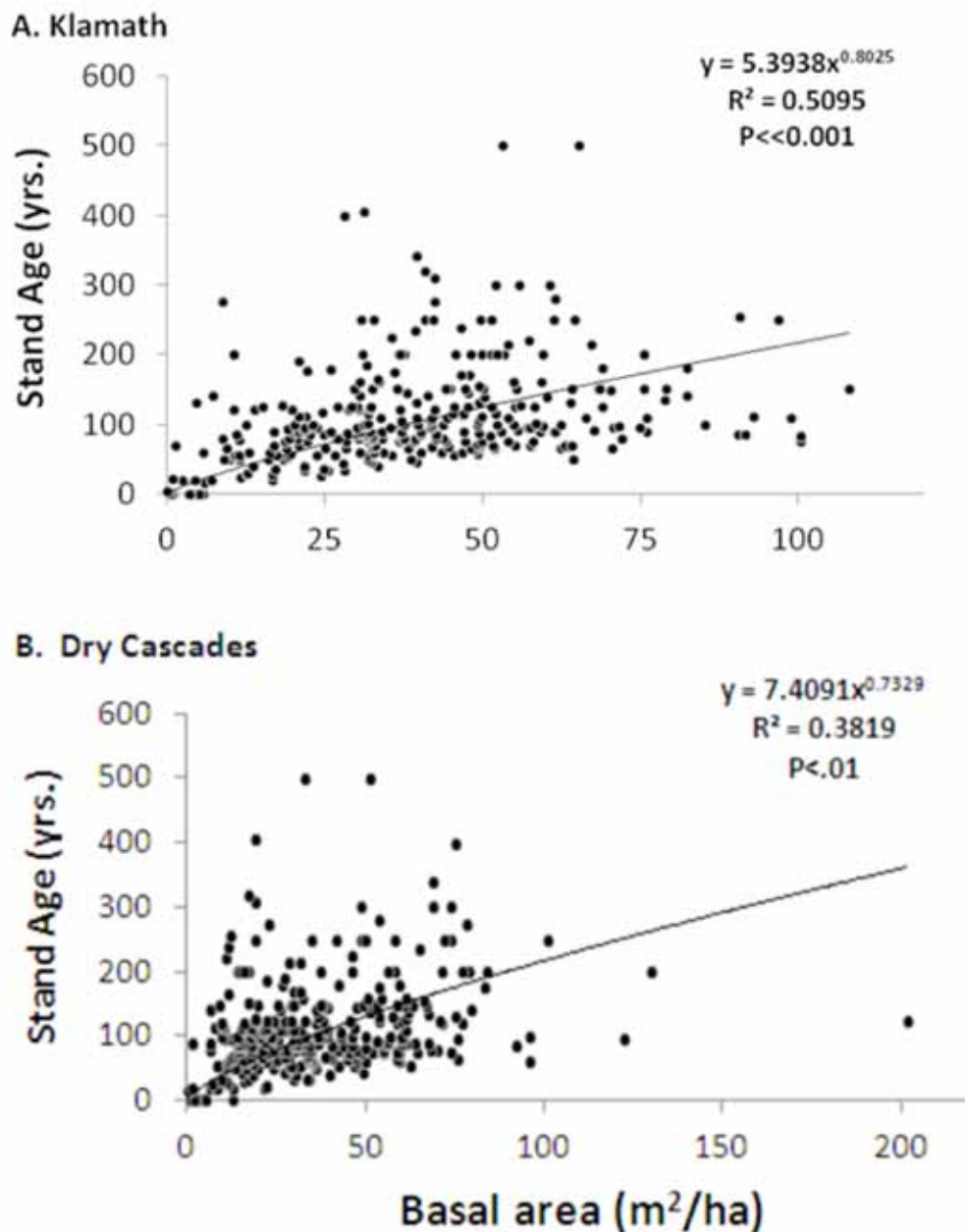


Fig. (2a-b). Scatterplots of live-tree basal area per hectare and stand age from US Forest Service FIA data for the A. Klamath region and B. dry Cascades region.

The only owl habitat we considered for impacts from thinning was suitable nesting, roosting, and foraging (so called NRF habitat). Because treatments aimed at demonstrating the type of thinning to be implemented in spotted owl habitat reduce basal area down to 13.75-27.5 m²/ha, mostly well-below the minimum amounts for NRF habitat (Pidgeon 1995, Buchanan and Irwin 1998, LeHaye and Gutiérrez 1999), and because treated forests also have reduced amounts of key habitat features like multi-canopy structure, down wood, small firs and mistletoe infections, the area affected by these treatments will largely correspond to the amount of habitat lost. Thinning may also render adjacent, unthinned forest unsuitable or less suitable (Seamans and Gutiérrez 2007), but we did not account for this effect. The lifespan for thinning treatments that we used was 20 years for one-time thinning (Rhodes and Baker

2008), and 40 years for maintained treatments. Transition from late- to early-successional vegetation due to high-severity fire also was considered habitat loss. This may overestimate the impacts of fire on Northern Spotted Owl foraging habitat (Bond *et al.* 2009, USFWS 2011), but the assumption is largely irrelevant due to the low rates of high-severity fire in both study regions in relation to forest regrowth, as described next.

RESULTS

We found a highly significant relationship between live-tree basal area and stand age in both regions (Figs. 2a-b, Klamath $n = 442$, dry Cascades $n = 304$). Much of the variance in the plot data was caused by a modest number of relatively old stands that had much lower basal area for their

Table 2. Forest Inventory and Analysis (FIA) plot parameters for the Klamath and dry Cascades provinces, California, Oregon, and Washington, based on most recent survey data from 2001-2009. Also shown are the amounts of time after fire that is takes forest to regrow to the specified live basal area (BA) thresholds using the regression equations shown in Figs. (2a-b).

^aThese plots have 2 or more stand ages associated with them due to different disturbance histories within the main FIA plot.

Entity	Klamath	Dry Cascades
Number of plots (total)	581	445
Number of plots excluded from analysis [†]	139	141
Initial (p_{t+0}^E) early-successional forest (%)	9	14.5
Initial (p_{t+0}^M) mid-successional forest (%)	14.4	26.9
Initial (p_{t+0}^L) late-successional forest (%)	76.6	55.6
Regrowth period, 0-13.5 m ² /ha live BA (yrs)	44	53
Regrowth period, 13.5-27.5 m ² /ha live BA (yrs)	32	36
Regrowth period, 0-27.5 m ² /ha live BA (yrs)	76	89
High-severity fire rotation	362	913

[†]These plots have 2 or more stand ages associated with them due to different-aged sub-plots within the main FIA plot.

age than did other plots. The amount of time following disturbance needed for regenerating forests to reach live-tree basal area >27.5 m²/ha was 77 and 90 years, respectively, for the Klamath and dry Cascades (Table 2).

Using the MTBS data, the rotation for high-severity fire from 1996-2011 was 362 to 913 years in the Klamath and dry Cascades, respectively (Table 2). At these rates, a total of 1,221 and 325 km² of high-severity fire would occur in Klamath and dry Cascades late-successional forests, respectively, in 40 years. With annual regrowth rates of late-successional forests that were 4.5 to >10 times greater than the rates of fire disturbances (i.e. (1/77)/(1/362) for the Klamath and (1/89)/(1/913) for the dry Cascades, and no disturbances other than fire, late-successional forests would eventually come to occupy 83% of the potential forested area in the Klamath and 91% in the Cascades. Thus, over 40 years, late-successional forests in the Klamath increased slightly over their current amount of 77% of the forested landscape FIA plots to 81% or from about 10,668 km² to 11,335 km² (Fig. 3a). In the dry Cascades, where late-successional forests were 59% of the forested landscape FIA plots, they increased relatively rapidly to 77% of the forested landscape, or from 6,253 km² to 8,234 km² in 40 years (Fig. 4a).

Simulated thinning of 21% of dense, late-successional forest of the Klamath landscape meant that a total of 2,225 km² would be reduced, while treatments in mid-successional forests would cover 840 km² to reach a treatment level of 22% of the whole landscape. After the one-time thinning, late-successional forests returned to slightly lower amounts than occurred without thinning after 40 years (Fig. 3a). The net effect of the one-time thinning was to reduce late-successional habitat by 10.7% over the 40-year period, or from an average of 11,086 km² to 9,996 km² over 40 years

(i.e., 1,090 km² less each year on average, Fig 3b). The amount of dense, late-successional forest that was prevented from burning at high severity was 16 km²/year, resulting in 320 km² of dense, late-successional forest, which would otherwise have been transformed into early-successional forest, in each year on average over the 40-year period. Therefore, in this scenario, thinning reduced 3.4 times more late-successional forest than it increased. The maintained treatment reduced habitat by 15.3%, from 11,086 km² on average over 40 years to 9,396 km² (i.e., 1,690 km² less each year on average, Fig. 3c). In both cases, 13% of the habitat loss was from thinning in mid-successional forest that prevented or slowed these forests from developing into dense, late-successional forest. The amount of dense, late-successional forest that was prevented from burning at high severity was 20 km²/year, resulting in 400 km² of dense, late-successional forest, which would otherwise have been transformed into early-successional forest, in each year on average over the 40-year period. Therefore, the combination of thinning and maintenance reduced 4.2 times more late-successional forest than it increased.

In the Cascades, to treat 22% of the landscape, the thinning scenario targeted 1,313 km² of dense, late-successional forest, and 1,036 km² of mid-successional forest. After the one-time thinning, late-successional forests again returned to slightly lower amounts than occurred without thinning after 40 years (Fig. 4a). The net effect of the one-time thinning treatment over 40 years was to reduce dense, late-successional forest by an average level of 11.1% (836 km² less each year on average, Fig. 4b). The amount of dense, late-successional forest that was prevented from burning at high severity from the one time treatment was 3.5 km²/year, resulting in 140 km² of dense, late-successional forest, which would otherwise have been transformed into

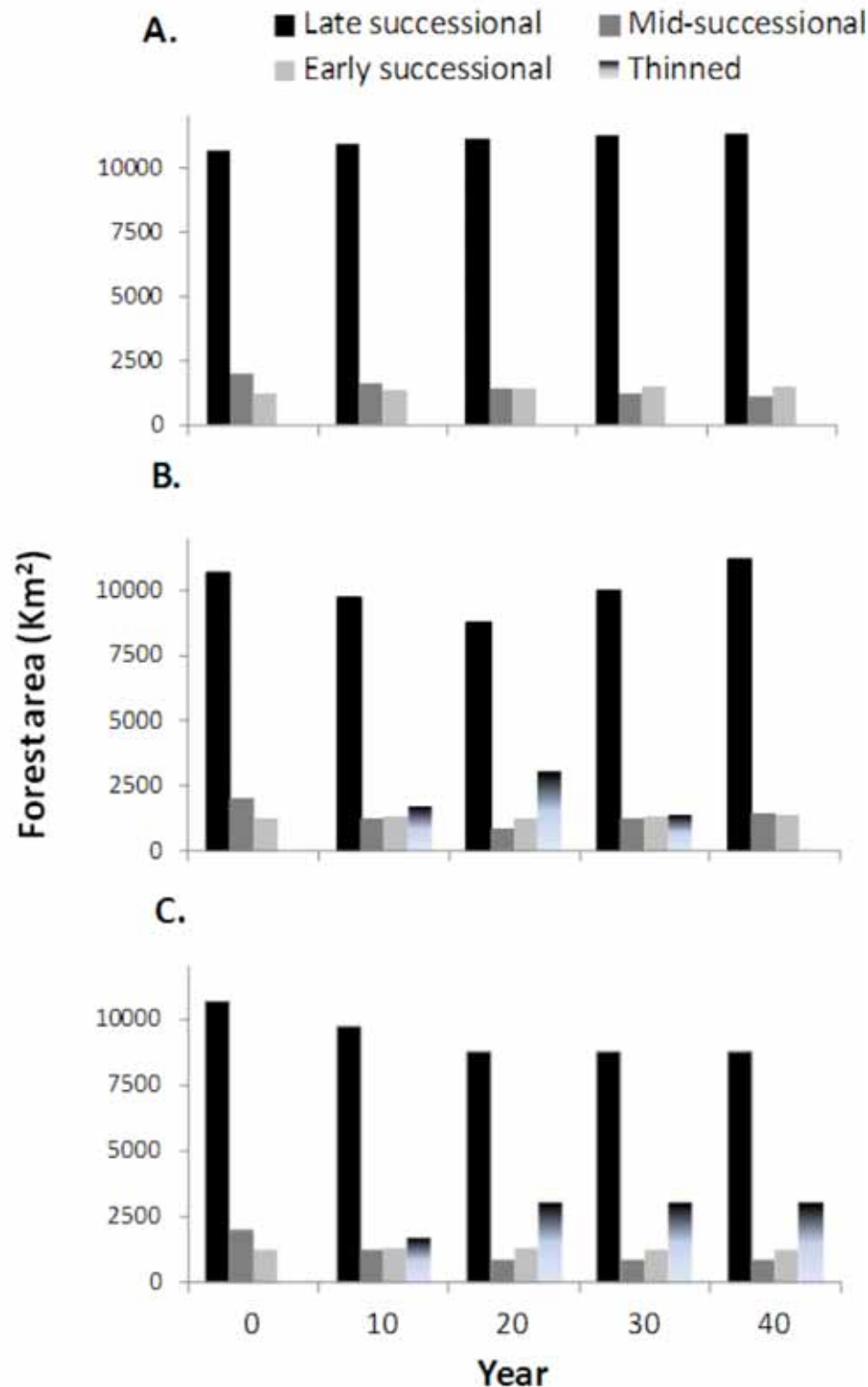


Fig. (3a-c). Amounts of the four forest types (early-, mid-, late-successional, and thinned) in the landscape over a 40-year period based on the states shown in (Fig. 1) and transition rates (Table 2) for the Klamath province, California, and Oregon, and the following scenarios: A) no treatment; B) one-time treatment of 21% of late-successional forests (>27.5 m²/ha live-tree basal area) and 42% of mid-successional forests (= total of 22% of landscape treated) followed by recovery in 20 years to late-successional forest; C) treatment of 21% of late-successional forests (>27.5 m²/ha live-tree basal area) and 42% of mid-successional (= total of 22% of landscape treated) forests with future maintenance. We converted proportions of forest types from modeling output to km² using the area estimate from FIA for the Klamath study region.

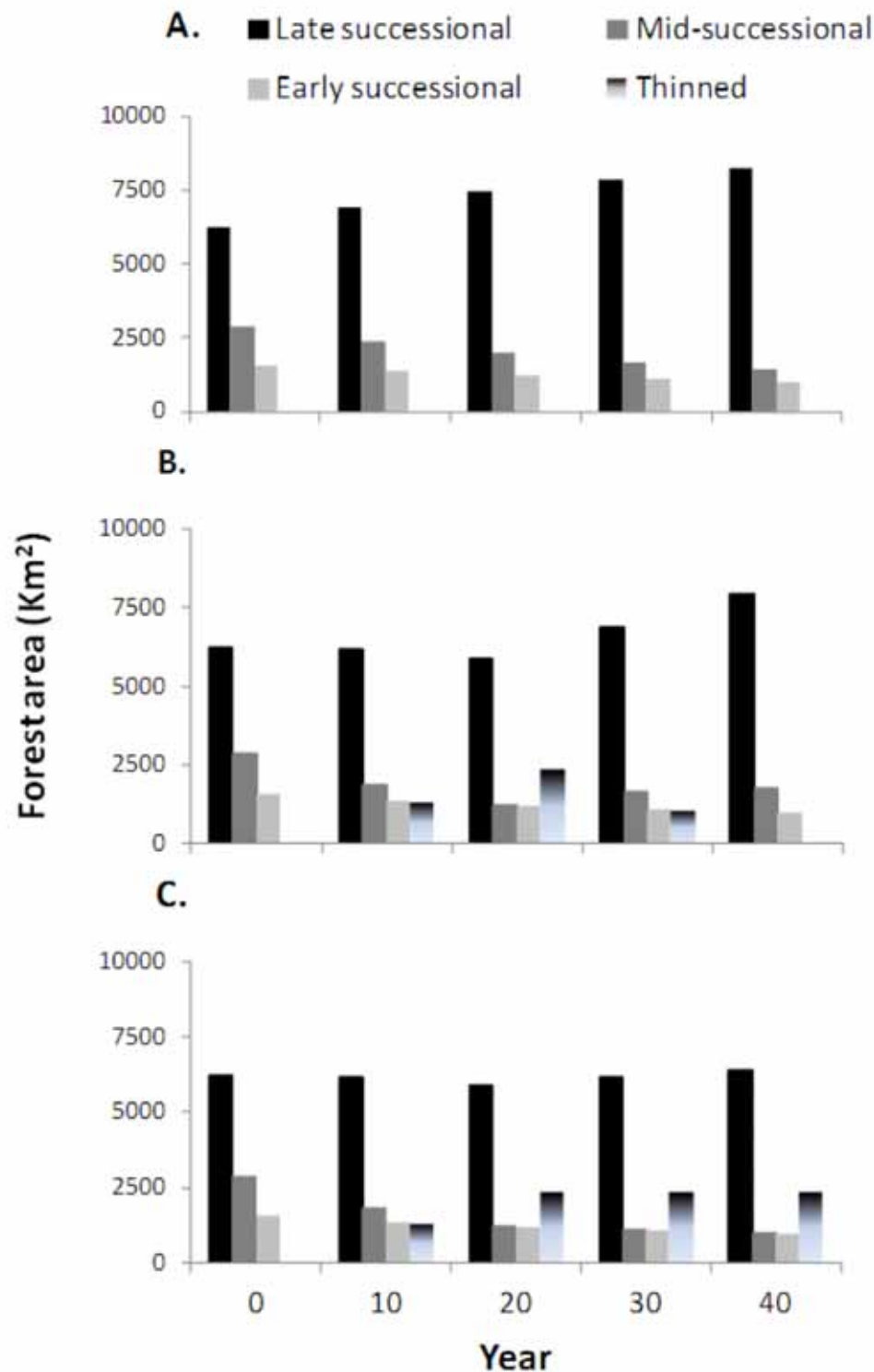


Fig. (4a-c). Amounts of the four forest types (early-, mid-, late-successional, and thinned) in the landscape over a 40-year period based on the states in (Fig. 1) and transition rates (Table 2) for the dry Cascades province, California, Oregon, and Washington and the following scenarios: **A)** no treatment; **B)** one time treatment of 21% of late-successional forests ($>27.5 \text{ m}^2/\text{ha}$ live tree basal area) and 36% of mid-successional forests ($=22\%$ of landscape treated) followed by recovery in 20 years to late-successional forest; **C)** treatment of 21% of late-successional forests ($>27.5 \text{ m}^2/\text{ha}$ live tree basal area) and 36% of mid-successional forests ($=22\%$ of landscape treated) in perpetuity. We converted proportions of forest types from modeling output to km^2 using the area estimate from FIA for the dry Cascades study region.

early-successional forest, in each year on average over the 40-year period. Therefore, thinning reduced 6.0 times more late-successional forest than it increased. The maintained treatment reduced dense, late-successional forest by an

average of 16.4% ($1,212 \text{ km}^2$ less each year on average, Fig. 4c). Of this reduction, 30% was from the indirect effect of thinning in mid-successional forests, more of which were treated in the Cascades scenario. The amount of dense, late-

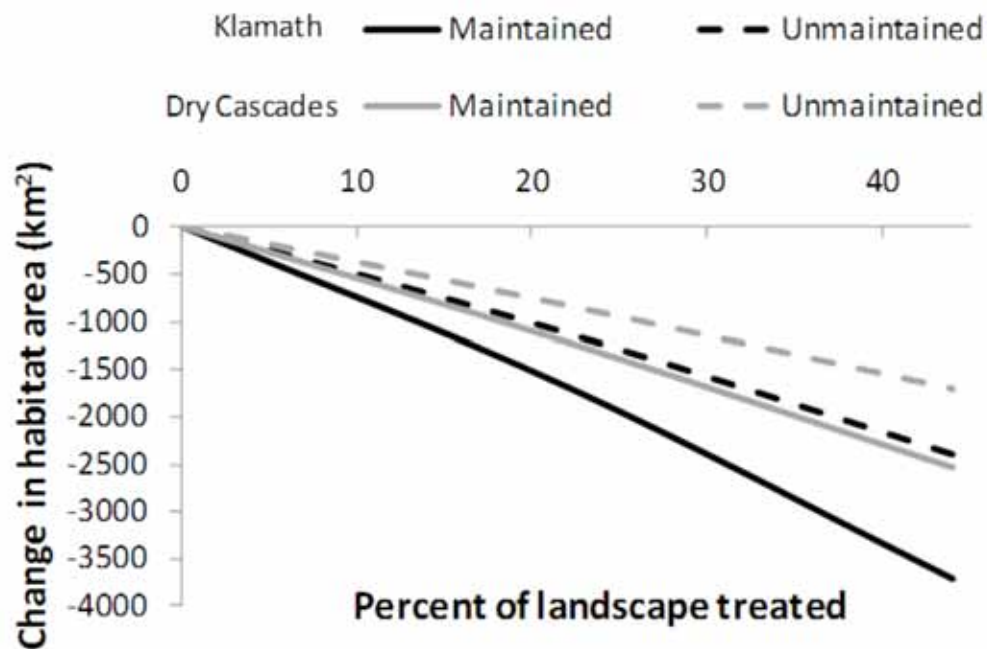


Fig. (5). Net amount of habitat lost over 40 years compared to the no-treatment scenario as a function of treatment of 0-45% of the landscape. The amount of late-successional forest treated was held constant at 21% of the area of this forest, except at very low levels of treatment. The amount of mid-successional forest treated varied from zero at very low treatment levels, to a large proportion of the mid-successional forests when 45% of the landscape was treated, particularly in the Klamath region.

successional forest that was prevented from burning at high severity from the maintained treatment scenario was 4.5 km²/year, resulting in 180 km² of dense, late-successional forest, which would otherwise have been transformed into early-successional forest, in each year on average over the 40-year period. Therefore, the combination of thinning and maintenance reduced 6.7 times more late-successional forest than it increased.

As treatment level increased from 11 to 22%, habitat loss doubled (Fig. 5). With 22% of the landscape treated, the effect of reducing fire by 50% in the rest of the landscape was reached, and there was no further reduction in fire with increasing treatment amount. With less fire prevented per km² treated, the rate of habitat loss increased as treatment went from 22 to 45% of the landscape.

We also assessed the effect of holding treatment level constant and varying the efficacy of treatments. Even if treatment efficacy was considerably greater than we assumed and rotations of high-severity fire substantially longer than twice their current length, the amount of dense, late-successional forest habitat that would be reduced due to thinning would only be slightly lower (Figs. 6a-b). With complete elimination of fire over 40 years as a result of treatments, the amount of dense, late-successional forest would be 9-10% less than with no treatment. This becomes a large amount of habitat loss over time.

DISCUSSION

We found that the habitat recruitment rate exceeded the rate of severe fire by a factor of 4.5 in the Klamath and 10 in the dry Cascades, leading to a deterministic increase in dense forest habitat over time, assuming no other disturbance

events. In contrast, previous published assessments of fire on spotted owls have not explicitly considered fire and forest regrowth rates (Wilson and Baker 1998, Lee and Irwin 2005, Roloff *et al.* 2005, 2012, Calkin *et al.* 2005, Hummel and Calkin 2005, Ager *et al.* 2007, Lehmkühl *et al.* 2007). Not including the probability of high-severity fire, which is low, leads to highly inflated projections of the effects of thinning versus not thinning on high-severity fire (Rhodes and Baker 2008, Campbell *et al.* 2012).

Our calculations of thinning effects included rates of forest regrowth along with high-severity fire. The calculations illustrate how the requirement that the long-term benefits of thinning clearly outweigh adverse impacts (USFWS 2011) is not attainable as long as treatments have adverse impacts on spotted owl habitat. This is because the amount of dense, late-successional forest that might be prevented from burning severely would be a fraction of the area that would be thinned. Under our “best case” scenario, thinning reduced dense, late-successional forest by 3.4 and 6.0 times more than it prevented such forest from experiencing high-severity fire in the Klamath and dry Cascades, respectively, similar to findings in a recent unpublished report by U.S. Forest Service scientists from the Pacific Northwest Research Station (Raphael *et al.* 2013). This would not be a concern if thinning effects were neutral, but the commercial thinning prescriptions being implemented call for forests with basal area reduced by nearly half to 13.5-27.5 m²/ha, which is mostly well below the minimum level known to function as nesting and roosting habitat (ca. 23 m²/ha) (Buchanan *et al.* 1995, 1998). Thus, if dense forests are subjected to these treatments, much of the impacted area would no longer have minimum basal area needed to function as nesting and roosting habitat. Even an immediate doubling of fire rates due to climate change or

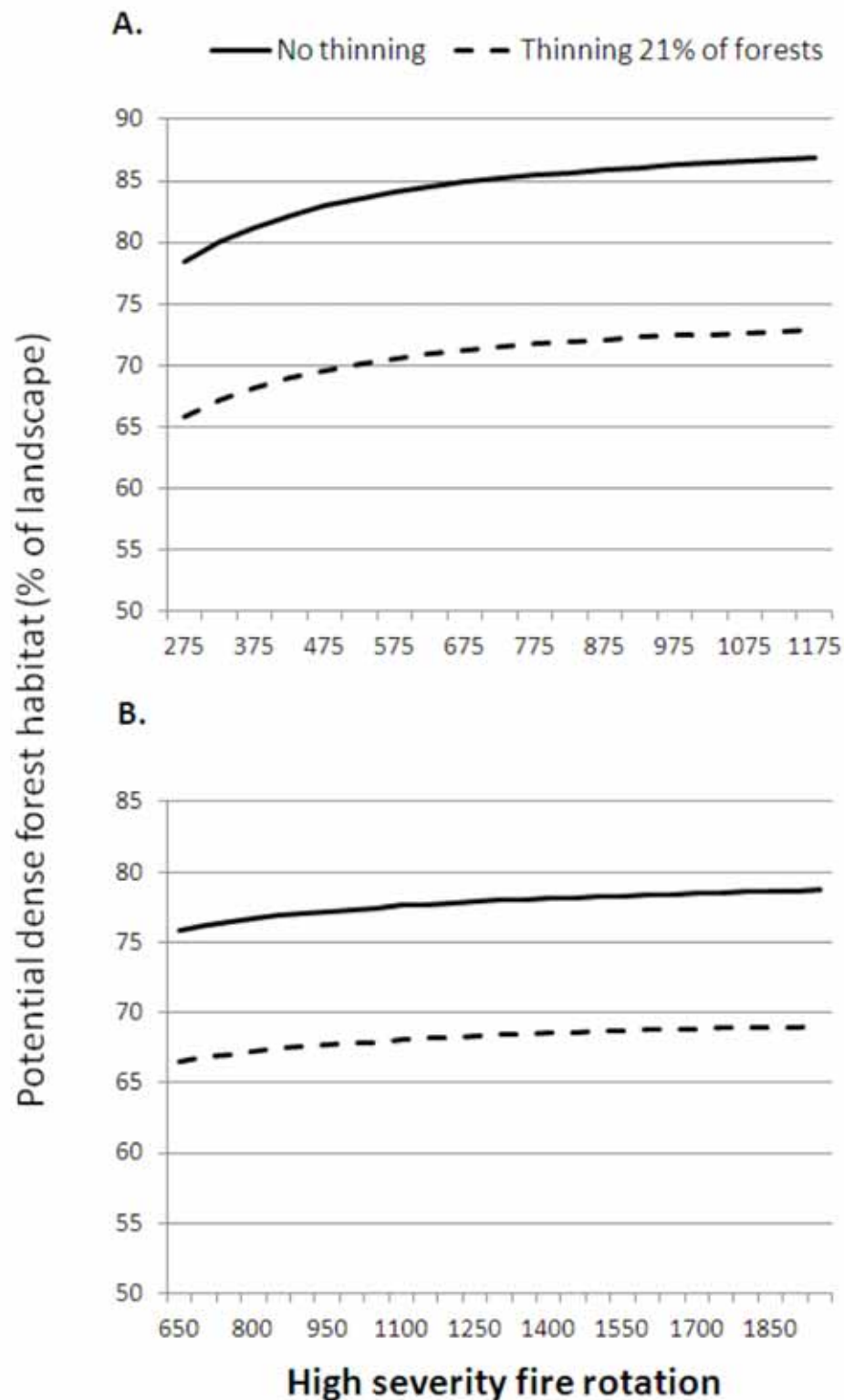


Fig. (6a-b). Amount of forest habitat in the range of the Northern Spotted Owl in the A. Klamath, and B. dry Cascades 40 years in the future as a function of the average high severity rotation over that time period, and longer rotations.

other factors would result in far less habitat affected by high-severity fire than thinning. In addition, much of the high-severity fire might occur regardless of thinning, especially if the efficacy of thinning in reducing high-severity fire is reduced as fire becomes more controlled by climate and weather (Cruz and Alexander 2010). Clearly, the strategy of

trying to maintain more dense, late-successional forest habitat by reducing fire does not work if the method for reducing fire adversely affects far more of this forest habitat than would high-severity fire, and the high-severity fire might occur anyway because it is largely controlled by climate and weather.

There may be silvicultural treatments that can be done in spotted owl habitat that may reduce adverse impacts. For example, thinning that maintains at least 23-27.5 m² ha basal area. However, given that key habitat elements such as small trees, down wood, and likely some intermediate-sized trees are going to be targeted in any forest fuel reduction treatment, it appears unlikely that any conventional fuels reduction treatment in spotted owl habitat would not have at least some adverse impacts. This is supported by research on thinning that was often less intensive than commercial thinning prescriptions. This research showed negative impacts on spotted owls or their prey, as summarized in our introduction (Waters and Zabel 1995, Waters *et al.* 2000, Carey 2001, Ransome and Sullivan 2002, Gomez *et al.* 2003, Suzuki and Hayes 2003, Ransome *et al.* 2004, Bull *et al.* 2004, Lehmkuhl *et al.* 2006, Meyer *et al.* 2007, Wilson 2010, Holloway and Smith 2011, Manning *et al.* 2012), and how spotted owls have been displaced by even very limited amounts of thinning or contemporary harvest near the nest or activity center (Forsman *et al.* 1984, King 1993, Hicks *et al.* 1999, Meiman *et al.* 2003, Seamans and Gutiérrez 2007). Even if adverse impacts were quite modest, the amount of dense, late-successional forest that might be prevented from experiencing high-severity fire is so much smaller than the area that would be treated in an effort to accomplish this reduction in fire, that the net impact of the thinning would still be much greater. In addition, it is becoming increasingly less clear whether a reduction in high-severity fire below current rates would necessarily be beneficial to spotted owls. The dry forests in which spotted owls are found were historically characterized by mixed-severity fires (see Hessburg *et al.* (2007), Baker (2012), and Odion *et al.* (2014) for historic fire in the dry Cascades of Washington and Oregon, Beaty and Taylor (2001) and Bekker and Taylor (2001, 2010) for the California Cascades, and Wills and Stuart (1994), Taylor and Skinner (1998, 2003), and Odion *et al.* (2014) for the Klamath). Recent research suggests that this historic fire may have neutral and beneficial effects to spotted owls.

Studies on the effects of fire on spotted owls are few and often focused on other owl subspecies and some studies are confounded by post-fire logging effects (Clark *et al.* 2013). Nonetheless, it has long been known that fire in woody vegetation causes an increase in small rodent populations and consequently raptor populations (Lawrence 1966), and studies on spotted owls and fire where no logging occurred suggest that high-severity fire at current rates may confer benefits or be neutral. Bond *et al.* (2009) found that California Spotted Owls in the Sierra Nevada preferentially foraged in severely burned forests more than unburned forests within about 1.5 km of a core-use area. The percentage of high-severity fire in burned Mexican Spotted Owl (*Strix occidentalis* ssp. *lucida*) sites had no significant influence (Jenness *et al.* 2004). Roberts *et al.* (2011) found no support for an occupancy model for California Spotted Owls that distinguished between burned and unburned sites in unmanaged forests; the mean "owl survey area" that burned at high-severity was 12%, with one survey area experiencing up to 52% high-severity fire, which is almost three times the current amount of severe fire in owl habitat, according to the MTBS data. In a longer-term (1997-2007) study of California Spotted Owl site-occupancy dynamics

throughout the Sierra Nevada, high-severity fire that burned on average 32% of forested vegetation around nests and core roosts had no significant effect on extinction or colonization probabilities, and overall occupancy probabilities were slightly higher in mixed-severity burned areas than in unburned forest (Lee *et al.* 2012), while other research found no significant difference in home range size between mixed-severity fire areas and unburned forest (Bond *et al.* 2013). Studies on reproduction in occupied sites of all three spotted owl subspecies indicated no difference between unburned sites and mixed-severity burned sites (excluding burn out areas created by fire suppression operations) (Jenness *et al.* 2004), or in some cases reproduction may have been greater in burned sites (Bond *et al.* 2002, Roberts 2008). The longer-term value of fire disturbances is in the creation of landscape heterogeneity with inclusions of young stands, improving habitat at the landscape scale. Fire also plays a vital role in creating snags, large down logs, and other key elements of the highest quality spotted owl habitat at the territory scale (Franklin *et al.* 2000). No assessments of fire and thinning effects on spotted owls, including this one, have accounted for any potential beneficial effects of mixed-severity fire, nor the potential negative effects of lack of mixed-severity fire in treated areas.

While much of the concern about fire and thinning in dry forests of the Pacific Northwest has focused on spotted owls, it may also apply to other biota associated with dense, old forests, including species of conservation concern, such as Pacific fisher (*Martes pennanti pacifica*), which research indicates may benefit from mixed-severity fire (Hanson 2013), the Northern Goshawk (*Accipiter gentilis*), and, following fire, the Black-backed Woodpecker (*Picoides arcticus*), which depends upon higher-severity fire in dense, older forest (Odion and Hanson 2013). Like the spotted owl, studies have documented that this woodpecker is also negatively affected by thinning (Hutto 2008). Also, like the spotted owl, the Black-backed Woodpecker, Pacific Fisher and Northern Goshawk occur in forests where the historic fire regime was not low-severity. Modeling for the fisher, similar to modeling for the spotted owl, has not used the actual rates of high-severity fire and forest regrowth to assess possible impacts of fire, and has assumed that fire represents a loss of fisher habitat (Scheller *et al.* 2011), contrary to more recent empirical findings (Hanson 2013). Not including the actual probability of fire leads to considerably inflated projections of the effects of thinning vs. not thinning in reducing high-severity fire (Rhodes and Baker 2008, Campbell *et al.* 2012). Our findings highlight the need to be cautious about conclusions that thinning treatments are needed for species found in dense forest and that they will not have unintended consequences (e.g., Stephens *et al.* 2012) until long-term, cumulative impacts are better understood. As we found with spotted owls, long-term and unintended consequences may be substantial for species that rely on dense, late-successional forests, especially when these species are sensitive to small amounts of thinning in their territory.

CONCLUSION

We used a quantitative approach that, unlike others, accounted for rates of high-severity fire and forest

recruitment, allowing assessment of future amounts of spotted owl habitat at current rates of fire, with and without thinning. We found that the long-term benefits of commercial thinning would not clearly outweigh adverse impacts, even if much more fire occurs in the future. This conclusion applies even if adverse impacts of treatments are quite modest because of the vastly larger area that would need to be treated compared to area of high-severity fire that might be reduced by thinning. Moreover, our results indicate that, even if a longer time interval is analyzed (e.g., 100 years), the declines in dense, late-successional habitat due to thinning would not flatten, as long as thinning is reoccurring. Thus, where spotted owl management goals take precedence, the best strategy for maintaining habitat will be to avoid thinning treatments that have adverse impacts in spotted owl habitat or potential habitat (Gaines *et al.* 2010). There is ample area outside of existing or potential spotted owl habitat where managers wishing to suppress fire behavior or extent may focus their efforts without directly impacting spotted owls (Gaines *et al.* 2010), such as in areas adjacent to homes or in dense conifer plantations with high fuel hazards (Odion *et al.* 2004). In addition, there are management approaches that may be more effective than thinning in helping accomplish these fire prevention goals, such as controlling human-caused fire ignitions (Cary *et al.* 2009). Lastly, emerging research suggests that fire is not the threat it has been assumed to be for spotted owls, suggesting that, rather than management that focuses on suppressing fire behavior, other, no regrets active management may be more appropriate (Hanson *et al.* 2010). Research is needed to determine if these findings might apply to other species that are characteristic of dense forests, particularly given the widespread and growing emphasis on thinning as a management tool for suppressing wildland fires.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interest.

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SUPPORTIVE/SUPPLEMENTARY MATERIAL

Supplementary material is available on the publishers Web site along with the published article.

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Principle Investigator:

Dr. Martin G. Raphael, USDA Forest Service, Pacific Northwest Research Station, 3625 93rd Ave SW, Olympia WA 98512. mraphael@fs.fed.us

Co-Principal Investigators:

Dr. Paul Hessburg, USDA Forest Service, Pacific Northwest Research Station, Wenatchee WA

Dr. Rebecca Kennedy (retired), USDA Forest Service, Pacific Northwest Research Station, Corvallis OR

Dr. John Lehmkuhl, USDA Forest Service, Pacific Northwest Research Station, Wenatchee WA (retired)

Dr. Bruce G. Marcot, USDA Forest Service, Pacific Northwest Research Station, Portland OR

Dr. Robert Scheller, Portland State University, Portland OR

Dr. Peter Singleton, USDA Forest Service, Pacific Northwest Research Station, Wenatchee WA

Dr. Thomas Spies, USDA Forest Service, Pacific Northwest Research Station, Corvallis OR

Research Assistants and Technicians:

Mr. Erik Haunreiter, Oregon State University, Corvallis OR

Mr. James Dickinson, USDA Forest Service, Pacific Northwest Research Station, Wenatchee WA

Mr. Michael Cibicki, USDA Forest Service, Pacific Northwest Research Station, Wenatchee WA

Mr. Shiloh Halsey, Portland State University, Portland, OR

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I. Abstract

National Forests in the dry forest provinces on the east-side of the Oregon and Washington Cascades have been managed under the guidelines of local Forest Plans and the Northwest Forest Plan (NWFP), both of which specify large areas of late-successional reserves (LSRs). In contrast, the recently-released USDI Fish and Wildlife Service Revised Recovery Plan (RRP) for the Northern Spotted Owl (NSO) calls for development of dynamic and shifting mosaics in the dry forests, and retention of LSRs in moist forests of eastern Cascades of Oregon and Washington, to address NSO habitat and wildfire concerns. Our objectives in this study were to develop and evaluate several key management approaches intended to reduce fire risk and conserve NSO habitat and to assess the relative merit of alternative management strategies in fire-prone stands and landscapes. We first sought to determine the current area and successional status of east-side forests across eastern Cascade forests in Oregon and Washington. Next, we simulated succession, wildfire, and fuel treatments using a state-and-transition model, *LADS*. Finally, we translated forest cover types into three levels of NSO habitat suitability (poor, moderate, and good) and applied an NSO population simulation model to investigate response of the NSO to vegetation trajectories over a 100-yr time series. To do so, we developed a spatially explicit, individual-based population model using HexSim software that integrated habitat maps with information on spotted owl population dynamics. We then compared the outcomes of several landscape management scenarios: no restoration management, restoration management under the Northwest Forest Plan reserve network, and several whole-landscape scenarios that vary the area and intensity of treatments without regard for current reserve allocations. All of our simulations assumed a wildfire regime that reflects the past 15 years of fire history, including the potential for large, rare fire events.

NSO population changes through time generally tracked changes in total NSO habitat (the combined amount of good and moderate NSO habitat) and showed similar patterns for the Wenatchee analysis area and the Deschutes NSO population scenarios without BDOW displacement. Decadal lambda (rate of population change was approximately stationary ($\lambda \sim 1$) from simulation years 0 to 30 for most scenarios excepting the large-area, high-intensity treatments, which resulted in decadal NSO population decline ($\lambda < 1$) for those years. NSO population bottlenecks (temporary periods of lower than average population levels) generally occurred in both analysis areas around year 30, after treatments had been applied but before the steep accumulation of good habitat in years 30-50. All of the NSO population modeling scenarios showed a spike in decadal lambda from years 30 to 60 in response to a steep, synchronous increase in the modeled amount of good and moderate habitat.

Higher-intensity, larger-area treatment scenarios created short-term NSO habitat and population bottlenecks, but had mixed effects on end-century NSO population sizes. Particularly for the Wenatchee analysis area, we did not find larger ending NSO population sizes from aggressive fuel reduction treatments relative to the No Treatment scenario. The presence of both good and moderate habitat contributed substantially to the suitability of an area for occupancy by a territorial NSO pair based on our analysis of habitat conditions surrounding documented NSO activity centers. Active fuel reduction activities in moderate habitat

contributed to substantial short-term (simulation years 0 to 30) population declines under the larger area, higher intensity scenarios. However, our landscape-scale analysis may have failed to detect local benefits of targeted fuel reduction treatments for habitat sustainability and recruitment in specific areas. More refined, finer-scale analysis may reveal more local benefits of fuel reduction treatments for recruiting and maintaining NSO habitat.

II. Background and Purpose

Land managers are faced with a conundrum when tasked with maintaining threatened northern spotted owl (*Strix occidentalis caurina*, NSO) populations, while reducing wildfire risk in dry, fire-prone forests of the Inland Northwest. Historical surface-fire-dominated regimes have given way to crown-fire-dominated regimes, with high rates of old forest loss, and potentially dire consequences for the multi-storied stands that are NSO habitat (Spies et al. 2006; Hessburg et al. 2005). Substantial areas of dry forest need to be treated to reduce fire risk and restore dry forest structure, but treatments can adversely impact NSO habitat quality and population viability. In addition, NSO populations appear to be declining in much of their range in part due to competitive interactions with recently established barred owls (*Strix varia*, BDOW; Gutierrez et al. 2004, Forsman et al. 2011).

At present, there remains high uncertainty and controversy over east-side (east of the Cascades crest) forest management and NSO population outcomes, especially with regard to effects of fuel treatments on NSO and reserve vs. non-reserve landscape strategies (TWS 2008, SCB and AOU 2008). To date, National Forests in the dry forest provinces on the east-side have been managed under the guidelines of local Forest Plans and the Northwest Forest Plan (NWFP), both of which specify large areas of late-successional reserves (LSRs). In contrast, the recently-released USDI Fish and Wildlife Service (USFWS) Revised Recovery Plan (RRP) for the Northern Spotted Owl (USFWS 2011) calls for development of dynamic and shifting mosaics in the dry forests, and retention of LSRs in moist forests of eastern Cascades of Oregon and Washington, to address NSO habitat and wildfire concerns. The RRP suggests that approximately a third of the total dry forest land area should be maintained in late-successional and old forest (LSOF) structural conditions of sufficient patch size and spatial distribution to provide for breeding pairs of NSOs. However, the spatial allocation and temporal dynamics of these forests has not been determined, nor is it described by the RRP. Complicating the successful implementation of Plan guidelines are the adverse effects from the BDOW (Livezey 2007), whose influence challenges the success of any NSO recovery plan based solely on vegetation or habitat characteristics.

We developed and evaluated several key management approaches intended to conserve NSO habitat, and reduce fire risk, at stand and landscape scales, throughout a large portion of the east-side NSO range (10 million ac), to assess risk of NSO habitat loss and related population processes. The goal of this project was to assess the relative merit of alternative management practices and conservation strategies to maintaining habitat and populations of the NSO in fire-prone stands and landscapes. Our study is unique in that it focuses not only on fire and fuels

management effects on NSO habitat, but also on NSO population viability and influences of the Barred Owl (BDOW) on NSO population processes.

III. Study Description and Location

Project Overview

We used a multi-model framework to simulate forest growth and disturbance dynamics, and NSO population responses, to evaluate the effect of different forest management treatment scenarios on NSO habitat and populations in the eastern Cascades. We also investigated various assumptions regarding competitive interactions with BDOWs, as well as habitat contributions from non-federal lands. We quantified landscape-scale habitat associations of NSOs and BDOWs by analyzing vegetation and topographic characteristics surrounding documented activity centers for each species (Singleton 2013). We used state-of-the-art fire spread models and existing fuels data to determine current burn probability and probable flame length in the vicinity of NSO habitats. Predicted burn probability and flame length maps were used along with topographic and other data to define fuels management treatment locations in the vicinity of NSO habitats for the purpose of their protection. We used a forest state-and-transition model (*LADS*: Wimberly 2002, Wimberly and Kennedy 2008) to simulate forest growth and disturbance processes over a 100-year period. We then used a spatially explicit individual-based population model (*HexSim*: Schumaker 2012) to simulate NSO population dynamics based on habitat maps derived from the forest growth and disturbance modeling. We compared the various forest management scenarios using the following metrics: (1) ending and minimum amounts of good and moderate NSO habitat, (2) ending and minimum NSO population sizes, (3) rate of NSO population change over 100 years (simulation-duration lambda), and (4) running 10-year rates of NSO population change (decadal lambdas) over each 100-year NSO population simulation.

Analysis Areas

We conducted our modeling in two analysis areas: the Wenatchee analysis area, and the Deschutes analysis area (Figure 1). These areas encompassed portions of the Okanogan-Wenatchee National Forest and Deschutes National Forest, respectively, within the range of the NSO, and included adjacent areas that had the potential to support NSOs. The Wenatchee analysis area was approximately 1.6 million ha characterized by rugged, mountainous topography, with elevations ranging from 210 to 2900 m (700 to 9500 ft). The Deschutes analysis area encompassed 0.4 million ha, dominated by volcanic landforms including broad pumice plains, cinder cones, and overall more gentle terrain than the Wenatchee. Elevations range from 600 to 3150 m (2000 to 10300 ft). Vegetation communities in both areas are influenced by the strong moisture gradient associated with the rain-shadow effect of the Cascade Range, with wetter areas near the crest of the range on the west and drier areas in the east.

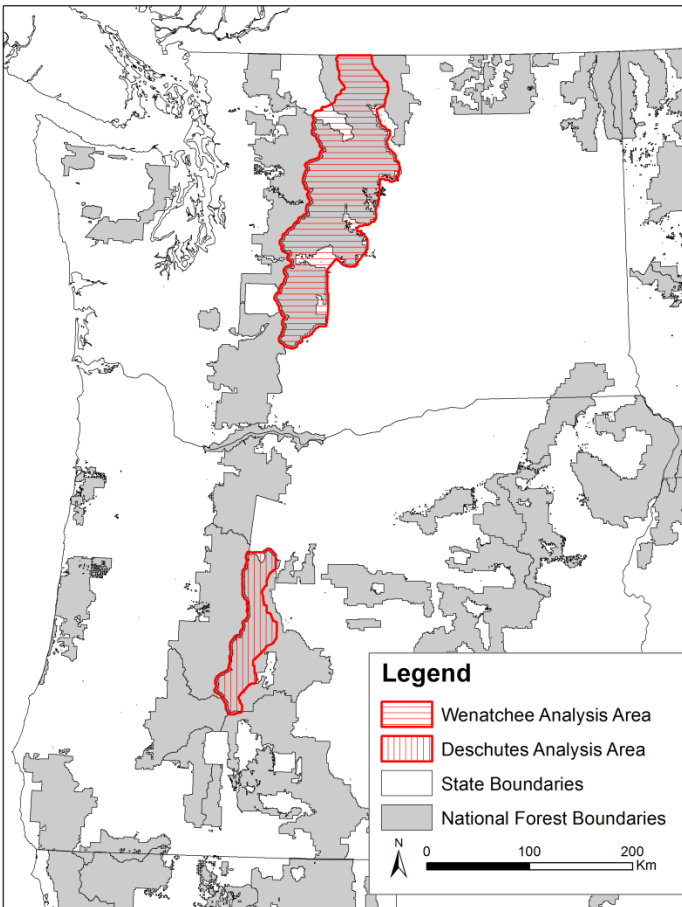


Figure 1. Analysis area locations within Washington and Oregon.

Our objectives were to develop and evaluate several key management approaches intended to reduce fire risk and conserve NSO habitat and to assess the relative merit of alternative management strategies in fire-prone stands and landscapes. We first sought to determine the current area and successional status of east-side forests across the eastern Cascade in Oregon and Washington. Next, we simulated succession, wildfire, and fuel treatments using a state-and-transition model, *LADS* (Wimberly 2002). We then compared the outcomes of several landscape management scenarios: no restoration management, restoration management under the Northwest Forest Plan reserve network, and several whole-landscape scenarios that vary the area and intensity of treatments without regard for current reserve allocations. All of our simulations assumed a wildfire regime that reflects the past 15 years of fire history, including the potential for large, rare fire events. We simulated 100 years of landscape change and structure to determine whether and when the landscape will become more or less heterogeneous.

Vegetation simulations

Our study sites occur in the eastern Cascade physiographic provinces designated by the RRP as areas potentially suitable for whole-landscape treatments. Vegetation in the study area consists of Ponderosa pine (*Pinus ponderosa*), mixed conifer, and mountain hemlock (*Tsuga mertensiana*)

forest types. Fire regimes range from low to high severity with frequencies ranging from <10 to >150 years. Vegetation is similar in type and current condition to the surrounding landscapes. Results derived from this research will be broadly applicable to surrounding forests in the range of the NSO. Resource managers on these forests have expressed a great interest in developing management approaches that will be conducive to recovering NSO populations.

Fire modeling

Wildfire risk analysis examines for a resource of interest (here, NSO habitat), the susceptibility of that resource to loss or damage by fire, and the probability of the loss. In this work, we used the underlying algorithms from *FlamMap* (Finney 2002) and *Randig* (Ager et al. 2012) to model wildfire ignitions, burn probability and flame lengths, and the Forest Vegetation Simulator (FVS) and stand table (tree list) data from the GNN database (Ohmann 2002) to simulate risk of loss to owl habitats.

On the Wenatchee and Deschutes analysis areas we used 150,000 and 50,000 (respectively) random ignitions to simulate the spread of a large number of fires across the study landscapes. The proportion of times a pixel burned in all fires and its predicted flame length at each occurrence were stored for later creation of burn probability and probable flame length maps (Ager et al. 2012). We used FVS to calculate flame length thresholds needed to make substantive changes in NSO habitat, and to determine whether those thresholds had been achieved in *FlamMap*. Results of this risk analysis were mapped and later used to assign fuels treatments in the vicinity of NSO habitats. Wildfire risk analyses for the Deschutes and Wenatchee were similar, except for local differences in weather and topography and locally established fuels data (Table 1).

The Wenatchee analysis used a fuels map created on national forests by local fuels specialists resampled to 90m to represent the 13 surface fire behavior fuel models (FBFMs, Anderson 1982). The Deschutes used *Landfire* (www.landfire.gov) fuels data, which is based on the Scott and Burgan (2005) 40 FBFMs. To predict crown fire ignition and spread potential and more realistically simulate surface fire behavior, additional raster layers defining the existing crown bulk density, canopy base height, canopy closure, and average canopy height were used to initialize the fire spread model. Elevation, slope and aspect were also used to account for topographic effects on pre-combustion heating and moisture content of fuels. Fuel moistures were assigned by particle size and time-lag class, assuming 97th percentile fire weather burn conditions (Table 1). We used Remote Automatic Weather Station (RAWS) weather data combined with local fire manager experience to establish wind parameter files for the wildfire simulations. The wind parameter file specifies the prevailing wind directions, speed, and duration, which are probabilistically drawn (Table 1) and assigned to each simulated ignition. To ensure that the simulations were capturing realistic fire sizes, we compared simulated fire sizes with recorded fire size data using methods of Ager et al. (2012).

Table 1: Summary of environmental variables used in fire simulation modeling for the Wenatchee and Deschutes study areas.

Wenatchee	Wind			Fuel Moisture (%)		
	Direction (°)	Speed (k h ⁻¹)	Probability	Size Class	-	All fuel models
	290	32.18	0.70	1-h	-	3
	290	32.18	0.25	10-h	-	4
	290	32.18	0.05	100-h	-	7
				Live Herbaceous	-	50
				Live Woody	-	80
Deschutes	Wind			Fuel Moisture (%)		
	Direction (°)	Speed (k h ⁻¹)	Probability	Size Class	Fuel Model GR2	All other fuel models
	270	40.2	0.35	1-h	1	1
	335	40.2	0.35	10-h	2	2
	225	32.2	0.25	100-h	5	5
	90	32.2	0.05	Live Herbaceous	60	40
				Live Woody	90	60

Vegetation Modeling (LADS)

We used the *LADS* state-and-transition model for all simulations of landscape change (Wimberly 2002, Kennedy and Wimberly 2008). *LADS* treats a landscape as a grid of interacting cells; each cell is associated with a dominant cover type and a fire zone. *LADS* simulates the transition of dominant cover type to larger sizes and higher cover class through time with transition times determined through empirical analysis and/or expert inputs. Simulated fires regimes are unique to each fire zone although an individual fire event can spread among zones. After a fire event is initialized, fire severity is determined by the probability of low, medium, and high fires associated with each combination of cover type, size class, and cover class (details below). Fuel treatments are simulated as events that alter the size and cover class (cover type is immutable) and have unique fire severity and spread rates. Fuel treatments are transitory and after a predefined duration revert back to an appropriate size and cover class (Wimberly 2002).

Our simulated successional trajectories were bounded by the dominant cover at the landscape scale, i.e., dominant cover type at a given location could not change. Nevertheless, our simulations indicate broad successional changes on the landscape that varied among the dominant cover types, among scenarios, and between the two landscapes.

NSO Population Modeling (HexSim)

We developed a spatially explicit, individual-based population model using *HexSim* software (version 2.4, Schumaker 2012) that integrated habitat maps with information on spotted owl population dynamics. Breeding pairs are the fundamental unit of population function for most large raptors, including spotted owls (Anthony et al. 2006, Forsman et al. 2011). We used a female-only, single-sex model structure, where territorial females were surrogates for breeding pairs. The general model structure was based on the work of Dunk et al. (2012, also see USFWS 2011: Appendix C), but was modified for our study area and questions. We adjusted NSO vital rate parameters to reflect local demographic information (Forsman et al. 2011), and we adjusted space use parameters (i.e., core area and home range sizes) to correspond to findings from local NSO radiotelemetry studies (Eric Forsman, USFS PNW Research Station, unpublished data).

Spatially explicit habitat maps formed the basis for the NSO population simulations. Each analysis area landscape was represented as a grid of 86.6 ha (1 km diameter) hexagons. Each hexagon was assigned a habitat resource value based on the amount of good and moderate NSO habitat within the hexagon. Hexagon resource values were updated at 10-year intervals based on the *LADS* landscape modeling outputs. During each annual time step in our simulations, animals moved through the landscape, attempted to establish territories, then reproduced and survived at rates influenced by the habitat quality within their territories (Figure 2).

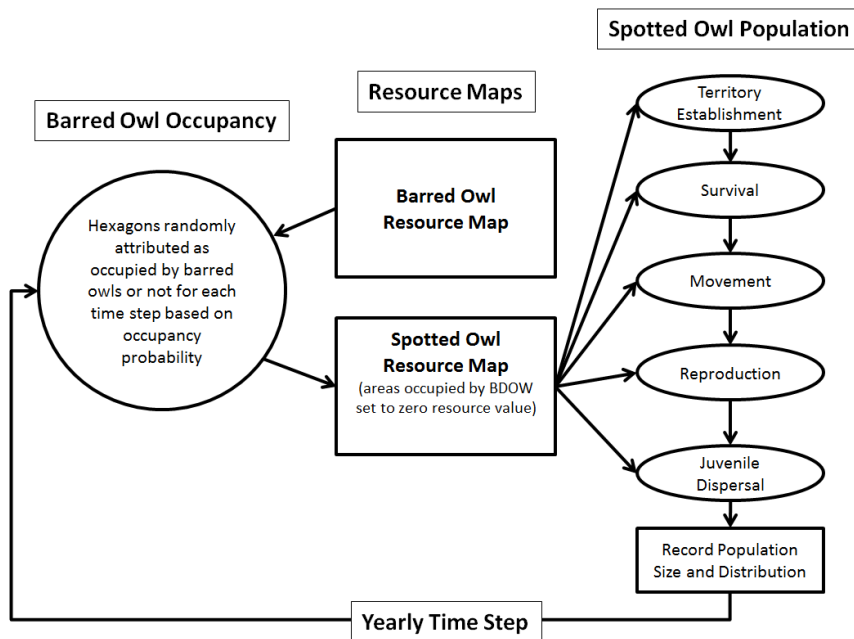


Figure 2. The NSO population model event sequence. The NSO *HexSim* population model simulated territory establishment, survival, reproduction, and movement for female spotted owls during each annual time step for our 100-year simulation period. Resource maps were updated at 10-year intervals based on habitat maps from *LADS* landscape modeling simulations.

Our habitat classification rules were based on habitat patterns observed around NSO activity centers as described by Singleton (2013). We identified areas with vegetation (i.e., tree size, canopy cover, and dominant tree species) and topographic characteristics (i.e., topographic position and slope) that corresponded to areas used by NSOs more than available, or in proportion to availability, within the analysis area landscapes (classified as good or moderate habitat respectively). Using the approach of Dunk et al. (2012), we employed maximum entropy models (*Maxent*: Phillips et al. 2006) to convert habitat characteristics within a hexagon into a single resource value for each hexagon in the *HexSim* base map (Singleton 2013). We then conducted additional spatial analyses so that habitat patterns within modeled NSO territories corresponded to observed habitat patterns around actual NSO activity centers documented in our analysis areas (Singleton 2013).

Model Experiments

We evaluated 12 landscape management scenarios and 4 NSO population scenarios. The landscape management scenarios included a No Treatment scenario, and 11 combinations of 3 strategies for spatial allocation of treatment, 3 sizes of areas treated, and 3 intensities of fuel reduction (Table 2). The 3 strategies for spatial allocation of treatment were: (1) Structured – no treatment in existing good NSO habitat, other areas were prioritized by fire risk and proximity to owl habitat (representing an integration of a critical habitat approach with an effort to create fire-breaks around existing habitat); (2) Naïve – treatment units were prioritized by existing fire risk only, with no consideration for owl habitat (representing aggressive management focused on minimizing fire risk); and (3) Reserve – areas within Late Successional Reserves identified by the Northwest Forest Plan were excluded from treatment, and treatment units outside of reserves were prioritized based on existing fire risk (representing a reserve-based approach, but not including management activities within reserves as provided for under the Northwest Forest Plan).

Table 2. Treatment scenario codes and descriptions.

Code	Strategy	Wen Treated ha	Des Treated ha	Intensity
NoTrt	No Treatment	None	None	None
N10H	Naïve	40553	16152	High
N10L	Naïve	40553	16152	Low
N20M	Naïve	80604	32242	Moderate
N40H	Naïve	161311	64616	High
N40L	Naïve	161311	64616	Low
S10H	Structured	40326	16079	High
S10L	Structured	40326	16079	Low
S20M	Structured	80806	32390	Moderate
S40H	Structured	127017	64530	High
S40L	Structured	127017	64530	Low
NWFP	Reserve	130320	59020	High

The three simulated fuel treatment intensities reduced fuel loads and retained large trees within the treated stands. High intensity treatments resulted in stands moving from a closed canopy (>60%) to an open (<40%) canopy condition and had the largest reduction in fuel, representing typical forest restoration thinning treatments. Light intensity treatments moved stands from closed (>60%) to moderate (40-60%) canopy closure and resulted in less reduction in fuel load, representing light thinning from below and removal of ladder fuels. Medium intensity treatments resulted in an intermediate impact on canopy and fuel load.

USFS lands were considered to be available for treatment if they were not in wilderness or administratively withdrawn (e.g., roadless) status, within 500 m of existing roads, and dominated by a forest type appropriate for fuel reduction treatment (e.g., subalpine fir and mountain hemlock types were not considered for treatment). The simulated treatments were only applied in areas that are currently available for treatment. The total treatable area for the Wenatchee analysis area was 402,769 ha. The total treatable area for the Deschutes analysis area was 161,150 ha. Three areas of treatment (approximately 10%, 20%, and 40% of the available area) were applied for several combinations of treatment intensity and allocation strategy (Table 2). Each treatment scenario landscape simulation was replicated 20 times in *LADS* to capture variation in outcomes resulting from stochastic disturbance events.

We evaluated four NSO population modeling scenarios to evaluate the range of potential population outcomes with and without interactions with competitive BDOWs, as well as with and without habitat contributions from non-federal lands. For the NSO population scenarios with BDOW interactions, hexagons attributed as occupied by BDOWs were set to zero resource value to simulate the effects of exclusion of NSOs from areas occupied by territorial BDOWs (Singleton 2013). We attributed hexagons as occupied by BDOWs or not based on the amount of good BDOW habitat in the area. BDOW habitat definitions and occupancy probability were based on Singleton (2013). We also conducted NSO population simulations with and without non-federal lands contributing NSO habitat resource values. The purpose of these scenarios was to evaluate the range of potential NSO population outcomes that might result from different approaches to habitat conservation on non-federal lands. We conducted 3 population scenario replicates in *HexSim* for each *LADS* landscape realization.

IV. Key Findings

Vegetation

Our results indicated that despite intense prior logging and the risk of very large fires (Irland 2013), there is considerable successional inertia on both landscapes that will eventually transition much of both landscapes to larger diameter classes and more closed canopy conditions. However, the transition from small/medium to large/very large sized trees varies widely depending upon dominant cover type, stochastic variation due to wildfires, and

landscape management. There is further uncertainty in that we assumed that logging would remain at its current very low rates (Healey et al. 2008) and that climate change (Westerling et al. 2006) would not substantially alter fire regimes from their recent (1985-2008) patterns. Nevertheless, our simulated transitions are robust and appear likely within a broad spectrum of future conditions and drivers.

At the landscape scale, fuel treatment altered forest transitions for select dominant cover types, primarily when the area treated within the treatment zone was at or close to 5% per year with high intensity (e.g., under the Northwest Forest Plan). By reducing fire severity, fuel treatments enabled individual cells to transition to larger and more fire resilient size and cover classes before the next wildfire occurred. Because of the stochastic nature of wildfire, the process itself is highly variable and the effect can appear relatively minor. Nevertheless, for some dominant cover types, fuel treatments accelerated transitioning from mid- to larger- tree size classes after 30 years.

Treatment effectiveness (Figure 3) is primarily limited by the small area treated in total. Given the relatively small area available for treatment, optimized treatment effects to reduce fire flow through the landscape could not be achieved (Finney et al. 2007). This suggests that current restrictions on the fuel treatment placement may be impeding managers ability to protect against wildfire and improve habitat. Faster transitions could be achieved and across more forest types if the treatable area was larger. Doing so would also reduce ‘treatment pressure’ on a subset of the landscape and the landscape would more broadly respond to the treatment ‘shadow’ effect (Finney et al. 2007, Schmidt et al. 2008).

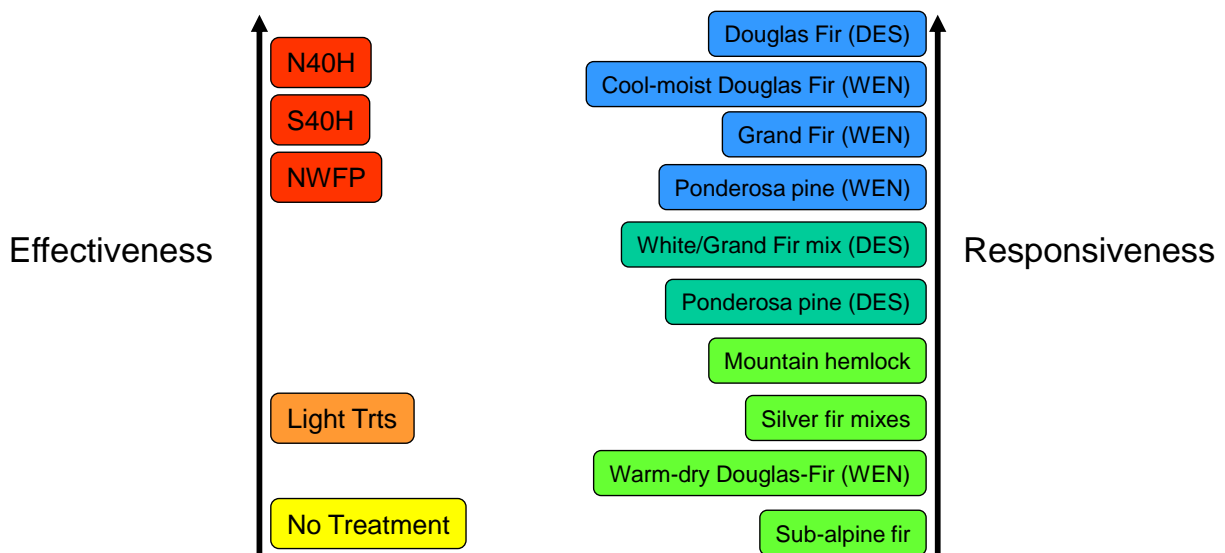


Figure 2. Relative treatment effectiveness and dominant cover type responsiveness for two study landscapes: Deschutes (DES) and Wenatchee (WEN). If location is not listed, the dominant cover type behaved similarly across both landscapes.

Treatment trajectories appeared to be a function of both the constant goal for level and intensity of treatment and the initial vegetation class distribution. We observed a bottleneck in

area treated (i.e., the treatment area dropped to zero) between year 15 and 30 in all scenario runs (especially the N40H runs). This pattern appeared to be a function of the initial distribution of vegetation conditions. Initially, the conditions were more synchronized and concentrated in small and medium closed conditions. Fuel treatments over the first 10 years reduced the amount of closed forest so that by year 20 most of the area was in an open condition, which was not eligible for treatment. Over time, this area of medium-open and large-open forest got larger and denser, so that by year 30 there was a fair amount of medium and closed forest which was eligible for treatment. In subsequent years, there was a large area of very large closed forest that never got fully treated and wildfires created a constant supply of younger and smaller forest vegetation classes that grew into pole and small and medium-closed classes that were eligible for treatment.

Our treatment scenarios were not designed to spatially optimize fuel conditions to significantly interrupt fire flow on the Wenatchee landscape; approximately three-quarters of the landscape was exempt from treatment due to existing land allocations or ownerships. Our most aggressive fuel treatment scenario treated 40% of 25% available area, net 10% of the Wenatchee analysis area was treated. Thus, our treatment scenarios did not produce substantial changes in fire patterns relative to the No Treatment scenario. This result is consistent with the experimental work of Finney *et al.* (2007).

In conclusion, to varying degrees under all management scenarios we analyzed, the two landscapes examined will be subjected to two countervailing trends: landscape successional inertia that will transition the forests to larger, closed-canopy conditions and landscape disturbance that will reset succession. Given the known processes and rates that we emphasized (as compared to less well-known processes including climate change and its cascading effects), the net balance will be an increase in late successional forest as compared to contemporary conditions. Fuel treatments can directly accelerate these transitions through active management and indirectly accelerate these transitions by protecting against the highest severity fires, although their effectiveness is currently limited by the relatively scant area available for treatment.

Spotted Owl Habitat and Populations

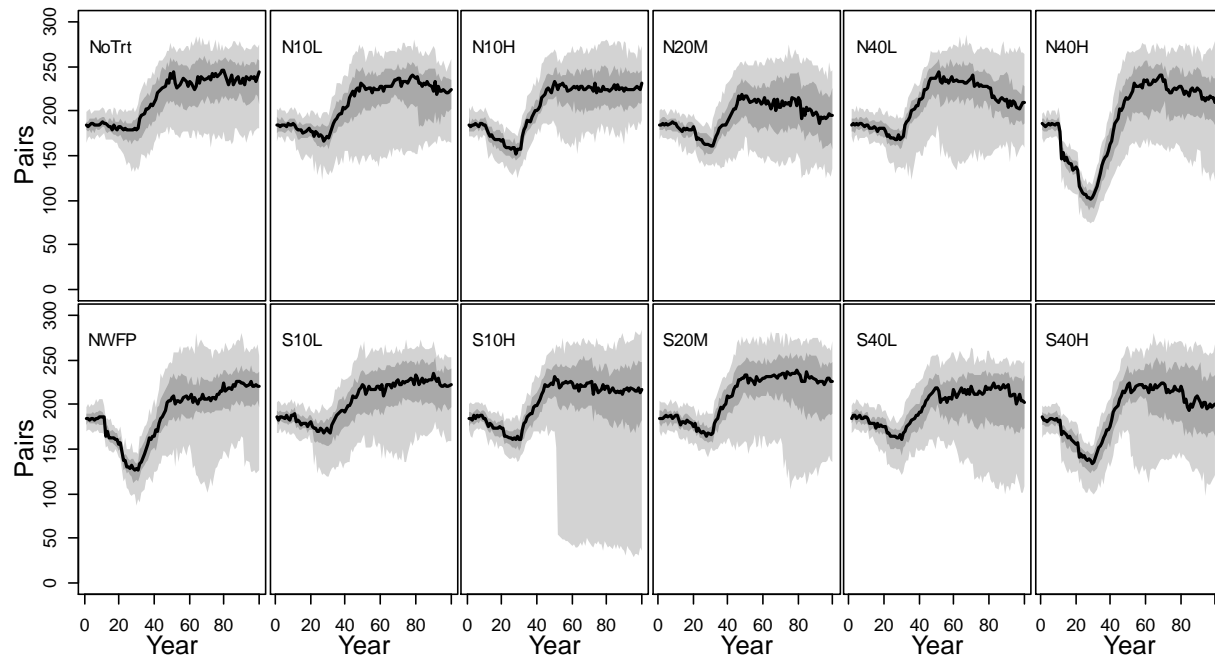
The amount of good NSO habitat increased over the 100-year simulation period for both analysis areas, but it increased much more in the Wenatchee analysis area than it did in the Deschutes. For the Wenatchee analysis area, the No Treatment scenario ended with average 275,318 ha of good NSO habitat (233% of the starting amount, averaged over 20 LADS model replicates). For the Deschutes analysis area, the No Treatment scenario ended with average 34,948 ha of good habitat (117% of starting), also averaged over 20 LADS model replicates.

Active treatment scenarios ended with more good quality NSO habitat than did the No Treatment scenario in the Deschutes analysis area, but not in the Wenatchee. The ending amount of good habitat under the treatment scenarios in the Wenatchee analysis area ranged from 235,064 ha (treatment scenario N20M: 200% of starting) to 265,779 ha (N10H: 226% of

starting). The ending amount of good habitat under the treatment scenarios in the Deschutes analysis area ranged from 35,509 ha (S40H: 119% of starting) to 41,078 ha (S10L: 138% of starting). The amount of moderate habitat increased over the simulation period on the Deschutes and decreased on the Wenatchee.

Owl populations did not increase at a rate corresponding to the increase in the amount of good habitat in the Wenatchee analysis area because of commensurate declines in the amount of moderate habitat impacted by fuels treatments (figure 3). Simulation-duration lambda (an index depicting rate of population change; $\lambda = 1$ indicates a stationary population; $\lambda < 1$ indicates declining and $\lambda > 1$ indicates increasing) was approximately 1.2 for the No Treatment scenario (without BDOW interactions) in the Wenatchee analysis area – that is, the 133% increase in the amount of good NSO habitat resulted in about 20% increase in the NSO population. In the Deschutes analysis area, NSO population growth corresponded more closely to the increase in the amount of good NSO habitat (figure 4). Simulation-duration lambda was 1.1 for the No Treatment scenario (without BDOW interactions) in the Deschutes analysis area – that is, the 17% increase in the amount of good NSO habitat resulted in a 10% increase in the NSO population.

No Barred Owls, with Private Lands, Wenatchee Analysis Area



With Barred Owls, with Private Lands, Wenatchee Analysis Area

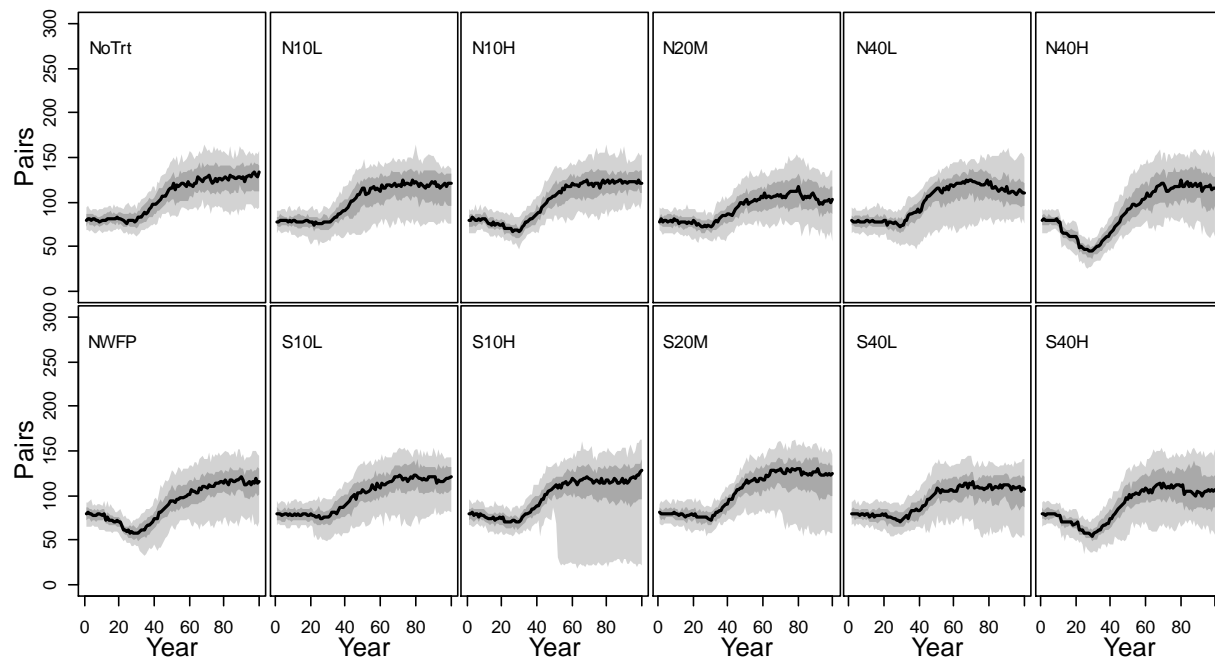
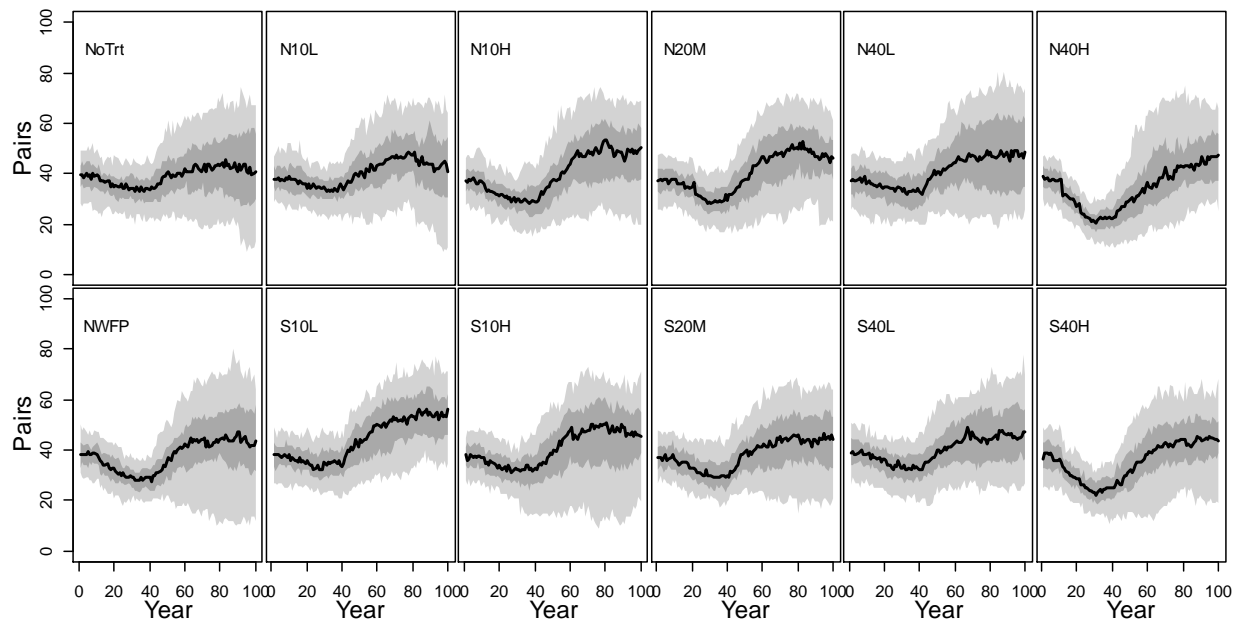


Figure 3. Simulated northern spotted owl population trajectories in the Wenatchee analysis area. Lines depict median (black line), 50% quantile range (dark grey shade), and 90% quantile range (light grey shade) of the estimated number of owls through the simulation for 60 *HexSim* replicates for each treatment scenario (see Table 2) with and without effects of barred owls.

No Barred Owls, with Private Lands, Deschutes Analysis Area



With Barred Owls, with Private Lands, Deschutes Analysis Area

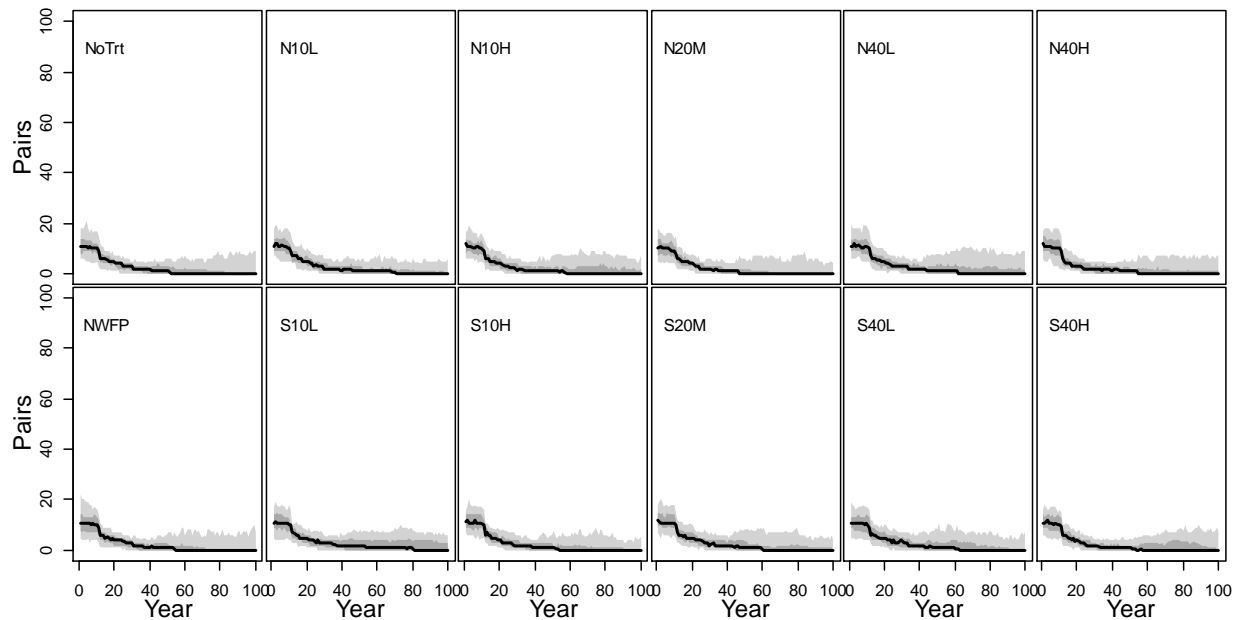


Figure 4. Simulated northern spotted owl population trajectories in the Deschutes analysis area. Lines depict median (black line), 50% quantile range (dark grey shade), and 90% quantile range (light grey shade) of the estimated number of owls through the simulation for 60 *HexSim* replicates for each treatment scenario (see Table 2) with and without effects of barred owls.

Last decade NSO population sizes broadly overlapped across the treatment scenarios, but minimum NSO population sizes were substantially different across scenarios. Last decade NSO population sizes were slightly smaller for the treatment scenarios as compared to the No Treatment scenario in the Wenatchee analysis area, and slightly larger for the Deschutes than for the Wenatchee. Minimum NSO population sizes were substantially different across treatment scenarios for all of the Wenatchee NSO population scenarios (ANOVA $p < 0.01$) and for the NSO population scenarios without BDOW interactions in the Deschutes analysis area (ANOVA $p < 0.01$). The larger-area, higher-intensity treatment scenarios (N40H, S40H, and NWFP) all had smaller minimum NSO population sizes across all of the NSO population scenarios. The N40H scenario produced the lowest minimum NSO population size of any treatment scenario for the Wenatchee analysis area and NSO population scenarios without BDOW interactions in the Deschutes. Minimum NSO population sizes were not different across treatment scenarios (ANOVA $p > 0.05$) for the Deschutes population scenarios with BDOW interactions because NSO populations went to extinction for most replicates of those scenarios.

NSO population changes through time generally tracked changes in total NSO habitat (the combined amount of good and moderate NSO habitat) and showed similar patterns for the Wenatchee analysis area and the Deschutes NSO population scenarios without BDOW displacement. Decadal lambda was approximately 1 from simulation years 0 to 30 for most scenarios excepting the large-area, high-intensity treatments (N40H, S40H, and NWFP) which resulted in decadal lambdas < 1 for those years. NSO population bottlenecks (temporary periods of lower than average population levels) generally occurred in both analysis areas around year 30, after treatments had been applied but before the steep accumulation of good habitat in years 30-50. All of the NSO population modeling scenarios showed a spike in decadal lambda from years 30 to 60 in response to a steep, synchronous increase in the modeled amount of good and moderate habitat.

V. Management Implications

The total area treated never exceeded 10% of each landscape analysis area, so the effects of fuel treatments on the landscape were limited by that fact alone. When we compared No Treatment with N40H for Wenatchee, we found a net reduction of about 7% in the amount of high severity fire for areas within 1 km of treatment areas. That means that the treatments, which reduce fire severity within the treated area also have the effect of reducing severity in the areas surrounding the treatments. This outcome makes sense, given the way the fire spread algorithm operates in *LADS* as a cellular automata approach that seeks to meet a fire area and size objective, and in which fuel treatments become a barrier to fire spread, creating wildfire “shadows” around treatments. *LADS* does not include time or weather conditions so it will not include decreases in fire behavior associated with longer-flow paths of fire through the landscape. Thus, our fire model cannot fully account for processes (weather and fire suppression) that would reduce fire spread, and potentially reduce fires severity, when fuel treatments are present in the landscape.

Initial landscape conditions strongly define the forest structural conditions that develop as suitable NSO habitat in the future. For example, mid-20th century selective harvesting practices in the Wenatchee analysis area resulted in relatively large areas of young forest with medium-sized trees. These areas of moderate NSO habitat in the Wenatchee analysis area became good NSO habitat over the duration of our simulations (much of it from simulation years 30 to 50). This pattern also occurred in the Deschutes analysis area, but did not produce as pronounced an increase in good NSO habitat because of the abundance of forest cover types that capable of growing into moderate but not good NSO habitat classes (e.g., ponderosa pine and mountain hemlock forests).

Higher-intensity, larger-area treatment scenarios created short-term NSO habitat and population bottlenecks, but had mixed effects on end-century NSO population sizes. Particularly for the Wenatchee analysis area, we did not find larger ending NSO population sizes from aggressive fuel reduction treatments relative to the No Treatment scenario. The presence of both good and moderate habitat contributed substantially to the suitability of an area for occupancy by a territorial NSO pair based on our analysis of habitat conditions surrounding documented NSO activity centers. Active fuel reduction activities in moderate habitat contributed to substantial short-term (simulation years 0 to 30) population declines under the larger area, higher intensity scenarios. However, our landscape-scale analysis may have failed to detect local benefits of targeted fuel reduction treatments for habitat sustainability and recruitment in specific areas. More refined, finer-scale analysis may reveal more local benefits of fuel reduction treatments for recruiting and maintaining NSO habitat.

The combination of BDOW interactions and high-intensity, larger-area treatments contributed to the most substantial NSO population bottlenecks. The combined effects of aggressive fuel reduction treatment approaches and interactions with BDOWs have the potential to contribute to increased extinction risk for NSOs in both analysis areas. We urge caution in the interpretation of our BDOW interaction modeling for the Deschutes analysis area. Due to the lack of empirical information on BDOW habitat associations in the Deschutes, we applied our BDOW habitat models from the Wenatchee analysis area to the Deschutes analysis area. Our finding that NSOs frequently became extinct under all of the scenarios that included BDOW interactions in the Deschutes analysis area suggests cause for concern regarding the effects of interactions of NSOs with BDOWs in this area. Additional information on BDOW habitat associations and interactions with NSOs in this area will be required.

Barred owl interactions had more impact on NSO population performance than treatment scenarios or assumptions regarding habitat values on non-federal lands, but NSO population growth rates (simulation-duration λ) were higher for scenarios including BDOW interactions in the Wenatchee analysis area partly because initial NSO population sizes were much smaller, so fewer additional NSO pairs were required to have a proportionately larger effect on its population growth rate. However, our results do suggest that widespread recruitment of NSO habitat could have the potential to enhance the chances of NSO population persistence in the face of detrimental effects of competitive interactions with barred owls in some landscapes (as also suggested by Dugger et al. 2011 and Forsman et al. 2011).

VI. Relationship to other recent findings and ongoing work

Our models show that treatments have opposite effects in the two study areas on the amount of good and moderate NSO habitat over the last decade. In the Wenatchee, the No Treatment scenario resulted in more good and moderate NSO habitat than all the treatments. In the Deschutes the story is reversed, where treatments generally resulted in more NSO habitat than under no treatments. One possible explanation may have to do with the initial vegetation structural class conditions. If the Wenatchee initially has significant areas in younger (non-habitat) vegetation that have potential to grow into NSO habitat, then the treatments, which would concentrate in non-habitat areas might be taking out potential future NSO habitat. Evidence for this interpretation is supported in our analysis of NSO habitat trends, which shows a steep increase in the amount of good NSO habitat on the Wenatchee (from a 100k to an average of more than 250k ha) during the first 7 decades and an equally steep decrease in moderate NSO habitat, which must be growing into good habitat. The relative change in the Deschutes of good habitat is much less (from 30k to an average of about 33k ha), and there is relatively little change in the amount of moderate habitat. The data from the Deschutes suggest that succession is producing relatively little new habitat and that most of the non-habitat that is treated is in environments or forests types that do not have potential to develop into owl habitat through succession. If these interpretations are correct then we may have discovered an important aspect of NSO habitat dynamics—namely the initial vegetation age and size structure of the landscape and the target of treatments relative to future NSO habitat. Ager (2007) (see below) did not grow NSO habitat and evaluated only the Deschutes. Our results are consistent with his for the Deschutes. Roloff et al. (2005) (see below) allowed treatments in owl habitat and found that that active management was not consistent with owl habitat production in that particular case. It appears that management regimes that take out owl habitat through treatments (either current or potential future) do not reduce the amount of habitat that is lost to wildfire enough to make up for the habitats lost through treatments.

Ager et al. 2007 found that fuel treatments would reduce expected loss of owl habitat when the treatment area reached at least 20% of the landscape. The reduction in expected loss of owl habitat in that study went from about 2.4% to 1.3% between 0% treated and 20% of landscape treated. The Ager analysis did allow treatment in areas that were defined as owl habitat and did not assume that succession or stand development would occur (static vegetation).

Roloff et al. 2005 modeled active and no-management in fire prone landscapes in SW Oregon. They found that active management in owl foraging areas reduced owl habitat compared with no management (only losses to wildfire). They attributed the lack of effect of active management in part on the limited area available at landscape scales to treat hazardous fuels but also to the fact that their treatments reduced owl habitat quality (from nesting to foraging) but did not reduce the amount of crown fire. Their model assumed vegetation dynamics (using FVS) and simulated fire using *FlamMap*. In a second paper Roloff et al. 2012 analyzed a different fuel management strategy for the same area. In that paper they found that active management “was more favorable to spotted owl conservation...than no management”

Although they used *FlamMap*, they did not actually burn up owl habitat with a landscape model. Instead they assumed that if 50% of the owl territory had crown fire *potential* then all of the territory would be lost to a fire. This assumption appears to overestimate loss of habitat to fire.

VII. Future Work Needed

- Conduct finer-scale analysis to evaluate responses to treatment within smaller landscape units (5th or 6th code hucs) and compare habitat trends across smaller landscape units that had different total proportions of area treated.
- Analysis of additional treatment scenarios that are not constrained by assumptions regarding access, ownership, and land use allocation to determine the area and spatial optimization of area that would be needed to affect habitat and NSO population outcomes. The fuel treatment scenarios that we analyzed in this project were constrained to a limited portion of the analysis landscape (the area presently available for treatment) and units were prioritized for treatment based on fire risk and other factors, not a true spatial optimization for limiting fire flow. Fewer limitations on treatment locations and using a formal spatial optimization approach to allocate treatments could produce different NSO population outcomes.
- We need more information on barred owl habitat associations and interactions with spotted owls on the Deschutes. Barred owls have been historically uncommon in this area, but detections have increased since 2010. Barred owl-specific surveys throughout the Deschutes (not just within NSO habitat) would provide important information on landscape-scale habitat associations of BDOW and overlap with NSO in this area.

VIII. Deliverables and Science Delivery

The team will deliver a full range of science and technology transfer products. We anticipate publishing 4-5 papers in peer-reviewed journals and presenting results at scientific and management conferences. A web page will describe the research progress and results. Workshops targeted at particular management and policy users will be held in OR and WA.

Deliverable Type	Description	Delivery Dates
Datasets and models	Integrated spatial (GIS) and modeling datasets on vegetation, fire, and Northern Spotted Owl habitat, in the eastern Cascade Mountains study area, for Forest Planning	in prep.

Deliverable Type	Description	Delivery Dates
	<i>LADS</i> model of landscape dynamics	in prep.
	<i>HexSim</i> model Northern Spotted Owl population dynamics	in prep.
Refereed publications	<p><i>Several refereed publications prepared on compatibility of fuel treatments and conservation of owl habitats and populations, and integrating fuel reduction with maintaining NSO prey, including papers on:</i></p> <p>Landscape scenario analysis. R. Scheller et al. Potential target journals: Ecological Applications, Landscape Ecology</p> <p>Future northern spotted owl habitat dynamics and population responses in the Eastern Cascade Range. Singleton, P.H., B.G. Marcot, M. Raphael, J. Lehmkuhl., R. Scheller, P. Hessburg. For: Conservation Biology.</p> <p>Landscape-scale habitat associations for barred owls and spotted owls in the Eastern Cascade Range, Washington. Singleton, P.H., (and others). For: Biological Conservation.</p> <p>Overlap of barred owl and spotted owl habitat influences spotted owl pair site occupancy dynamics. Singleton, P.H., (and others). For: Journal of Wildlife Management.</p> <p>Simulated population-level impacts of territorial interactions with barred owls on northern spotted owls in the Eastern Cascade Range, Washington. Singleton, P.H. (and others). For: Conservation Biology.</p> <p>Spotted Owls, Barred Owls, and Fire Risk. P. Singleton, P. Hessburg, B. Salter, T. Flowe. Potential target journals: Forest Ecology and Management</p> <p>Fire risk and owl habitat. P. Hessburg et al. Potential target journal: International Journal of Wildl. Fire</p> <p>Analysis of sensitivity and uncertainty in an individual-based movement model of a threatened wildlife species. B. Marcot et al. Target journal: Environmental Modelling & Software</p> <p>Other reports or journal manuscripts to be determined.</p>	<p>in prep.</p> <p>in prep.</p> <p>in prep.</p> <p>in prep.</p> <p>in prep.</p> <p>in prep.</p> <p>in prep.</p> <p>in initial review</p> <p>in prep.</p>
Dissertation	Barred Owls and Northern Spotted Owls in the Eastern Cascade Range, Washington. Singleton, P.H. 2013. Ph.D. Dissertation. University of Washington. Seattle WA.	2013

Deliverable Type	Description	Delivery Dates
Agency report	US Forest Service General Technical Report submitted to JFSP with details of results by draining, etc.; or, as used in supplemental material for journal papers	in prep.
Workshops	<p>A public workshop on dry forest restoration/fuels reduction and spotted owl management was held in Redmond, Oregon, during 2009. There were 225 attendees. A full report and recommendations can be found at: http://www.fws.gov/oregonfwo/ExternalAffairs/Topics/DryForestWorkshop/2009DryForestWorkshop.asp</p> <p>Two one-day workshops were held with staff of the Okanogan-Wenatchee and the Deschutes National Forests during 2010 to discuss management strategies they use and felt necessary for us to model.</p> <p>Development of stand silvicultural prescriptions that integrate fuel reduction and forest restoration, and NSO prey and nesting/roosting/foraging structural habitat. This workshop of 25 select managers and scientists was held during 2012 in Hood River, Oregon. A GTR listed below is in progress with expected publication at the end of 2013.</p>	<p>2009</p> <p>2010</p> <p>2012</p>
Website	Summarize progress and display interim maps and other products: https://sites.google.com/a/pdx.edu/vegetation-fire-owl/	ongoing
Non-refereed publications	<p>Silviculture and Monitoring Guidelines for Integrating Restoration of Dry Mixed-Conifer Forest and Spotted Owl Habitat Management in the Eastern Cascade Range. PNW GTR in prep for publication in late 2013. The results of the Workshop listed above.</p> <p>US Forest Service, Pacific Northwest Research Station <i>Science Update</i> article</p> <p>US Forest Service, Pacific Northwest Research Station <i>Science Findings</i> article</p>	<p>2013</p> <p>to be developed</p> <p>to be developed</p>
Presentations	<p>2009:</p> <p>Kennedy, R. S. H., A. A. Ager, P. F. Hessburg, J. F. Lehmkuhl, B. G. Marcot, M. G. Raphael, N. H. Schumaker, P. H. Singleton, and T. A. Spies. 2009. Assessing the compatibility of fuel treatments, wildfire risk, and conservation of Northern Spotted Owl habitats and populations in the eastern Cascades. Invited poster presented at: 4th International Fire Ecology & Management Congress: Fire as a Global Process. 30 November - 4 December 2009, Savannah, Georgia.</p>	presented

Deliverable Type	Description	Delivery Dates
	<p>2010:</p> <p>Lehmkuhl, J. F. and P. F. Hessburg. 2010. A Whole-Landscape Strategy to Restore Inland Northwest Dry Forests and Recover the Northern Spotted Owl. 24th International Congress for Conservation Biology: Conservation for a Changing Planet. 3-7 July 2010, Edmonton, Alberta, Canada.</p>	presented
	<p>2011:</p> <p>Kennedy, R., P. Hessburg, B. Marcot, P. Singleton, M. Raphael, J. Lehmkuhl, A. Ager, and T. Spies. 2011. Conserving Northern Spotted Owl habitat and populations while mitigating wildfire risk and increasing resiliency of forest structure and function: balancing among conflicting ecosystem services in landscapes characterized by disturbance. Presented at: 2011 US-IALE (U.S. Regional Association of the International Association for Landscape Ecology) Annual Symposium, Portland, Oregon.</p>	presented
	<p>Singleton, P.H. 2011. Habitat overlap for northern spotted owls and barred owls in the eastern Cascades, Washington. Presented at: 2011 US-IALE (U.S. Regional Association of the International Association for Landscape Ecology) Annual Symposium. April 5, 2011. Portland, Oregon.</p>	presented
	<p>Singleton, P.H. 2011. Barred owls and northern spotted owls in the eastern Cascades, Washington. Presented at: The Washington State Chapter, Society of American Foresters Annual Meeting. May 12, 2011. Portland, Oregon.</p>	presented
	<p>Lehmkuhl, J. 2011. A foundation for integrating wildlife and restoration objectives in Cascadian dry forests. The Society of American Foresters, Northwest Chapter, Conference: Forest Restoration Beyond Fuel Reduction: What is the Vision? October 12-14, 2011, Bend, OR</p>	presented
	<p>2012:</p> <p>Lehmkuhl, J. 2012. Overview: Creating Stand-Level Silvicultural Prescriptions & Monitoring Templates for Restoration & the Northern Spotted Owl in the Eastern Cascades. PNW Station & U.S. Fish and Wildlife Workshop on Creating Stand-level Silvicultural Prescriptions that Integrate Restoration and Ecological Objectives in the Eastern Cascade Range. Hood River, Oregon, Sept. 5-7, 2012</p>	presented
	<p>Lehmkuhl, J. 2012. An overview of alternatives for dry forest restoration and Northern Spotted Owl conservation in the eastern Cascade Range and their</p>	presented

Deliverable Type	Description	Delivery Dates
	<p>analysis by the Veg-Fire-Owl Project. The Wildlife Society 19th Annual Conference. Oct. 17, 2012, Portland, Oregon.</p> <p>Lehmkuhl, J. and others. 2012. Strategies for integrating dry forest restoration and Northern Spotted Owl conservation in the eastern Cascade Range. 5th International Fire Congress. Dec. 5, 2012, Portland, Oregon.</p> <p>Singleton, P. H., B. G. Marcot, J. Lehmkuhl, M. Raphael, R. Kennedy, and N. H. Schumaker. 2012. Modeling interactions between Spotted Owl and Barred Owl populations in fire-prone forests. Presentation at: 97th Annual Meeting of the Ecological Society of America, 5-10 August 2012, Portland, Oregon.</p> <p>Scheller, R.M., E. Haunreiter, R. Kennedy, P. Singleton. 2012. Projected dry forest landscape dynamics and the implications for Northern Spotted Owl habitat under alternative management scenarios. Invited Speaker at Symposium of The Wildlife Society 75th Annual Meeting. October, 2012. Portland, OR.</p> <p>Singleton, P. H., B. G. Marcot, M. Raphael, J. Lehmkuhl, N. Schumaker. 2012. Distribution and abundance of Northern Spotted Owls under alternative dry forest management scenarios. Presentation at: The Wildlife Society 19th Annual Conference, October 12-18, 2012, Portland, Oregon.</p> <p>Spies, T., P. Hessburg, and J. Lehmkuhl. 2012. Strategies for integrating dry forest restoration and conservation of the Northern Spotted Owl in the eastern Cascade Range. The Wildlife Society 19th Annual Conference. Oct. 17, 2012, Portland, Oregon. (Spies gave the presentation).</p> <p>2013:</p> <p>Raphael, M.G. 2013. The Vegetation, Fire, Owl project: applications to Region 6 restoration initiatives. Presentation to Regional biologists and planners, POortland, OR.</p>	<p></p> <p>presented</p> <p>presented</p> <p>presented</p> <p>presented</p> <p>presented</p>

Citations

- Ager, A.A, N.M. Vaillant, M.A. Finney, H.K. Preisler. 2012. Analyzing wildfire exposure and source sink relationships on a fire prone forest landscape. *Forest Ecology and Management*. 267:271 – 283.
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Acronyms and abbreviations used in this report:

BDOW = barred owl, *Strix varia*
DES = Deschutes landscape analysis area
GNN = gradient nearest neighbor vegetation inventory
LSOF = late-successional and old forest
LSR = late-successional [forest] reserve
NSO = northern spotted owl, *Strix occidentalis caurina*
RAWS = Remote Automatic Weather Stations
RRP = Revised Recovery Plan
USFS = U.S. Forest Service
USDA = U.S. Department of Agriculture
USFWS = U.S. Fish and Wildlife Service
WEN = Wenatchee landscape analysis area

Model names used in this report:

FBFM = fire behavior fuel model
FlamMap = fire simulation model
FVS = Forest Vegetation Simulator
HexSim = spatially explicit individual-based population simulation model
LADS = forest state-and-transition simulation model



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EDITED BY

Arshad Ali,
Hebei University, China

REVIEWED BY

Osbert Jianxin Sun,
Beijing Forestry University, China
Tanzeel J. A. Farooqi,
Yibin University, China

*CORRESPONDENCE

Brendan M. Rogers
brogers@woodwellclimate.org

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Using ecosystem integrity to maximize climate mitigation and minimize risk in international forest policy

Brendan M. Rogers^{1*}, Brendan Mackey²,
Tatiana A. Shestakova^{1,3}, Heather Keith², Virginia Young⁴,
Cyril F. Kormos⁵, Dominick A. DellaSala⁵, Jacqueline Dean¹,
Richard Birdsey¹, Glenn Bush¹, Richard A. Houghton¹ and
William R. Moomaw⁶

¹Woodwell Climate Research Center, Falmouth, MA, United States, ²Climate Change Response Program, School of Environment and Science, Griffith University, Gold Coast, QLD, Australia, ³Department of Crop and Forest Sciences, University of Lleida, Lleida, Spain, ⁴International Forests and Climate Programme, Australian Rainforest Conservation Society, Milton, QLD, Australia, ⁵Wild Heritage, Berkeley, CA, United States, ⁶Global Development and Environment Institute, Fletcher School of Law and Diplomacy, Tufts University, Medford, MA, United States

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 (through 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).

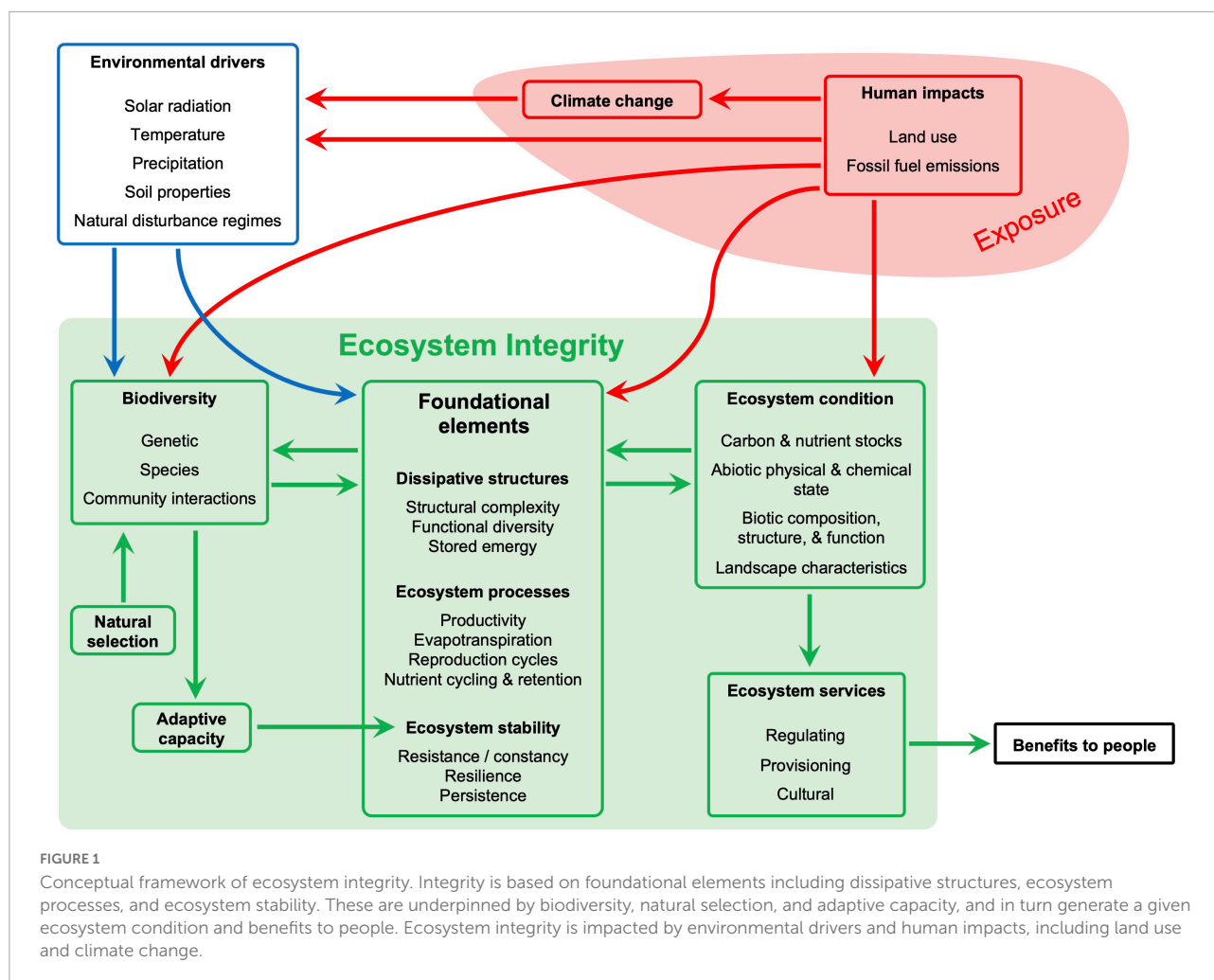
Components of ecosystem integrity

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 energy (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



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 emery as manifested in biomass and carbon stocks in section “Ecosystem condition”). High-integrity forests that have been allowed time to respond to their emery 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; Bourgoïn 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 CO₂ 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; Holtmark, 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 (Fussler 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 (Vioreck, 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; Brien 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; Ehrlén 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 m² 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

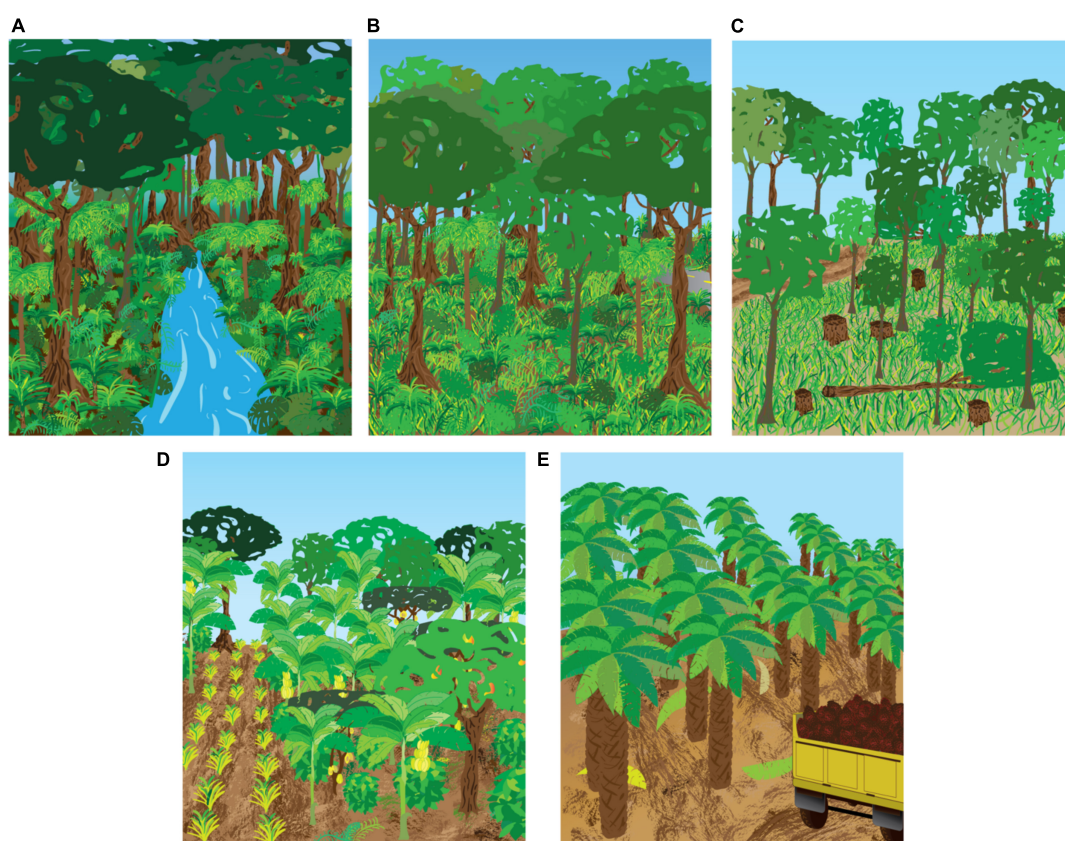


FIGURE 2

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			
<ul style="list-style-type: none"> • 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 			
<i>Dissipative structures</i>	<i>• Ecosystem processes</i>	<i>• Stability and risk profiles</i>	<i>• Ecosystem integrity level</i>
<ul style="list-style-type: none"> • Canopy trees dominated by large, old trees • In wet tropics, closed canopies • Dense soil organic stocks • Typically significant quantities of dead biomass 	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • High levels for all three factors
Secondary forest			
<ul style="list-style-type: none"> • 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 			
<i>• Dissipative structures</i>	<i>• Ecosystem processes</i>	<i>• Stability and risk profiles</i>	<i>Ecosystem integrity level</i>
<ul style="list-style-type: none"> • In wet tropics, canopy closure can occur within 1–2 decades • Aboveground living significantly less than primary forests • Some dead biomass may remain 	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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) 	<ul style="list-style-type: none"> • Moderate depending on time since disturbance
Production forest			
<ul style="list-style-type: none"> • 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 			
<i>• Dissipative structures</i>	<i>• Ecosystem processes</i>	<i>• Stability and risk profiles</i>	<i>Ecosystem integrity level</i>
<ul style="list-style-type: none"> • Logging regimes maintain a predominantly even-aged, younger age structure (~20–60 years) • Simplified vertical vegetation structure 	<ul style="list-style-type: none"> • Canopy tree species natural regenerated but some level of assisted regeneration common • Ongoing soil loss 	<ul style="list-style-type: none"> • More flammable forest conditions • Greater exposure to invasive species 	<ul style="list-style-type: none"> • Low to moderate depending on intensity of logging regimes and biodiversity loss
Agro-forestry (commercial, subsistence)			
<ul style="list-style-type: none"> • 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 			
<i>Dissipative structures</i>	<i>Ecosystem processes</i>	<i>Stability and risk profiles</i>	<i>Ecosystem integrity level</i>
<ul style="list-style-type: none"> • A curated canopy of trees, often remnant from primary forest or planted from local stock • Little if any understory • Ground cover are food crops 	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • Intensive small-scale management and modest level of biodiversity provides assisted resilience and adaptive capacity 	<ul style="list-style-type: none"> • 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)

<i>Dissipative structures</i>	<i>Ecosystem processes</i>	<i>Stability and risk profiles</i>	<i>Ecosystem integrity level</i>
<ul style="list-style-type: none"> • Typically mono-cultures that are harvested at around a young age (~10–20 years) 	<ul style="list-style-type: none"> • Soil water and nutrient retention • Can utilize natural pollinators from neighboring or remnant natural forests 	<ul style="list-style-type: none"> • Exposed to extreme weather events, invasives, pests, and disease • Intensive large-scale management needed 	<ul style="list-style-type: none"> • 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 (≤ 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 IPCC 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

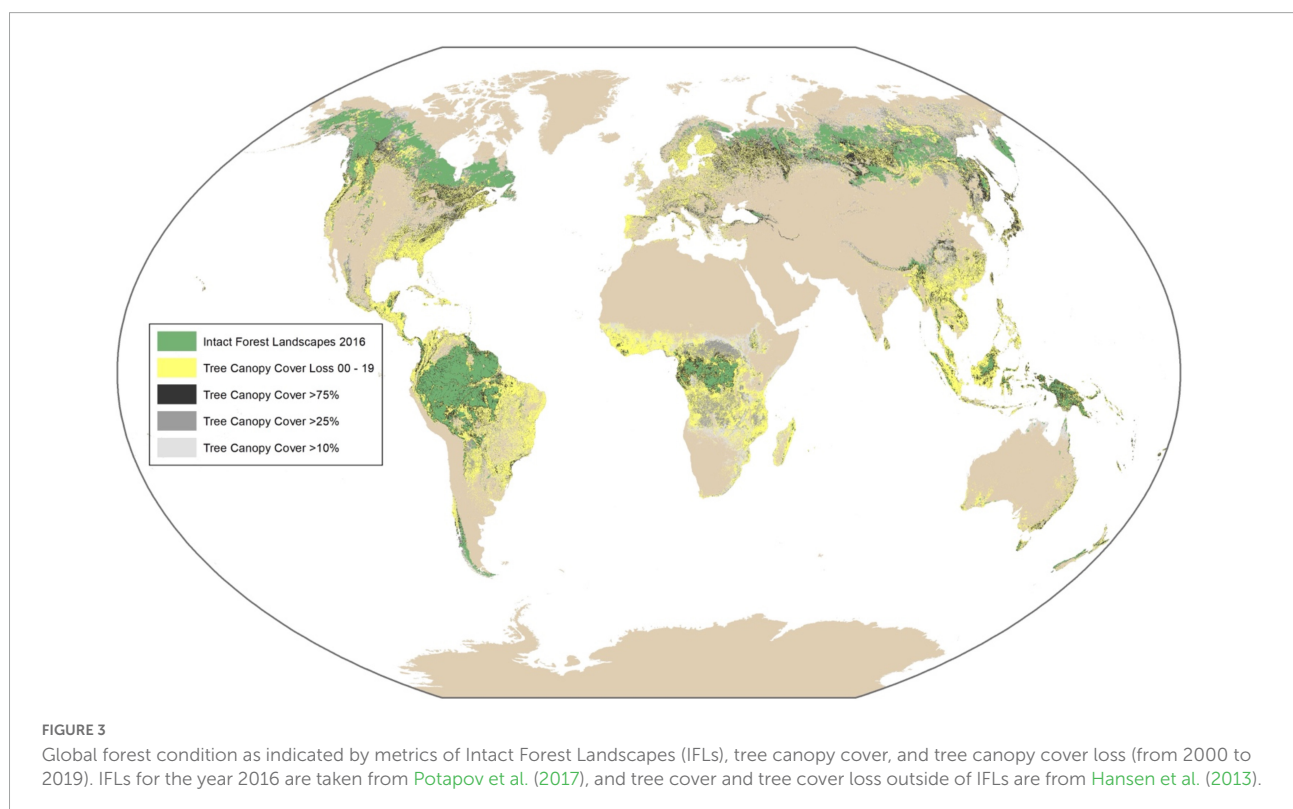
Because ecosystem integrity is such an integrative and multidisciplinary concept, research gaps are relatively extensive. We therefore do not offer an exhaustive list, but rather a prioritized assessment of future research directions to improve the understanding, valuation, and operationalization of 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.



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.

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A review of the effects of wildfire smoke on the health and behavior of wildlife

O V Sanderfoot^{*} , S B Bassing , J L Brusa, R L Emmet, S J Gillman , K Swift and B Gardner

School of Environmental & Forest Sciences, University of Washington, Seattle, WA, United States of America

^{*} Author to whom any correspondence should be addressed.E-mail: oliviavs@uw.edu**Keywords:** wildfires, smoke, air pollution, wildlife, monitoring, conservation, climate change

Abstract

Climate change is intensifying global wildfire activity, and people and wildlife are increasingly exposed to hazardous air pollution during large-scale smoke events. Although wildfire smoke is considered a growing risk to public health, few studies have investigated the impacts of wildfire smoke on wildlife, particularly among species that are vulnerable to smoke inhalation. In this review, we synthesized research to date on how wildfire smoke affects the health and behavior of wildlife. After executing a systematic search using Web of Science, we found only 41 relevant studies. We synthesized findings from this literature and incorporated knowledge gained from fields outside wildlife science, specifically veterinary medicine and air pollution toxicology. Although studies that directly investigated effects of smoke on wildlife were few in number, they show that wildfire smoke contributes to adverse acute and chronic health outcomes in wildlife and influences animal behavior. Our review demonstrates that smoke inhalation can lead to carbon monoxide poisoning, respiratory distress, neurological impairment, respiratory and cardiovascular disease, oxidative stress, and immunosuppression in wildlife, including terrestrial and aquatic species, and these health effects can contribute to changes in movement and vocalization. Some species also use smoke as a cue to engage in fire-avoidance behaviors or to conserve energy. However, our review also highlights significant gaps in our understanding of the impacts of wildfire smoke on wildlife. Most notably, the lack of robust air pollution measurements in existing studies limits meta-analyses and hinders construction of dose-response relationships, thereby precluding predictions of health outcomes and behaviors under different air quality conditions, especially during extreme smoke events. We recommend that future studies leverage existing data sets, infrastructure, and tools to rapidly advance research on this important conservation topic and highlight the potential value of interdisciplinary collaborations between ecologists and atmospheric chemists.

1. Introduction

As climate change intensifies the frequency and severity of wildfires, communities around the world are increasingly vulnerable to smoke pollution (Jacob and Winner 2009). Increased wildfire activity has been linked to declines in average regional air quality and greater incidence of extreme air pollution episodes. For example, wildfires contributed to a recent increase in annual concentrations of fine particulate matter (PM_{2.5}, particles smaller than 2.5 µm in aerodynamic diameter) in the United States (McClure and Jaffe 2018, Clay and Muller 2019), and smoke

events in the Pacific Northwest, United States in 2018 and 2020 caused PM_{2.5} to spike to concentrations well above the National Ambient Air Quality Standards (Washington State Academy of Sciences 2019, Liu *et al* 2021a). Wildfire smoke directly contributes to adverse respiratory and cardiovascular health outcomes and mortality in humans (Cascio 2018, Chen *et al* 2021); in fact, studies have shown that the chemical composition of PM_{2.5} in wildfire smoke is more toxic than that of urban ambient PM_{2.5} (Franzi *et al* 2011, Aguilera *et al* 2021).

Wildfire smoke also sickens non-human animals, as illustrated by numerous case studies in veterinary

medicine that document morbidity and mortality in domestic animals exposed to smoke, including pets and livestock (Fitzgerald and Flood 2006, Marsh 2007). These case studies demonstrate that, like people, animals can suffer from carbon monoxide poisoning, thermal and chemical damage to lung tissue, and greater susceptibility to respiratory disease as a result of smoke inhalation (Wohlsein *et al* 2016). In fact, animal models, including mice, rats, rabbits, sheep, and monkeys, are often used to study the onset and progression of human disease following exposure to the toxic gases and aerosols found in smoke (David *et al* 2009). Although many animals in fire-prone habitats are able to detect and avoid wildfires, fires still pose direct threats to wildlife (Engstrom 2010, Nimmo *et al* 2021), including exposure to extreme heat and smoke. Yet, the impacts of wildfire smoke on the health and behavior of wildlife are largely unknown (Hovick *et al* 2017, Lee *et al* 2017, Erb *et al* 2018, Geiser *et al* 2018).

This paucity of research on how wildfire smoke affects the health and behavior of wild animals hinders full consideration of the direct and indirect effects of wildfires when conducting risk assessments for wildlife and developing conservation plans. In addition, research on the impacts of wildfire smoke on wildlife is published in disparate journals spanning numerous disciplines (e.g. ecology, physiology, animal behavior, veterinary medicine, etc); as such, ecologists, wildlife managers, and other stakeholders may be challenged to identify relevant studies. To date, review papers have synthesized findings on first-order effects of fire on animals, including injury, morbidity, and mortality (Engstrom 2010), considered behavioral responses of mammals to fire, specifically torpor (Geiser *et al* 2018), and discussed fire as an evolutionary force driving animal behavior and survival (Nimmo *et al* 2021), but none have focused specifically on the effects of smoke from wildfires on the health and behavior of wildlife.

Wildfires are an important type of natural disturbance (Turner 2010) in forests, grasslands, and deserts around the world, and many wildlife species benefit from resources available in post-fire landscapes (Smith 2000). However, just as people now grapple with health risks posed by routine smoke events, even in airsheds where smoke pollution was previously uncommon (Wilmot *et al* 2021), wildlife must also contend with greater—perhaps even novel—exposure to wildfire smoke with more intense wildfire activity. The magnitude of smoke events in the 21st century further underscores the urgent need to study the impacts of wildfire smoke on wildlife. Wildfire smoke persists in the atmosphere even after flames have subsided and can travel hundreds of miles, creating hazardous air quality conditions and degrading visibility across large geographic areas (figure 1). As a result, smoke from a single wildfire could impact the health and behavior of wildlife

at a much larger spatial scale than the area burned. Direct effects of wildfire smoke on individuals could scale to influence the demography of wildlife populations, with cascading community- and ecosystem-level impacts (figure 2).

In this review, we synthesized research to date on the effects of wildfire smoke on the health and behavior of wildlife. We focused specifically on the impacts of wildfire smoke rather than describing all immediate effects of wildfires on wildlife in order to more deeply investigate physiological and behavioral responses of wildlife to the large-scale smoke events that are becoming increasingly common around the world. Below, we (1) identify relevant literature on the effects of wildfire smoke on the health and behavior of wildlife, (2) highlight knowledge gaps, and (3) present opportunities for rapidly advancing research on this important topic, all of which should serve as a useful resource for guiding ecological studies and conservation actions.

2. Methods

In January 2021, we conducted two keyword searches using Web of Science (figure 3). Search terms included (1) ‘wildfire* AND smoke*’ and (2) ‘fire* AND smoke*’. We performed a basic search and entered search terms into the topic field. We excluded ‘news items’ and ‘meeting abstracts’ as document types to focus on peer-reviewed literature, then further refined our search results to include only articles from categories relevant to our review (e.g. environmental science, ecology, biology, physiology, toxicology, health sciences, veterinary sciences, etc) A complete list of topic areas is provided in the [appendix](#).

We reviewed the titles of articles in both sets of search results ($n = 4314$) (figure 3). We earmarked articles with titles that included any of the following for further review: (1) the name of a specific domestic animal, wildlife species, or taxa (e.g. mammals, birds); (2) a general reference to animals or wildlife; (3) an example of an animal behavior (e.g. migration); or (4) an example of a health effect (e.g. mortality). We did not further review papers with titles suggestive of inquiry into ecosystem-level impacts of wildfires or the effects of fire or smoke on vegetation. We also excluded titles with clear references to human demographic groups (e.g. children) or epidemiological study (e.g. hospitals, emergency rooms). Next, we reviewed abstracts of articles earmarked in the review of titles ($n = 295$) to assess their eligibility for a full-text review (figure 3). We assessed whether or not these papers presented research on the responses of animals to smoke from fires—regardless of the specific type of exposure investigated. Those that met these criteria were included in the list of papers that were read for this review ($n = 72$; figure 3).

We sorted papers into three categories: (1) experiments using animal models; (2) case studies from

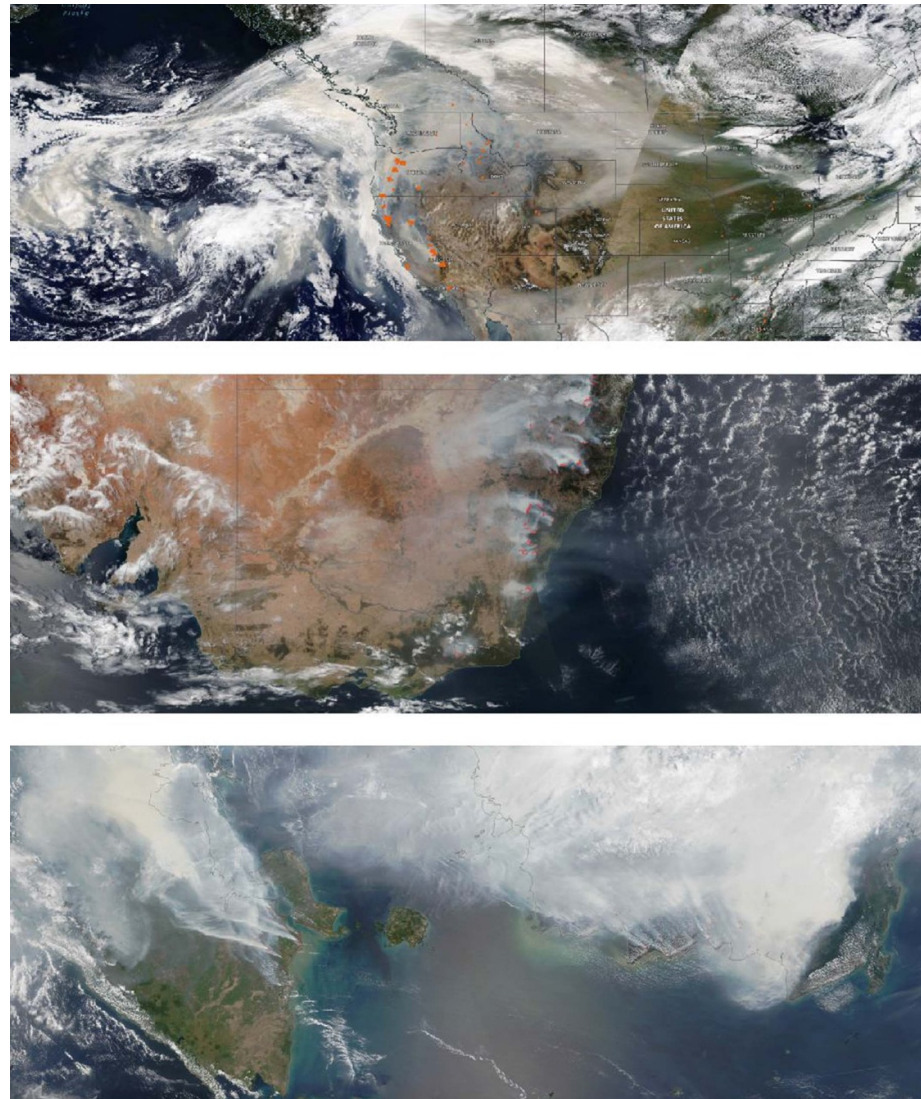


Figure 1. Satellite images of large-scale wildfire smoke events around the world. Orange points indicate locations of fires or thermal anomalies. Top: smoke blows across the Western United States on 13 September 2020. Middle: wildfires in southeast Australia send up smoke plumes on 17 December 2020. Bottom: smoke blankets much of Indonesia on 24 September 2015. We acknowledge the use of imagery from the NASA Worldview application (<https://worldview.earthdata.nasa.gov>), part of the NASA Earth Observing System Data and Information System (EOSDIS).

veterinary medicine; and (3) research on the effects of smoke on wildlife species (figure 3). For the last category, we considered ‘wildlife’ to include all non-domesticated fauna in terrestrial environments, including insects, as well as aquatic animals that breathe air, such as marine mammals. This allowed us to focus on the direct effects of smoke on wildlife, rather than explore all possible indirect effects that could arise from atmospheric deposition of airborne toxins found in wildfire smoke. At least one of the co-authors of this review read and documented findings from studies of animal models ($n = 36$) and case studies from veterinary medicine ($n = 18$). However, we focused our review on studies of the impacts of smoke on wildlife ($n = 18$). At least two co-authors of this review read and documented findings from each of these papers. In addition, we used Web of Science to conduct forwards searches, noting

any citations of these studies that referenced all of the following in the title: (1) smoke, or more generally air pollution associated with fires; (2) animals, wildlife, or the name of a particular species or taxa; and (3) an animal behavior or health effect. We also conducted backwards searches using two different approaches: (1) we noted citations that may be relevant to our review while reading a paper, and (2) we conducted a backwards search of all works cited in the paper using the same criteria described for the forwards search. All additional studies on the effects of smoke on wildlife species identified in forwards and backwards searches were also reviewed ($n = 16$) (figure 3). In addition to noting major findings from these papers, we pulled out several key pieces of information to characterize the research and compare results across studies, including publication year, field of study, location, type of exposure,

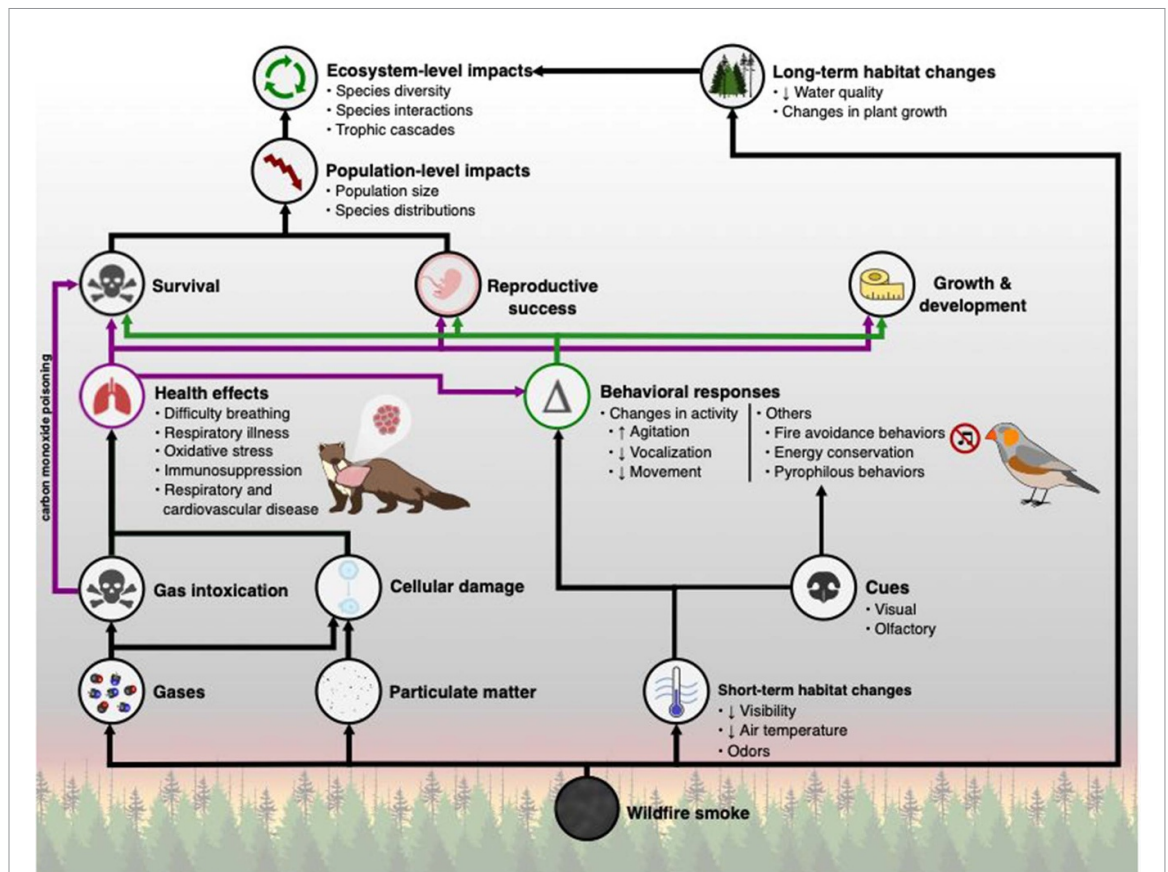


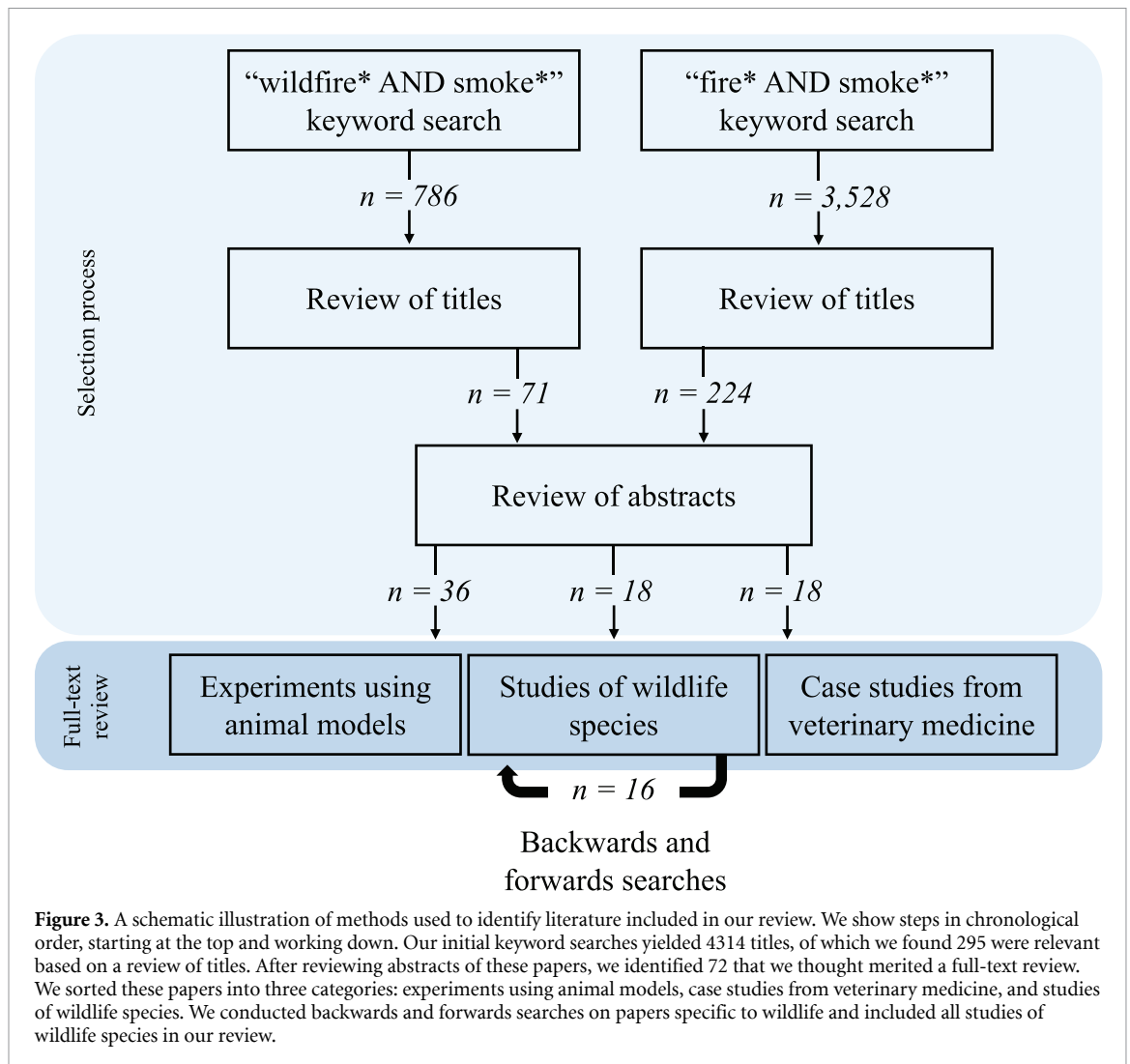
Figure 2. A conceptual model illustrating the various pathways by which wildfire smoke could influence wildlife populations and ecosystems. We hypothesize how effects of smoke on individual health and behavior could contribute to shifts in demographic rates, including growth and development, survival, and reproductive success. These parameters determine population growth, ultimately leading to community- and ecosystem-level impacts.

concentrations of air pollutants (if provided), and taxa and species of animals studied, as well as whether the animals were captive (i.e. kept in a laboratory or outdoor enclosure), or free-living (i.e. in the wild). Finally, we noted whether the ultimate goal of the study was to investigate effects of smoke in people or non-human animals. While preparing this manuscript, we learned of seven additional studies that considered the impacts of wildfire smoke on wildlife, which we also included in our review. Although we did not restrict our initial keyword searches in Web of Science by language, each subsequent step of our review was limited to text available in English. In addition, we were only able to review articles available through the University of Washington library system. All together, we reviewed 41 studies that considered the effects of wildfire smoke on wildlife (figure 3, table 1).

3. Results

We found that although research to date on the impacts of wildfire smoke on wildlife is limited, existing evidence suggests that smoke pollution has wide-ranging direct and indirect effects on both terrestrial and aquatic wildlife. Studies have linked smoke

inhalation to acute and chronic health outcomes in animals and sought to characterize how smoke influences animal behavior. Whereas the designs of these studies are highly variable, two general approaches have emerged in the literature: (1) experiments in which animals were intentionally exposed to smoke or constituents of smoke in a controlled environment (i.e. ‘controlled exposure’) and (2) opportunistic monitoring of free-living animals or animals in captivity during wildfire smoke events (i.e. ‘*in situ* exposure’). The studies we reviewed were conducted on five continents, including North America, Australia, Europe, Asia, and Africa (figure 4), and published between 1968 and 2021. They explored responses in a wide variety of taxa, including mammals, birds, reptiles, and insects, in both controlled and *in situ* settings (figure 5). A complete list of studies reviewed is provided in table 1. In sections 4 through 6, we detail findings from this literature while also incorporating knowledge gained from fields outside wildlife science, specifically veterinary medicine and air pollution toxicology. Finally, in section 7, we briefly summarize studies of indirect effects of smoke on wildlife and consider how a species’ life-history strategy mediates its exposure to smoke pollution.



4. Acute and chronic health outcomes

Few studies have explicitly considered the impact of wildfire smoke on the health of wildlife (table 1); however, research from veterinary medicine and air pollution toxicology clearly demonstrates that smoke inhalation contributes to acute and chronic health outcomes in animals. Case studies detailing the symptoms, treatment, and recovery of pets and livestock following structural fires establish that animals are vulnerable to negative health outcomes from smoke inhalation (e.g. Drobatz *et al* 1999a, 1999b, Marsh 2007). In addition, there are numerous examples of laboratory experiments designed to investigate the effects of inhalation exposure to wildfire smoke in humans using animal models (e.g. Hargrove *et al* 2019, Martin *et al* 2020) including mice, rats, rabbits, and sheep. Although the objective of these studies is to characterize the underlying physiological mechanisms that contribute to respiratory and cardiovascular disease in humans, their findings allude to health effects we could observe in other mammalian species.

These experiments have incorporated *in vivo*, *ex vivo*, and/or *in vitro* approaches. Some studies have also used animal models to study possible treatment interventions to improve health outcomes in humans following smoke inhalation (e.g. Janssens *et al* 1994, Wang *et al* 1999, Wong *et al* 2004, Syrkinia *et al* 2007, Hamahata *et al* 2008, Dunn *et al* 2018).

Research has largely focused on mammals, but all animals that breathe air—whether terrestrial or aquatic—are vulnerable to inhalation exposure to airborne toxins, including the reactive gases and aerosols that make up smoke (e.g. carbon monoxide (CO), hydrogen cyanide (HCN), and coarse and fine particulate matter (PM)). Many animals are susceptible to CO poisoning during smoke inhalation (Chaturvedi *et al* 1995, Fitzgerald and Flood 2006, Kent *et al* 2010, Ashbaugh *et al* 2012, Dörfelt *et al* 2014, Stern *et al* 2014), which can be fatal (Wohlsein *et al* 2016). CO binds to hemoglobin, a protein molecule containing iron that nearly all vertebrates (Ruud 1954) and many invertebrates depend on to carry oxygen through the bloodstream. This limits oxygen transport, resulting

Table 1. Summary of studies of wildlife species included in our review. For each paper, we provided the in-text citation, broad taxonomic category and specific species studied, and type of exposure (i.e. *in situ* or controlled) investigated. We also indicated whether a study assessed impacts in captive or free-living animals. In addition, we included the location and continent where each study took place. If locations for studies of captive animals were not provided, we noted the location of the research institution of the first author. We also provided a description of smoke exposure. Finally, we indicated if a health outcome and/or a behavioral response was observed. Citations are listed in alphabetical order.

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Álvarez <i>et al</i> (2015)	Insects	Pine sawyer (<i>Monochamus galloprovincialis</i>)	Controlled (excised antennae)	Insects captured in Valencia, Spain. Experiment conducted in Palencia, Spain	Europe	Excised antennae exposed to six smoke volatiles	No	Yes
Álvarez-Ruiz <i>et al</i> (2021)	Reptiles	Large psammodromus (<i>Psammodromus algirus</i>)	Controlled (captive)	Lizards captured on the eastern Iberian Peninsula in Spain. Study conducted in Valencia, Spain	Europe	Smoke generated from burning pine	No	Yes
Bova <i>et al</i> (2011)	Birds	Red-cockaded woodpecker (<i>Dryobates borealis</i>)	Controlled	Ohio, United States	North America	Smoke generated by burning maple twigs, branches, and leaf litter	No (only effects on habitat studied)	
Braun De Torres <i>et al</i> (2018)	Mammals	Florida bonneted bat (<i>Eumops floridanus</i>)	<i>In situ</i> (free-living)	Fred C. Babcock-Cecil M. Webb Wildlife Management Area and Florida Panther National Wildlife Refuge, Florida, United States	North America	Smoke from prescribed burns	No	Yes
Cahill and Walker (2000)	Birds	Red-knobbed Hornbill (<i>Aceros cassidix</i>)	<i>In situ</i> (free-living)	Tangkoko-Dua Saudara Nature Reserve, Sulawesi, Indonesia	Asia	Smoke from 1997 wildfire	Yes	Yes
Cheyne (2008)	Mammals	Bornean white-bearded gibbon (<i>Hyllobates albibarb</i>)	<i>In situ</i> (free-living)	Natural Laboratory of Peat-swamp Forest, Indonesia	Asia	Smoke from 2006 wildfire. Months were categorized as 'smoky' if the Indeks Standar Pencemar Udara (ISPU), an air quality index, exceeded Category 3—indicative of unhealthy air quality ($PM_{10} > 100 \mu g m^{-3}$)—on more than 75% of days	No	Yes
Dickinson <i>et al</i> (2009)	Mammals	Indiana bat (<i>Myotis sodalis</i>) and Northern long-eared bat (<i>Myotis septentrionalis</i>)	<i>In situ</i> (free-living)	Daniel Boone National Forest, Kentucky, United States	North America	Smoke from prescribed burns. CO peaked at ≥ 400 parts per million	No	Yes

(Continued.)

Table 1. (Continued.)

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Dickinson <i>et al</i> (2010)	Mammals	Indiana bat (<i>Myotis sodalis</i>)	N/A (modeling exercise; data on air pollution from prescribed burns in Tar Hollow State Forest and Daniel Boone National Forest, United States)	United States			No (no animals or specimens observed)	
Doty <i>et al</i> (2018)	Mammals	Gould's long-eared bat (<i>Nyctophilus gouldi</i>)	Controlled (captive)	Armidale, New South Wales, Australia	Australia	Smoke generated by burning eucalyptus leaves. Air quality measured using a smoke meter. Smoke level was measured at 6 (on a scale of 0–6), indicative of thick smoke	No	Yes
Engstrom (2010)	Multiple	Multiple	N/A (review, focused on first-order effects of fire in animals)				Yes	Yes
Erb <i>et al</i> (2018)	Mammals	Bornean orangutans (<i>Pongo pygmaeus wurmbii</i>)	<i>In situ</i> (free-living)	Tuanan Research Station, Central Kalimantan, Indonesia	Asia	Smoke from 2015 wildfire During wildfire season, daily mean concentrations of PM ₁₀ exceeded unhealthy levels (i.e. 150 $\mu\text{g m}^{-3}$) most days (79%). PM ₁₀ peaked at 1829 $\mu\text{g m}^{-3}$	Yes	Yes
Geiser <i>et al</i> (2018)	Mammals	Multiple (focus on small mammals)	N/A (review, focused on data from the southern hemisphere)				Yes	Yes
Hinz <i>et al</i> (2018)	Insects	Australian 'firebeetle' (<i>Merimna atrata</i>)	Controlled (captive)	Insects collected in Perth, Western Australia. Experiment carried out in Bonn, Germany	Europe	Insects exposed only to visual cues of smoke (e.g. projected image of a smoke plume)	No	Yes
Höcherl and Tautz (2015)	Insects	European paper wasp (<i>Polistes dominula</i>)	Controlled (free-living)	Wüzberg, Germany	Europe	Smoke generated by burning poplar wood	No	Yes

(Continued.)

Table 1. (Continued.)

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Hovick <i>et al</i> (2017)	Birds	Multiple (raptors)	<i>In situ</i> (free-living)	The Nature Conservancy Tallgrass Prairie Preserve and Oklahoma State University Cross Timbers Experimental Range, Oklahoma, United States	North America	Smoke from prescribed burns	No	Yes
Jordaan <i>et al</i> (2020)	Reptiles	Multiple (6 lizard and 8 snake species)	<i>In situ</i> (free-living)	Tembe Elephant Park, South Africa	Africa	Smoke from prescribed burns	Yes	Yes
Klocke <i>et al</i> (2011)	Insects	<i>Microsania australis</i> , <i>Hypocentides nearticus</i> , and <i>Anabarhynchus hyalipennis</i>	<i>In situ</i> (free-living)	Perth, Western Australia, Australia	Australia	Smoke from wildfires in 2006–2009	No	Yes
Layne (2009)	Mammals	Eastern red bat (<i>Lasiurus borealis</i>)	Controlled (captive)	Animals captured within and studied in outdoor enclosures at the Peck Ranch Conservation Area, Missouri, United States	North America	Smoke generated by burning leaf litter. CO peaked at 40 ppm	No	Yes
Lee <i>et al</i> (2017)	Multiple (ecoacoustics study, soundscape likely dominated by birds and insects)		<i>In situ</i> (free-living)	'EcoLink' wildlife overpass connecting Bukit Timah Nature Reserve and Central Catchment Nature Reserve, Singapore	Asia	Smoke from 2015 wildfire. During smoke event, the Pollutant Standards Index (PSI) ranged from 97 to 267, indicative of moderate to very unhealthy air quality	No	Yes
Liu <i>et al</i> (2021b)	Insects	Painted lady butterfly (<i>Vanessa cardui</i> L.)	Controlled (captive)	London, England, United Kingdom	Europe	Smoke generated by burning incense. Concentrations of PM _{2.5} during experiments ranged from 0.15 mg m ⁻³ to 1.28 mg m ⁻³	No	Yes
Mendyk <i>et al</i> (2020)	Reptiles	Pinecone lizards (<i>Tiliqua rugosa</i>)	<i>In situ</i> (captive)	Audubon Zoo, New Orleans, Louisiana, United States	North America	Smoke not generated intentionally. Animals exposed to smoke when a pastry burned in a nearby toaster	No	Yes
Milberg <i>et al</i> (2015)	Insects	Multiple	Controlled (free-living)	Ostergotland County, Sweden	Europe	Smoke generated by burning birch wood	No	Yes
Nimmo <i>et al</i> (2021)	Multiple	Multiple	N/A (review, focused on behavioral responses to fire)				No	Yes

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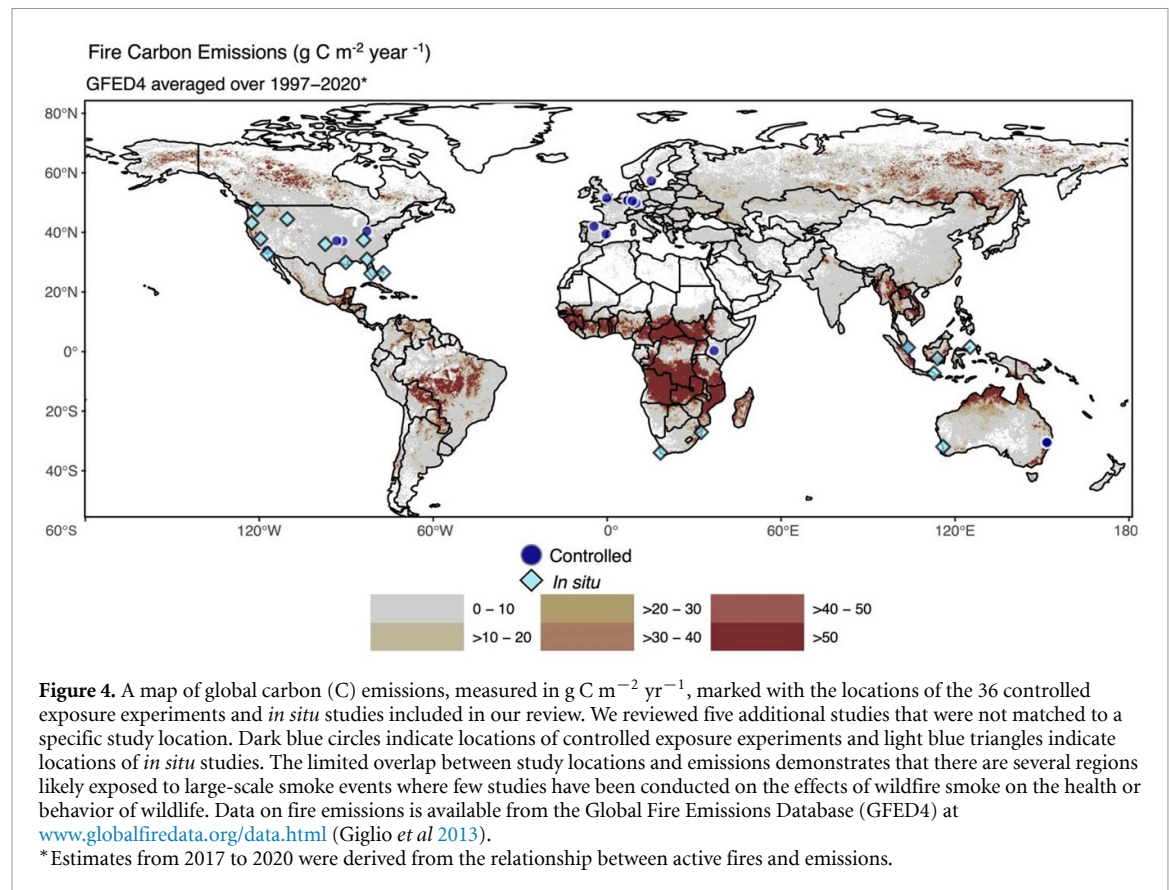
Table 1. (Continued.)

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Nowack <i>et al</i> (2016)	Mammals	Eastern pygmy possum (<i>Cercartetus nanus</i>)	Controlled (captive)	Animals captured in Dorrigo, New South Wales, Australia. Study conducted in Armidale, New South Wales, Australia	Australia	Possums exposed only to olfactory cues of smoke, specifically the scent of wood smoke	No	Yes
Nowack <i>et al</i> (2018)	Mammals	Sugar gliders (<i>Petaurus breviceps</i>)	Controlled (captive)	Animals captured in the Dorrigo and Imbota Nature Reserves in New South Wales, Australia. Study conducted in Armidale, New South Wales, Australia	Australia	Smoke generated by burning branches, sawdust, and leaves. Air quality measured using a smoke meter. Smoke level was measured between 3.2 and 4.1 (on a scale of 0 = clean air to 6 = thick smoke)	No	Yes
O'Brien <i>et al</i> (2006)	Birds	Cuban parrot (<i>Amazona leucocephala</i>)	<i>In situ</i>	Great Abaco, Bahamas	North America	Smoke from a prescribed burn. The maximum CO ₂ concentration in the surrogate nesting cavity was 2092 ppm	No (only effects on habitat)	
Sanderfoot and Gardner (2021)	Birds	71 common bird species	<i>In situ</i> (free-living)	Washington, United States	North America	Smoke from wildfires in 2015–2018. Daily mean concentration of PM _{2.5} ranged from 0 to 295.8 $\mu\text{g m}^{-3}$, with an average value of 8.6 $\mu\text{g m}^{-3}$	No (only effects on detection studied)	
Sanderfoot and Holloway (2017)	Birds	Multiple	N/A (review, focused on effects of air pollution on birds)				Yes	Yes
Scesny (2006)	Mammals	Eastern red bat (<i>Lasiurus borealis</i>)	Controlled (captive)	Animals captured in the Peck Ranch Conservation Area in Missouri, United States. Study conducted in Springfield, Missouri, United States	North America	Smoke generated by burning leaf litter	No	Yes
Schütz <i>et al</i> (1999)	Insects	Black fire beetle (<i>Melanophila acuminata</i>)	Controlled (excised antennae)	Giessen, Germany	Europe	Excised antennae exposed to volatiles generated from burning pine	No	Yes
Sensenig <i>et al</i> (2017)	Insects	<i>Crematogaster sjostedii</i> , <i>C. mimosae</i> , <i>C. nigriceps</i> , and <i>Tetraponera penzigi</i>	Controlled (free-living)	Mpala Research Centre, Kenya	Africa	Smoke generated by burning elephant dung	No	Yes

(Continued.)

Table 1. (Continued.)

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Singer <i>et al</i> (1989)	Mammals	Elk (<i>Cervus elaphus</i>)	<i>In situ</i> (free-living)	Yellowstone National Park, United States	North America	Smoke from the 1988 wildfires	Yes	Yes
Snoddy and Tippins (1968)	Insects	<i>Microsania imperfecta</i>	<i>In situ</i> (free-living)	Clinch County, Georgia, United States	North America	Smoke from an incinerator	No	Yes
Stawski <i>et al</i> (2015)	Mammals	Fat-tailed dunnart (<i>Sminthopsis crassicaudata</i>)	Controlled (captive)	Armidale, New South Wales, Australia	Australia	Smoke generated by burning eucalyptus	No	Yes
Stawski <i>et al</i> (2017)	Mammals	Yellow-footed antechinus (<i>Antechinus flavipes</i>)	Controlled (captive)	Animals captured in the Aberlaidie Nature Reserve, New South Wales, Australia. Study conducted in Armidale, New South Wales, Australia	Australia	Air quality measured using a smoke spot tester. Smoke level was measured at 5 (on a scale of 0–6), indicative of thick smoke	No	Yes
Tan <i>et al</i> (2018)	Insects	Squinty bush brown (<i>Bicyclus anynana</i>)	Controlled (captive)	National University of Singapore, Singapore	Asia	Smoke generated from burning incense. Average concentration of PM _{2.5} was 117 $\mu\text{g m}^{-3}$	Yes	No
Thompson and Purcell (2016)	Mammals	Fisher (<i>Pekania pennanti</i>)	<i>In situ</i>	Yosemite National Park and Sierra National Forest, United States	North America	Smoke from prescribed burns. The maximum CO concentration in dens ranged from 5.5 to 563.5 ppm, with a mean value of 170.8 ppm	No (only effects on habitat studied)	
Tribe <i>et al</i> (2017)	Insects	Cape honeybee (<i>Apis mellifera capensis</i>)	<i>In situ</i> (free-living)	Table Mountain National Park, South Africa	Africa	Smoke from 2015 wildfire	No	Yes
Venn-Watson <i>et al</i> (2013)	Mammals	Bottlenose dolphin (<i>Tursiops truncatus</i>)	<i>In situ</i> (free-living)	San Diego, California, United States	North America	Smoke from wildfires in 2003 and 2007. Maximum daily mean concentrations of PM _{2.5} reported for study years: 170 mg m^{-3} (2003) and 70 mg m^{-3} (2007)	Yes	No
Visser <i>et al</i> (1995)	Insects	Honey bee (<i>Apis mellifera</i>)	Controlled (excised antennae)	Riverside, California, United States	North America	Smoke generated by burning burlap	No	Yes
Yang <i>et al</i> (2021)	Birds	Multiple species	<i>In situ</i> (free-living)	Western United States	North America	Smoke from 2020 wildfires	Yes	No

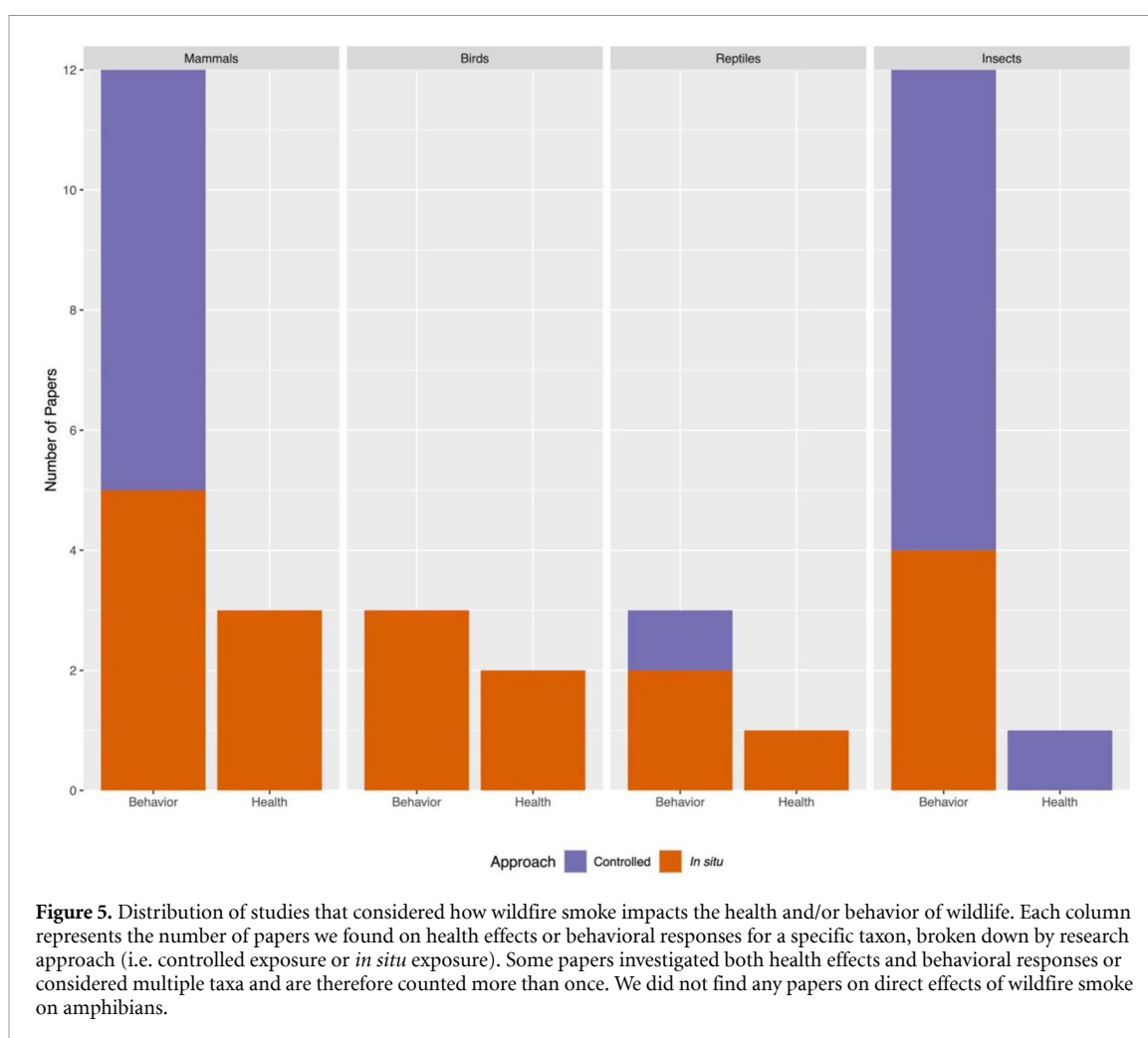


in low blood oxygen levels (i.e. hypoxemia) and insufficient supply of oxygen to tissues and organs (i.e. hypoxia) (Wohlsein *et al* 2016). Neurological symptoms of hypoxic brain damage could include confusion and stupor (Drobatz *et al* 1999a, 1999b, Mariani 2003, Kent *et al* 2010, Weiss *et al* 2011, Guillaumin and Hopper 2013). Hypoxia could also make animals more vulnerable to predation as they attempt to flee wildfires (Braithwaite and Estbergs 1987).

Smoke inhalation also causes both thermal and chemical damage to lung tissue in terrestrial and aquatic vertebrates (Fitzgerald and Flood 2006, Marsh 2007, Wohlsein *et al* 2016). As a result of this injury, fluid can accumulate in the lungs, a condition known as pulmonary edema (Bidani *et al* 1998, Jordaan *et al* 2020), which has been documented in pets and livestock exposed to smoke during structural fires (Verstappen and Dorrestein 2005, Fitzgerald and Flood 2006, Marsh 2007). Symptoms of smoke inhalation injury can be immediate or delayed and include labored breathing (i.e. dyspnea) (Verstappen and Dorrestein 2005, Fitzgerald and Flood 2006), rapid breathing (i.e. tachypnea) (Mariani 2003, Fitzgerald and Flood 2006), wheezing (Kemper *et al* 1993), panting (i.e. polypnea) (Dörfelt *et al* 2014), coughing (Kemper *et al* 1993, Fitzgerald and Flood 2006, Dörfelt *et al* 2014), foaming at the nostrils (McPherson 1993, Wohlsein *et al* 2016), and rapid heart rate (i.e. tachycardia) (Dörfelt *et al* 2014), which are consistent with acute respiratory distress syndrome (Guillaumin and Hopper 2013). If untreated, smoke

inhalation injury can quickly impair gas exchange, resulting in hypoxemia (Wohlsein *et al* 2016) and elevated levels of acid in the blood (i.e. acidosis) (Bidani *et al* 1998). For example, in a retrospective analysis of health records of captive bottlenose dolphins (*Tursiops truncatus*), researchers found that blood carbon dioxide (CO_2) levels were elevated in the month following a wildfire smoke event in 2003, possibly due to respiratory acidosis (Venn-Watson *et al* 2013). Air-breathing invertebrates might also be vulnerable to smoke inhalation. Tan *et al* (2018) investigated effects of smoke exposure in captive squinty bush brown butterflies (*Bicyclus anynana*) and found that particles accumulated in the entryway of spiracles—external openings in the exoskeleton that vent the insect respiratory system—but did not enter the trachea.

Wildfire smoke contributes to chronic respiratory and cardiovascular health outcomes in animals. Smoke inhalation can jeopardize an animal's immune system, which is designed to protect the body from foreign matter, such as bacteria, viruses, and toxins. In mammals, smoke inhalation immediately triggers production of immune cells, including lymphocytes (e.g. T cells) and macrophages (Bidani *et al* 1998, Barrett *et al* 2006, Syrkinia *et al* 2007, Hamahata *et al* 2008, Hargrove *et al* 2019)—a type of white blood cell that engulfs and digests (i.e. phagocytizes) foreign particles. However, exposure to wildfire smoke can alter (Venn-Watson *et al* 2013) or weaken (Black *et al* 2017) the immune response in animals. For example, whereas macrophages are able to sequester



toxic particles in wildfire smoke, they are unable to destroy them; this precludes macrophages from helping to prevent infection (Wohlsein *et al* 2016). Furthermore, toxins in smoke also destroy antioxidants, substances that neutralize free radicals—highly reactive, oxygen-containing compounds that damage tissue (Shalini *et al* 1994, Hamahata *et al* 2008, Wegesser *et al* 2010). Oxidative stress can ultimately contribute to compromised immune function by destroying macrophages or other types of immune cells (Franzi *et al* 2011, Williams *et al* 2013). Lung injury and a weakened immune response can leave animals more vulnerable to respiratory infection and illness, such as pneumonia (Attwood *et al* 1996a, 1996b, Marsh 2007, Simone-Freilicher 2008, Lange *et al* 2010, Guillaumin and Hopper 2013, Wohlsein *et al* 2016) or laryngotracheitis (Morris *et al* 1986). For example, captive bottlenose dolphins were three times more likely to have bacterial pneumonia at time of death after exposure to smoke during a wildfire in 2003 (Venn-Watson *et al* 2013). However, age also influenced the incidence of pneumonia, and after controlling for age, the effect of fires was no longer statistically significant (Venn-Watson *et al* 2013). A study of rhesus macaque monkeys (*Macaca mulatta*) housed in outdoor enclosures found that newborn monkeys

exposed to wildfire smoke exhibited reduced lung capacity and weakened immune responses in adolescence compared to those born in a subsequent year with good air quality (Black *et al* 2017). Whereas this study was designed to investigate pediatric health outcomes in humans associated with wildfire smoke, these results suggest that wildlife could experience long-term, adverse health outcomes from a single smoke event. Smoke inhalation can also impair cardiovascular function in vertebrates (Kim *et al* 2014, Wohlsein *et al* 2016, Thompson *et al* 2018, Sharpe *et al* 2020) and repeated or prolonged exposure to smoke can lead to chronic heart disease (Thompson *et al* 2018, Martin *et al* 2020).

Health outcomes associated with inhalation of wildfire smoke vary as a function of its toxicity. Research from air pollution toxicology demonstrates that toxicity of biomass smoke is dependent on its chemical and biological composition (Franzi *et al* 2011, Kim *et al* 2019), which is determined by the substrate burned (e.g. peat, oak, eucalyptus, etc) and combustion conditions (e.g. flaming, smoldering) (Hargrove *et al* 2019, Kim *et al* 2019). Smoke is also subject to chemical transformation during long-range transport (Jalava *et al* 2006). This suggests that the specific types of vegetation burned during

wildfires, the stage and severity of the fires, and the distance smoke travels ultimately affect respiratory and cardiovascular health outcomes associated with smoke inhalation in wildlife.

5. Impacts on demography

Negative health outcomes associated with inhalation exposure to wildfire smoke could ultimately influence demographic rates in wildlife populations, including survival, growth, and reproductive success (figure 2). *In vivo* studies of animal models (e.g. Bidani *et al* 1998, Dubick *et al* 2002, Lee *et al* 2005, Syrkin *et al* 2007, Lange *et al* 2010) and case studies from veterinary medicine (e.g. Morris *et al* 1986, Drobatz *et al* 1999b, Kent *et al* 2010, Dörfelt *et al* 2014, Stern *et al* 2014) provide clear evidence that animals can die from smoke inhalation. For example, Anderson *et al* (2020) linked elevated concentrations of PM_{2.5} during a large-scale smoke event to increased mortality in dairy cows, specifically calves. Yet, we found only four studies that considered the effect of smoke on survival of wildlife species. A study of captive butterflies reared in smoky conditions found that caterpillars exposed to smoke exhibited a higher mortality rate than those in the control group, likely due to gas intoxication (Tan *et al* 2018). Gas intoxication was also hypothesized as a contributing factor to the death of lizards and snakes that did not survive prescribed burns in Tembe Elephant Park, South Africa (Jordaan *et al* 2020). Few specimens exhibited signs of burn injury, yet Jordaan *et al* found that 61% of specimens collected at the site of one fire exhibited pulmonary edema and noted particles accumulated in the lungs of two of these specimens. These findings suggest that reptiles that did not survive the fire died from asphyxiation, CO or HCN poisoning, or heat-induced cardiac arrest. Large mammals are also vulnerable to smoke inhalation—Singer *et al* (1989) reported that smoke inhalation injury or gas intoxication likely killed 246 elk (*Cervus elaphus*) that perished in the 1988 wildfires in Yellowstone National Park. Finally, Yang *et al* (2021) found that smoke from extensive wildfires in the Western United States contributed to a mass avian mortality event in 2020.

Wildfire smoke could also reduce growth rates and reproductive success. Tan *et al* (2018) reported that captive squinty bush browns exposed to smoke developed more slowly and weighed less as pupae. Cahill and Walker (2000) reported that the nesting success of Red-knobbed Hornbills (*Aceros cassidix*) declined at the Tangkoko Nature Reserve in Indonesia following extensive wildfires in 1997, possibly due to exposure to extreme heat and smoke. Although the Red-knobbed Hornbill example was the only study we found that considered the impacts of wildfire smoke on reproductive success in wild animals, a case study of domestic chickens exposed to smoke during a structural fire suggests that smoke inhalation

could reduce egg production (Morris *et al* 1986). Previous research has linked other types of air pollution to reduced hatching success and lower clutch size in birds (e.g. Eeva and Lehikoinen 1995), which suggests that wildfire smoke could also impair avian reproductive success. In addition, PM—a major component of wildfire smoke—dirty bird feathers, which can render them less attractive to potential mates (Griggio *et al* 2011) and interfere with other color-based signaling or camouflage.

6. Behavioral responses

Wildfire smoke can also trigger shifts in animal behavior, including movement and vocalization. Such behavioral changes could be due to underlying health effects (Erb *et al* 2018) or serve to limit exposure to airborne toxins (Singer *et al* 1989, Dickinson *et al* 2009, Liu *et al* 2021b). Some species rely on smoke as an early-warning signal that helps them to avoid wildfires (Engstrom 2010, Höcherl and Tautz 2015, Álvarez-Ruiz *et al* 2021) or prepare to conserve energy in a post-fire landscape (Geiser *et al* 2018), whereas others use smoke as a cue to navigate toward newly available resources in burned habitats (Schütz *et al* 1999, Klocke *et al* 2011, Milberg *et al* 2015). Animals could also change their behavior in response to alterations in the physical environment that result from smoke pollution (Cheyne 2008, Lee *et al* 2017), such as reduced visibility (Haider *et al* 2019) or cooler air temperatures (Robock 1991). Emerging evidence suggests that behavioral responses to wildfire smoke could ultimately influence the short- and long-term fitness of wildlife (Cheyne 2008, Erb *et al* 2018).

6.1. Effects of smoke on wildlife activity

Exposure to smoke can influence wildlife activity, including movement and vocalization. Case studies from veterinary medicine demonstrate that animals sometimes alter their behavior due to acute, adverse health effects associated with smoke inhalation; for example, pets and livestock exposed to smoke from structural fires can become agitated (Fitzgerald and Flood 2006, Marsh 2007, Weiss *et al* 2011, Guillaumin and Hopper 2013, Mendyk *et al* 2020), vocalize more (Fitzgerald and Flood 2006, Weiss *et al* 2011), reduce their activity (Simone-Freilicher 2008) or exhibit signs of neurological impairment, such as disorientation (Marsh 2007, Weiss *et al* 2011, Guillaumin and Hopper 2013). Researchers observed that pinecone lizards (*Tiliqua rugosa*) in captivity exhibited rapid tongue-flicking when exposed to smoke near their enclosure, a sign of agitation (Mendyk *et al* 2020). Animals in the wild could also alter their behavior in response to smoke pollution, possibly due to underlying health effects, as noted in one of the only studies to directly link wildfire smoke exposure to specific health outcomes for a wildlife species

(Erb *et al* 2018). In this study, researchers documented the daily activity of male Bornean orangutans (*Pongo pygmaeus wurmbii*) before, during, and after an extensive wildfire smoke event in Indonesia. They also collected urine samples opportunistically to test for ketones, a marker of fat catabolism associated with energy expenditure. The researchers found that orangutans rested more both during and after the smoke event. Furthermore, after the smoke event, orangutans traveled shorter distances and increased their caloric intake, but expended more energy (i.e. increased fat catabolism). Despite conserving energy and eating more food, orangutans still burned more calories than they consumed after an extended period of smoke exposure, which suggests that smoke inhalation negatively affected their energy budgets. The researchers postulated this could have been due to stress or a heightened immune response (Erb *et al* 2018).

In addition to movement, smoke can also influence animal vocalization. For example, a study of singing behavior in Bornean white-bearded gibbons (*Hylobates albibarbis*) in Indonesia found that gibbons sang less when it was smoky—during months when wildfire smoke led to unhealthy air quality, both the number of days gibbons sang and the length of singing bout decreased (Cheyne 2008). Changes in vocalization during wildfire smoke events may ultimately influence entire soundscapes (Lee *et al* 2017). An analysis of audio recordings collected in Singapore during a haze event brought on by wildfires showed that wildlife acoustic activity, as measured by four acoustic indices, was negatively correlated with smoke pollution. Although the mechanisms driving this response were beyond the scope of the study, its authors hypothesized that several factors could have contributed to a decrease in acoustic activity, including reduced vocalization, a shift in ecological activity outside the recording period, or mortality due to direct effects of smoke exposure or reduced foraging success. Acoustic activity was suppressed for months following the smoke event, illustrating that smoke could have long-term impacts on species and communities (Lee *et al* 2017).

6.2. Use of smoke as a cue

6.2.1. Fire avoidance behaviors

Wildlife across taxa, including insects, reptiles, and mammals, rely on smoke as a cue to engage in fire avoidance behaviors (Nimmo *et al* 2021). Insects may relocate after detecting smoke to evade fires. Researchers in Germany exposed European paper wasps (*Polistes dominula*) to biomass smoke and found that the insects increased their thorax temperature in response to this stressor (Höcherl and Tautz 2015). Many insects must warm up their thoraxes before flying; as such, the results of this experiment suggest that smoke prompts a pre-flight warm-up behavior in wasps that prepares them for a quick

escape from nearby fire (Höcherl and Tautz 2015). Researchers exposed ants in Kenya to smoke generated by burning elephant dung and found that two of the four study species evacuated in response to smoke, relocating up to 1800 m (Sensenig *et al* 2017). Of the two ant species that responded to smoke, the subordinate ant species (*Crematogaster nigriceps*) evacuated twice as quickly as the dominant competitor (*C. mimosae*). These results suggest that subordinate species may be more willing to adopt a colonist strategy following disturbance and therefore are better equipped to escape and survive wildfires (Sensenig *et al* 2017). However, some insects, such as the Cape honeybee (*Apis mellifera capensis*), may not attempt to evade fire and instead use smoke as a cue to retreat to protective nest structures, (Tribe *et al* 2017). Regardless of their fire avoidance strategy, smoke could compromise the ability of insects to escape fires by impairing flight performance (Liu *et al* 2021b). Liu *et al* (2021b) found that the duration, distance, and speed flown by painted lady butterflies (*Vanessa cardui* L.) decreased following exposure to smoke, which could adversely impact other insect behaviors as well, such as foraging and migration (Liu *et al* 2021b).

Studies of captive lizards suggest that smoke can also trigger fire avoidance behaviors in reptiles (Mendyk *et al* 2020, Álvarez-Ruiz *et al* 2021). For example, captive *Psammmodromus* lizards (*Psammmodromus algirus*) exhibited a variety of escape behaviors when exposed to smoke, including running and scratching at their terrariums (Álvarez-Ruiz *et al* 2021). Furthermore, lizards were more likely to increase their activity in response to smoke if they were captured in habitats prone to wildfires, regardless of an individual's previous experience with fire. These results indicate that in areas that experience frequent fires, selective pressure drives greater sensitivity to smoke, increasing the ability of local populations to detect and evade fires (Álvarez-Ruiz *et al* 2021).

Smoke can also prompt mammals to arouse from torpor, enabling them to escape fires (Scesny 2006, Layne 2009, Stawski *et al* 2015, Nowack *et al* 2016, Doty *et al* 2018). However, not all torpid mammals flee in response to smoke, or react quickly enough to survive; responses to fire stimuli are likely to vary by species, sex, and individual (Layne 2009, Nowack *et al* 2016, 2018). In addition, lower ambient temperatures slow torpor arousal following smoke exposure, which suggests that torpid mammals are less able to evade fires on colder days (Layne 2009, Nowack *et al* 2016, Doty *et al* 2018). Furthermore, animals that detect smoke and arouse from torpor at cooler temperatures might not return to steady-state torpor, which increases their energy expenditure (Doty *et al* 2018).

To avoid fires, small animals might seek shelter underground or in rock crevices (Engstrom 2010); however, burrowing may not always protect animals

from extreme heat and smoke. For example, Jordaan *et al* (2020) noted that fossorial species were well-represented in their samples of dead reptile specimens collected after prescribed burns in Tembe Elephant Park, South Africa. They hypothesized that cause of death was likely asphyxiation, gas intoxication, or heat-induced cardiac arrest, which suggests that even burrowing animals are susceptible to smoke inhalation during fires (Jordaan *et al* 2020).

6.2.2. Energy-saving behaviors

Some animals rely on smoke as an indicator of impending food scarcity, prompting them to engage in energy-saving strategies. Small mammals must maintain high metabolic rates, which is difficult after fires due to limited availability of food and water. Studies of captive small mammals show that smoke can increase use of torpor in some species, allowing animals to conserve energy and survive post-fire conditions (Geiser *et al* 2018). For example, exposure to smoke and a substrate of charcoal and ash increased duration of torpor in captive yellow-footed antechinuses (*Antechinus flavipes*) (Stawski *et al* 2017) and captive sugar gliders (*Petaurus breviceps*) (Nowack *et al* 2018). However, use of torpor after fires depends on food availability, and is likely to vary by species (Nowack *et al* 2018) and sex (Stawski *et al* 2017).

6.2.3. Resource availability

Pyrophilous insects (i.e. fire-associated species that benefit from resources available in post-fire landscapes) can use smoke as a cue to navigate toward fires, responding to thermal and/or olfactory signals (Schütz *et al* 1999, Klocke *et al* 2011, Álvarez *et al* 2015, Milberg *et al* 2015). Some are even known to swarm in smoke plumes, such as 'smoke flies' of the genera *Microsania* and *Hormopeza*, possibly to mate near burned trees where they deposit their eggs (Evans 1966, Snoddy and Tippins 1968, Sinclair and Cumming 2006). Schütz *et al* (1999) found that the antennae of fire bugs (*Melanophila acuminata*) respond to volatiles generated in the combustion of pine, suggesting that the smell of smoke helps some beetles detect and locate burned trees. Insects may also respond to visual cues of smoke plumes but results from experimental studies are ambiguous (Hinz *et al* 2018). An influx of aerial insects to burned habitats could enhance foraging opportunities for bats (Braun De Torrez *et al* 2018) and insectivorous birds; unlike small, quadrupedal mammals, bats might actually decrease their use of torpor after fires to take advantage of this increase in food availability (Geiser *et al* 2018). Raptors may also be attracted to smoke plumes, which could signal an opportunity to prey on insects and small mammals fleeing fire (Hovick *et al* 2017).

Whereas pyrophilous insects appear to rely on olfaction to locate burned areas, exposure to smoke can impair detection of other scents. Visscher *et al*

(1995) found that the antennae of honey bees (*Apis mellifera*) exposed to smoke were less responsive to both a floral odor and alarm pheromones. This suggests that detection of smoke could have short-term impacts on foraging and defensive behaviors in insects (Visscher *et al* 1995).

7. Effects on wildlife habitat

Several studies have sought to quantify potential exposure to smoke for species that use specific habitats, although they did not evaluate the impact of smoke on animal health or behavior (e.g. O'Brien *et al* 2006, Bova *et al* 2011, Thompson and Purcell 2016). O'Brien *et al* (2006) measured air quality in a hole that could be used as a nesting cavity by Cuban parrots (*Amazona leucocephala*) during a prescribed burn. They found that as flames passed the cavity entrance, smoke accumulated inside for about 20 min, and CO₂ concentrations sharply increased to 2092 parts per million (ppm). O'Brien *et al* (2006) described these conditions as 'benign,' but pointed to the lack of research to date on inhalation exposure to air pollution in birds. Thompson and Purcell (2016) took a similar approach to assess the vulnerability of fishers (*Pekania pennanti*) to smoke during prescribed burns, measuring the concentration of CO in tree cavities that were previously used or could be used as den sites. They found that whereas levels of CO during burns might not be harmful to adult fishers, they are hazardous to developing fetuses and newborns. Dickinson *et al* (2010) used air quality data collected during prescribed burns to determine if smoke exposure endangered Indiana bats (*Myotis sodalis*). They determined that CO concentrations during low-intensity prescribed burns were unlikely to be dangerous but suggested that bats that roost in foliage or under bark could be more vulnerable to gas intoxication during fires than bats that roost in cavities or crevices where concentrations of poisonous gases are lower (Dickinson *et al* 2010). Dickinson *et al* (2009) found that CO concentrations during a prescribed burn did not exceed the threshold at which incapacitation of bats would likely occur; however, they noted that bats that roost closer to the ground would be more at risk of exposure to elevated concentrations of toxic gases. Cave-roosting bats in particular could be in danger of smoke inhalation because caves could fill with smoke before bats have a chance to escape (Dickinson *et al* 2009, Geiser *et al* 2018). These findings illustrate that exposure to air pollution during wildfires varies widely, depending on the specific habitats used by wildlife.

Although we primarily focused our review on the direct effects of wildfire smoke on the health and behavior of wildlife, it is worth considering how smoke pollution indirectly affects wildlife by driving short-term changes in habitat. Smoke limits visibility

(Haider *et al* 2019) and cools air temperatures (Robcock 1991)—changes in the physical environment that could influence the health and behavior of wild animals. While vegetative succession following wildfires generates habitat for a wide variety of fauna (Smith 2000, Jones and Tingley 2021, Stillman *et al* 2021), smoke from wildfires also has immediate impacts on plant growth. For example, wildfire smoke triggers seed germination in plants that grow in fire-prone habitats (Van Staden *et al* 2000). Smoke can also positively or negatively influence plant productivity, depending on the extent to which aerosols absorb or scatter sunlight, as well as ambient concentrations of co-pollutants that damage plants (Hemes *et al* 2020). Furthermore, pollutants in smoke can deposit on soils or vegetation, which can indirectly affect wildlife (Phaneuf *et al* 1995). Plants can absorb toxins in smoke that, if consumed, could compromise the health of herbivorous animals (Tan *et al* 2018). Wildfire smoke also affects aquatic habitats (Jaafar and Loh 2014). Smoke limits how far light penetrates underwater, which can influence the vertical distribution of microorganisms (Urmy *et al* 2016) or primary productivity of coral reefs (Risk *et al* 2003). Atmospheric deposition of aerosols in smoke can also degrade water quality (Phaneuf *et al* 1995, Earl and Blinn 2003, Corbin 2012), which can in turn alter the composition of macroinvertebrate communities (Earl and Blinn 2003) and negatively affect the health of fish or other water-breathing animals (Gresswell 1999, Gonino *et al* 2019).

8. Discussion

We found that the available literature clearly demonstrates that wildfire smoke has direct and indirect effects on wildlife, including terrestrial and aquatic species (figure 2, table 1). Smoke inhalation contributes to adverse acute and chronic health outcomes in animals (Venn-Watson *et al* 2013, Black *et al* 2017), including CO poisoning, respiratory distress, neurological impairment, respiratory and cardiovascular disease, oxidative stress, and immunosuppression. These health effects could contribute to changes in wildlife activity, including movement (Erb *et al* 2018) and vocalization (Cheyne 2008). Animal behavior could also be influenced by changes in the physical environment that co-occur with smoke pollution, such as reduced sunlight or cooler air and water temperatures. Finally, many species that depend on fire-prone habitats have evolved to use smoke as a cue to engage in fire avoidance (Nimmo *et al* 2021) or energy-conserving behaviors (Geiser *et al* 2018) or perceive smoke as a signal of resource availability (Schütz *et al* 1999). Both the immediate, direct effects of wildfire smoke on the health and behavior of animals and the long-term impacts of smoke on wildlife habitat could ultimately influence the demography of wildlife populations (figure 2).

However, our review also demonstrates that a limited number of studies have investigated—or even considered—the impacts of wildfire smoke on wildlife (table 1). For decades, naturalists have observed how wildlife respond to smoke from wildfires (e.g. Komarek 1969, Braithwaite and Estbergs 1987) and noted the vulnerability of animals exposed to smoke during wildfires or prescribed burns (e.g. Geluso *et al* 1986). Yet, we found few peer-reviewed studies that directly investigated health outcomes or behavioral responses in wildlife associated with inhalation or detection of biomass smoke. After conducting a comprehensive search, we only identified 41 relevant studies, several of which did not explicitly test for an effect of smoke on animals and, instead, only considered how the presence of smoke could explain the responses observed (e.g. Cahill and Walker 2000, Jordaan *et al* 2020). Furthermore, research to date is unequally distributed across taxa (figure 5) and world regions (figure 4), with most studies conducted on mammals (39%) or insects (29%) in North America (37%), followed by Europe (17%) and Australia (15%) (figure 4). Our keyword searches were conducted in English, which could have influenced the geographic distribution of the studies we reviewed.

Researchers have used a variety of methods to investigate the impacts of smoke on wildlife, which makes it challenging to compare findings across existing studies. Monitoring animals before, during, and after wildfires or prescribed burns (e.g. Dickinson *et al* 2009, Jordaan *et al* 2020) allows researchers to study how free-living animals respond to the onset and progression of a smoke event and enables direct inference about the impacts of biomass smoke on wildlife. However, such studies are difficult to plan, tend to be logistically complicated, and can jeopardize the health and safety of the research team (Erb *et al* 2018). Alternatively, researchers have studied how animals respond to smoke generated in a controlled environment, such as a laboratory or outdoor enclosure (e.g. Nowack *et al* 2018, Tan *et al* 2018). This approach may be easier to implement because it does not require coordination with a fire management team or planning fieldwork around unpredictable wildfires. Controlled conditions also allow researchers to investigate specific health outcomes and behaviors in animals that would be difficult to assess in the wild. However, despite attempts to simulate biomass smoke that is representative of what animals would be exposed to during a wildfire smoke event in their natural habitat (e.g. Layne 2009), controlled exposure experiments cannot reproduce the exact air quality and visibility conditions animals are likely to encounter in the wild. In addition, controlled studies are often limited to smaller species that are relatively easy to capture (e.g. insects, small mammals), and captive animals could exhibit behavioral changes during experiments that arise from confinement and should not be attributed to air pollution

exposure (Sterner 1993a, 1993b). In sum, the experience of smoke exposure for animals is likely to be vastly different between *in situ* and controlled studies, which makes it difficult to compare their findings.

Another limiting factor in connecting findings from existing research is the lack of robust air pollution measurements during field studies and experiments. Primary components of wildfire smoke include water vapor, CO₂, CO, PM, volatile organic compounds, nitrogen oxides, and hazardous air pollutants, such as acrolein, benzene, and formaldehyde (De Vos *et al* 2009). However, the exact biological (Kobziar and Thompson 2020) and chemical composition of smoke—and therefore its toxicity (Franzi *et al* 2011, Kim *et al* 2019)—is determined by fuel source (e.g. peat, oak, eucalyptus, etc), combustion conditions (e.g. flaming, smoldering) (Hargrove *et al* 2019, Kim *et al* 2019), weather, topography, and long-range transport (Jalava *et al* 2006). Without measuring the concentrations of reactive gases and aerosols animals are exposed to, it is impossible to construct dose-response relationships for specific health outcomes (Jaafar and Loh 2014, Sanderfoot and Holloway 2017). Furthermore, the composition of smoke could affect the visual and olfactory cues that elicit behavioral responses in wildlife. For example, Komarek observed that the behavior of Carolina grasshoppers (*Dissotera carolina*) varied depending on smoke conditions—when exposed to dense, white smoke, the grasshoppers ceased all activity, yet when exposed to black smoke, grasshoppers exhibited fire avoidance behaviors. To facilitate comparisons and meta-analyses of findings across studies, it is critical that future investigations move beyond qualitative descriptions of smoke and actually quantify exposure by measuring concentrations of specific gases and aerosols (Engstrom 2010, Sanderfoot and Holloway 2017).

More research is needed to identify which taxa and species are most threatened by wildfire smoke and determine how their vulnerability is influenced by physiology, behavior, and life-history strategy. It is well-established that birds are more sensitive to air pollution than other taxa (Brown *et al* 1997) and therefore more likely to be susceptible than other animals to direct health effects associated with smoke inhalation. Cetaceans, like birds, exchange most of the air in their lungs with each breath, which might put them at greater risk than other mammals of experiencing adverse health outcomes during smoke events (Venn-Watson *et al* 2013). Animal behavior and habitat use within and across species can also influence smoke exposure, thereby mediating risks. For example, bats that roost at higher heights are more protected from toxic gases during prescribed burns, and bats in torpor are less exposed to airborne toxins than they would be if they were active (Dickinson *et al* 2009). Furthermore, overlap between the timing of smoke pollution episodes and life-history events

likely contributes to species-specific vulnerability to wildfire smoke. For instance, birds attending to chicks (Cahill and Walker 2000) or bats caring for pups (Dickinson *et al* 2009) are likely more threatened by heat and smoke during fires than adults not tending to offspring, and fossorial reptiles are in greater danger when they come to the surface to feed or seek a mate (Jordaan *et al* 2020). Comparing species distributions with spatial and temporal trends in air pollution could help wildlife managers determine if smoke should be considered alongside other threats, such as habitat degradation, when developing wildlife conservation plans.

Animals have evolved alongside wildfires for thousands of years, but megafires driven by climate change are generating novel disturbance stressors, such as large-scale smoke events, that could exert selective pressure on wildlife (Nimmo *et al* 2021). The fire regimes species are adapted to are changing, and the traits that allow them to co-exist with fire and smoke may not be sufficient in the age of megafires (Nimmo *et al* 2021). For example, typical fire avoidance behaviors might not be sufficient to protect wildlife from injury or morbidity during more severe, fast-moving fires (Engstrom 2010, Nimmo *et al* 2021), and even animals that are not in the direct path of fires can still be exposed to dangerous levels of wildfire smoke (Erb *et al* 2018) (figure 1). As climate change intensifies smoke pollution, more animals are at risk of acute and chronic health outcomes associated with smoke inhalation, which could lower survival and reproductive success (figure 2). Over time, animals may adapt behavioral responses to detect hazardous air quality and limit their exposure to toxic gases and aerosols; however it is also possible that during large-scale smoke events, even well-adapted species may not find any refuge. Fire-adapted species might respond to visual and olfactory cues during large-scale smoke events even when fires are far away, which could have cascading impacts on wildlife communities. Pyrophilous species that rely on smoke as a cue to navigate toward burned areas may become disoriented during large-scale smoke events that occur hundreds of miles from fires, which could lead to reduced fitness and increased vulnerability to predation. Other species that use visual and olfactory cues from smoke to initiate fire-avoidance behaviors may do so at the expense of unnecessary energy expenditure when a fire is not an immediate threat (Dickinson *et al* 2009). Animals that exhibit escape behaviors when it is smoky could also be more vulnerable to predation; natural history observations suggest that raptors hunt insects and small mammals at the edge of fires (Braithwaite and Estbergs 1987) and may be attracted to smoke plumes as a signal of prey availability (Hovick *et al* 2017). Additionally, prey species often use scent cues to detect and avoid predators (Blumstein *et al* 2002); large-scale smoke events may mask olfactory signals and affect the ability of

prey to detect predators, further increasing their predation risk. Shifts in predator-prey interactions during smoke events could ultimately influence wildlife populations and community dynamics (figure 2).

Earlier and more prolonged wildfire seasons might pose novel threats to species that now encounter wildfire smoke during a critical stage of their life cycle, such as reproduction or migration. For example, the breeding phenology of songbirds may increasingly overlap with the smoke season, which could adversely impact songbirds in a reproductive state. Individuals that breed earlier, thereby avoiding reproductive activities during peak smoke season, could have higher reproductive success. This could lead to the evolution of traits, such as more synchronous or asynchronous breeding (Iwasa and Levin 1995), depending on the risks and benefits associated with the timing of breeding in relation to the threats posed by smoke events. Similarly, climate change is thought to be driving earlier breeding periods in many songbirds (Hällfors *et al* 2020), a trend that could be reinforced as smoke pollution worsens air quality during the summer months. Although wildfire smoke could function as an ecological disturbance that forces some species to adapt their life-history strategies, it is unlikely that all species threatened by smoke pollution will be able to adapt their phenology to match changing environmental conditions (Both and Visser 2001). More research is needed to assess how the frequency and timing of massive smoke events affects species adaptations to fire across different fire regimes.

We did not find any studies that explicitly linked wildfire smoke to demographic rates in wildlife populations (figure 2); however, emerging evidence suggests that the impact of large-scale smoke events on survival of wildlife species could be substantial. Yang *et al* (2021) found that air quality contributed to the spatial distribution of bird deaths in a mass avian mortality event in the Western United States in late summer 2020 (Yang *et al* 2021). This was not the first study to suggest that air pollution has negative demographic consequences for bird populations—a recent study also found that reductions in ozone (O_3) pollution in the United States prevented the loss of more than one billion birds (Liang *et al* 2020). Although O_3 is not a component of wildfire smoke, concentrations of O_3 can be higher on smoky days (Brey and Fischer 2016). Smoke inhalation has also been implicated in the death of insects (Tan *et al* 2018), reptiles (Jordaan *et al* 2020), and mammals (Singer *et al* 1989). Taken together, these findings emphasize the need to consider if and how wildfire smoke affects demographic rates in wildlife populations (figure 2).

Shifts in animal behavior during wildfire smoke events might ultimately affect the probability of observing wildlife, which has important implications for wildlife research and monitoring. For example,

animals that use smoke as cue to engage in fire-avoidance (e.g. burrowing) or energy-conserving behaviors (e.g. torpor) could be more difficult to observe during wildfire smoke events (Geiser *et al* 2018). Sanderfoot and Gardner (2021) investigated how wildfire smoke affected detection of 71 common bird species in Washington, United States and found that particle pollution during the wildfire season influenced the probability of observing 37% of study species—as $PM_{2.5}$ increased, 16 species were less likely to be observed and 10 species were more likely to be observed. These results suggest that species-specific behavioral responses to wildfire smoke ultimately influence researchers' ability to detect wildlife. Failing to account for how smoke affects observations of wildlife could bias inference about wildlife activity and population demographics (Sanderfoot and Gardner 2021).

To develop effective policy for wildlife conservation, we must rapidly expand our understanding of the effects of wildfire smoke on wildlife. We believe that ecologists and wildlife managers are well-positioned to tackle this challenge by leveraging pre-existing resources and infrastructure to address critical knowledge gaps. For example, camera traps, GPS tags, and acoustic recorders are often deployed in fire-prone areas as part of long-term monitoring projects, many of which are likely to overlap with the wildfire season (figure 6). Data collected by these instruments could be paired with long-term air quality monitoring data to investigate how wildfire smoke drives shifts in observations of wildlife (e.g. Lee *et al* 2017) or explore specific behavioral responses to smoke pollution, such as movement and vocalization. This equipment could also be deployed to monitor wildlife before, during, and after prescribed burns. Studies of marked individuals pre- and post-fire could also provide insight into the direct effects of fires on demographic rates (Engstrom 2010). In addition, retrospective analyses of health records of captive animals housed in outdoor enclosures at zoos and aquariums could be used to assess how sudden, extreme smoke events influence the health of wildlife across a wide variety of taxa (Venn-Watson *et al* 2013, Black *et al* 2017). Finally, data from existing large-scale databases, such as the North American Breeding Bird Survey, eBird, eMammal, iNaturalist, Movebank, and Map of Life, could be used in correlative studies to link smoke exposure to observations of wildlife.

To facilitate comparison of future studies, we recommend that researchers at minimum (1) identify the primary type of vegetation burned during prescribed burns or wildfires, or alternatively the substrate burned to generate smoke in controlled experiments and (2) incorporate measurements of $PM_{2.5}$ during exposure. $PM_{2.5}$ is often the focus of epidemiological investigations into the impacts of wildfire smoke on public health (McClure and Jaffe 2018,



Figure 6. Photo captures of wildlife in eastern Washington during the 2018 and 2020 wildfire seasons. (A) Smoke settles in the valley behind a male white-tailed deer (*Odocoileus virginianus*). (B) A group of mule deer (*Odocoileus hemionus*) navigate through thick smoke. (C) Smoke obscures the view over a ridge as a coyote (*Canis latrans*) carries its prey. (D) A wild turkey (*Meleagris gallopavo*) forages through haze. All photos were taken by camera traps deployed as part of the Washington Predator-Prey Project, a collaboration between the Washington Department of Fish & Wildlife and the University of Washington.

Aguilera *et al* 2021, Liu *et al* 2021a); as such, there is a multitude of resources available to characterize particle pollution during smoke events or controlled experiments, including data from ground-based air pollution sensors, air quality models, and satellite instruments (Diao *et al* 2019). Data from ground-based air quality monitors are considered the ‘gold standard’ for estimating exposure to air pollution (Diao *et al* 2019) and are often available to the public—for example, the U.S. Environmental Protection Agency provides data on air pollution across the United States, Puerto Rico, and the U.S. Virgin Islands on the web at www.epa.gov/outdoor-air-quality-data. If data from ground-based monitors is not available at relevant spatial and temporal scales, atmospheric scientists might rely on statistical interpolation or Land-Use Regression (LUR) models to build $PM_{2.5}$ exposure estimates (Jerrett *et al* 2005, Zou *et al* 2009). Alternatively, output from chemical transport models (CTMs) can be used in retrospective analyses and forecasting (Zou *et al* 2009). CTMs simulate air pollution by modeling transformation and transport of emissions (Jerrett *et al* 2005); examples of CTMs include the Community Model for Air Quality (CMAQ) and the Weather Research and Forecasting Model—Chemistry (WRF-Chem). Satellite data are also increasingly used to build $PM_{2.5}$ exposure estimates, although measurements from instruments on polar-orbiting satellites are only available once or

twice a day (West *et al* 2016, Diao *et al* 2019). Some of these approaches could be readily implemented with minimal training (Diao *et al* 2019), but others require technical knowledge. Regardless, careful consideration of the location and behavior of the target population is essential in determining exposure to specific pollutants. We recommend that ecologists studying the impacts of wildfire smoke on wildlife collaborate with atmospheric scientists to build $PM_{2.5}$ exposure estimates using the best available tools.

9. Conclusion

The frequency and severity of large-scale smoke events are increasing as climate change intensifies global wildfire activity (Westerling *et al* 2011, Abatzoglou and Williams 2016), posing new risks to wildlife (Nimmo *et al* 2021). Despite substantial research linking wildfire smoke to adverse health outcomes in humans, few studies have investigated the physiological and behavioral responses to wildfire smoke in animals (figure 4, table 1) (Erb *et al* 2018, Geiser *et al* 2018). However, research to date suggests that smoke inhalation contributes to negative acute and chronic health outcomes in a diversity of air-breathing animals, including mammals, birds, reptiles, and insects (figure 2, table 1). Detection of smoke triggers fire-avoidance and/or energy-conserving behaviors in some wildlife species, and

some species use smoke as a cue to navigate toward fires to take advantage of resources available in burned habitats (figure 2). However, even species that are adapted to fire-prone habitats are at risk of health outcomes linked to smoke inhalation, and it is unclear how they will cope with more extreme smoke pollution episodes. To inform the study and conservation of wildlife in a rapidly warming world, it is imperative that we expand our knowledge of wildfire smoke impacts on wildlife. Bridging the divide between the disciplines of ecology and atmospheric science will be essential in meeting this goal. We strongly recommend that scientists and managers build interdisciplinary partnerships and leverage existing data sets, infrastructure, and tools to quickly and efficiently address knowledge gaps and tackle research questions of global importance.

Data availability statement

No new data were created or analysed in this study.

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Author contributions

O V S: conceptualization, methodology, investigation, writing—original draft, writing—review & editing, visualization, project administration, funding acquisition; S B B, J L B, R L E, S J G, and K S: methodology, investigation, writing—review & editing, visualization; B G: methodology, investigation, writing—review & editing, visualization, funding acquisition.

Conflict of interest

We have no conflicts of interest to declare.

Appendix

We refined results from our initial keyword search in Web of Science to include only articles from categories deemed relevant to our literature review. We considered the top 100 Web of Science categories for each keyword search. Articles from the following categories were included from each keyword search.

fire* AND smoke*

Environmental Sciences, Public Environmental Occupational Health, Forestry, Plant Sciences, Ecology, Geosciences Multidisciplinary, Toxicology, Medicine General Internal, Multidisciplinary Sciences, Remote Sensing, Respiratory System, Environmental Studies, Oceanography, Water Resources, Biodiversity Conservation, Cardiac Cardiovascular Systems, Mathematics Interdisciplinary Applications, Biochemistry Molecular Biology, Computer Science Interdisciplinary Applications, Agriculture Multidisciplinary, Oncology, Biotechnology Applied Microbiology, Veterinary Sciences, Agronomy, Physiology, Biology, Infectious Diseases, Allergy, Genetics Heredity, Immunology

wildfire* AND smoke*

Environmental Sciences, Public Environmental Occupational Health, Forestry, Geosciences Multidisciplinary, Remote Sensing, Toxicology, Ecology, Multidisciplinary Sciences, Environmental Studies, Respiratory System, Plant Sciences, Water Resources, Oceanography, Medicine General Internal, Biodiversity Conservation, Biochemistry Molecular Biology, Geography, Agriculture Multidisciplinary, Allergy, Biology, Cardiac Cardiovascular Systems, Immunology, Marine Freshwater Biology, Agronomy, Cell Biology, Communication, Computer Science Interdisciplinary Applications, Development Studies, Genetics Heredity, Mathematics Interdisciplinary Applications, Physiology, Statistics Probability, Area Studies, Behavioral Sciences, Biotechnology Applied Microbiology, Developmental Biology, Entomology, Evolutionary Biology, Horticulture, Limnology, Mathematical Computational Biology

ORCID iDs

O V Sanderfoot  <https://orcid.org/0000-0003-1729-3826>

S B Bassing  <https://orcid.org/0000-0001-6295-6372>

S J Gillman  <https://orcid.org/0000-0002-9263-0522>

B Gardner  <https://orcid.org/0000-0002-9624-2981>

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Rate of tree carbon accumulation increases continuously with tree size

N. L. Stephenson¹, A. J. Das¹, R. Condit², S. E. Russo³, P. J. Baker⁴, N. G. Beckman^{3†}, D. A. Coomes⁵, E. R. Lines⁶, W. K. Morris⁷, N. Rüger^{2,8†}, E. Álvarez⁹, C. Blundo¹⁰, S. Bunyavejchewin¹¹, G. Chuyong¹², S. J. Davies¹³, Á. Duque¹⁴, C. N. Ewango¹⁵, O. Flores¹⁶, J. F. Franklin¹⁷, H. R. Grau¹⁰, Z. Hao¹⁸, M. E. Harmon¹⁹, S. P. Hubbell^{2,20}, D. Kenfack¹³, Y. Lin²¹, J.-R. Makana¹⁵, A. Malizia¹⁰, L. R. Malizia²², R. J. Pabst¹⁹, N. Pongpattananurak²³, S.-H. Su²⁴, I.-F. Sun²⁵, S. Tan²⁶, D. Thomas²⁷, P. J. van Mantgem²⁸, X. Wang¹⁸, S. K. Wiser²⁹ & M. A. Zavala³⁰

Forests are major components of the global carbon cycle, providing substantial feedback to atmospheric greenhouse gas concentrations¹. Our ability to understand and predict changes in the forest carbon cycle—particularly net primary productivity and carbon storage—increasingly relies on models that represent biological processes across several scales of biological organization, from tree leaves to forest stands^{2,3}. Yet, despite advances in our understanding of productivity at the scales of leaves and stands, no consensus exists about the nature of productivity at the scale of the individual tree^{4–7}, in part because we lack a broad empirical assessment of whether rates of absolute tree mass growth (and thus carbon accumulation) decrease, remain constant, or increase as trees increase in size and age. Here we present a global analysis of 403 tropical and temperate tree species, showing that for most species mass growth rate increases continuously with tree size. Thus, large, old trees do not act simply as senescent carbon reservoirs but actively fix large amounts of carbon compared to smaller trees; at the extreme, a single big tree can add the same amount of carbon to the forest within a year as is contained in an entire mid-sized tree. The apparent paradoxes of individual tree growth increasing with tree size despite declining leaf-level^{8–10} and stand-level¹⁰ productivity can be explained, respectively, by increases in a tree's total leaf area that outpace declines in productivity per unit of leaf area and, among other factors, age-related reductions in population density. Our results resolve conflicting assumptions about the nature of tree growth, inform efforts to understand and model forest carbon dynamics, and have additional implications for theories of resource allocation¹¹ and plant senescence¹².

A widely held assumption is that after an initial period of increasing growth, the mass growth rate of individual trees declines with increasing tree size^{4,5,13–16}. Although the results of a few single-species studies have been consistent with this assumption¹⁵, the bulk of evidence cited in support of declining growth is not based on measurements of individual tree mass growth. Instead, much of the cited evidence documents either the well-known age-related decline in net primary productivity (hereafter 'productivity') of even-aged forest stands¹⁰ (in which the trees are all of a similar age) or size-related declines in the rate of mass gain per

unit leaf area (or unit leaf mass)^{8–10}, with the implicit assumption that declines at these scales must also apply at the scale of the individual tree. Declining tree growth is also sometimes inferred from life-history theory to be a necessary corollary of increasing resource allocation to reproduction^{11,16}. On the other hand, metabolic scaling theory predicts that mass growth rate should increase continuously with tree size⁶, and this prediction has also received empirical support from a few site-specific studies^{6,7}. Thus, we are confronted with two conflicting generalizations about the fundamental nature of tree growth, but lack a global assessment that would allow us to distinguish clearly between them.

To fill this gap, we conducted a global analysis in which we directly estimated mass growth rates from repeated measurements of 673,046 trees belonging to 403 tropical, subtropical and temperate tree species, spanning every forested continent. Tree growth rate was modelled as a function of log(tree mass) using piecewise regression, where the independent variable was divided into one to four bins. Conjoined line segments were fitted across the bins (Fig. 1).

For all continents, aboveground tree mass growth rates (and, hence, rates of carbon gain) for most species increased continuously with tree mass (size) (Fig. 2). The rate of mass gain increased with tree mass in each model bin for 87% of species, and increased in the bin that included the largest trees for 97% of species; the majority of increases were statistically significant (Table 1, Extended Data Fig. 1 and Supplementary Table 1). Even when we restricted our analysis to species achieving the largest sizes (maximum trunk diameter > 100 cm; 33% of species), 94% had increasing mass growth rates in the bin that included the largest trees. We found no clear taxonomic or geographic patterns among the 3% of species with declining growth rates in their largest trees, although the small number of these species (thirteen) hampers inference. Declining species included both angiosperms and gymnosperms in seven of the 76 families in our study; most of the seven families had only one or two declining species and no family was dominated by declining species (Supplementary Table 1).

When we log-transformed mass growth rate in addition to tree mass, the resulting model fits were generally linear, as predicted by metabolic scaling theory⁶ (Extended Data Fig. 2). Similar to the results of our main

¹US Geological Survey, Western Ecological Research Center, Three Rivers, California 93271, USA. ²Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Republic of Panama. ³School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588, USA. ⁴Department of Forest and Ecosystem Science, University of Melbourne, Victoria 3121, Australia. ⁵Department of Plant Sciences, University of Cambridge, Cambridge CB2 3EA, UK. ⁶Department of Geography, University College London, London WC1E 6BT, UK. ⁷School of Botany, University of Melbourne, Victoria 3010, Australia. ⁸Spezielle Botanik und Funktionelle Biodiversität, Universität Leipzig, 04103 Leipzig, Germany. ⁹Jardín Botánico de Medellín, Calle 73, No. 51D-14, Medellín, Colombia. ¹⁰Instituto de Ecología Regional, Universidad Nacional de Tucumán, 4107 Yerba Buena, Tucumán, Argentina. ¹¹Research Office, Department of National Parks, Wildlife and Plant Conservation, Bangkok 10900, Thailand. ¹²Department of Botany and Plant Physiology, Buea, Southwest Province, Cameroon. ¹³Smithsonian Institution Global Earth Observatory—Center for Tropical Forest Science, Smithsonian Institution, PO Box 37012, Washington, DC 20013, USA. ¹⁴Universidad Nacional de Colombia, Departamento de Ciencias Forestales, Medellín, Colombia. ¹⁵Wildlife Conservation Society, Kinshasa/Gombe, Democratic Republic of the Congo. ¹⁶Unité Mixte de Recherche—Peuplements Végétaux et Bioagresseurs en Milieu Tropical, Université de la Réunion/CIRAD, 97410 Saint Pierre, France. ¹⁷School of Environmental and Forest Sciences, University of Washington, Seattle, Washington 98195, USA. ¹⁸State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, China. ¹⁹Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331, USA. ²⁰Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California 90095, USA. ²¹Department of Life Science, Tunghai University, Taichung City 40704, Taiwan. ²²Facultad de Ciencias Agrarias, Universidad Nacional de Jujuy, 4600 San Salvador de Jujuy, Argentina. ²³Faculty of Forestry, Kasetsart University, Chatuchak Bangkok 10900, Thailand. ²⁴Taiwan Forestry Research Institute, Taipei 10066, Taiwan. ²⁵Department of Natural Resources and Environmental Studies, National Dong Hwa University, Hualien 97401, Taiwan. ²⁶Sarawak Forestry Department, Kuching, Sarawak 93660, Malaysia. ²⁷Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331, USA. ²⁸US Geological Survey, Western Ecological Research Center, Arcata, California 95521, USA. ²⁹Landcare Research, PO Box 40, Lincoln 7640, New Zealand. ³⁰Forest Ecology and Restoration Group, Department of Life Sciences, University of Alcalá, Alcalá de Henares, 28805 Madrid, Spain. †Present addresses: Mathematical Biosciences Institute, Ohio State University, Columbus, Ohio 43210, USA (N.G.B.); German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, 04103 Leipzig, Germany (N.R.).

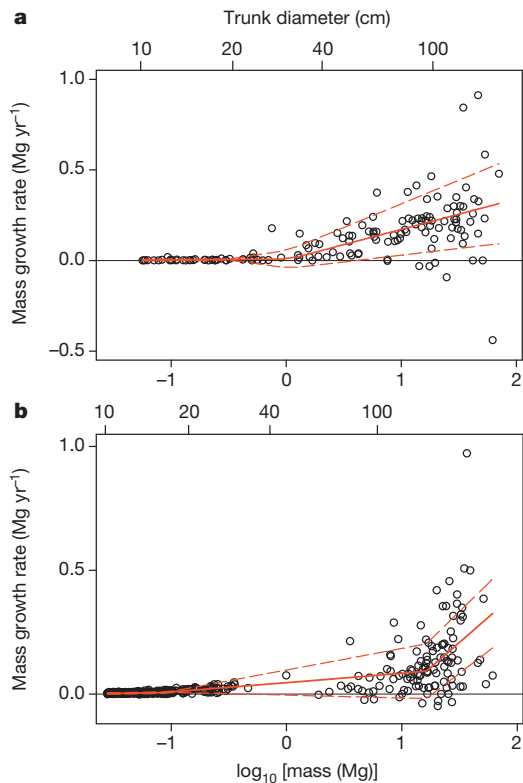


Figure 1 | Example model fits for tree mass growth rates. The species shown are the angiosperm species (*Lecomtedoxa klaineana*, Cameroon, 142 trees) (a) and gymnosperm species (*Picea sitchensis*, USA, 409 trees) (b) in our data set that had the most massive trees (defined as those with the greatest cumulative aboveground dry mass in their five most massive trees). Each point represents a single tree; the solid red lines represent best fits selected by our model; and the dashed red lines indicate one standard deviation around the predicted values.

analysis using untransformed growth, of the 381 log-transformed species analysed (see Methods), the log-transformed growth rate increased in the bin containing the largest trees for 96% of species.

In absolute terms, trees 100 cm in trunk diameter typically add from 10 kg to 200 kg of aboveground dry mass each year (depending on species), averaging 103 kg per year. This is nearly three times the rate for trees of the same species at 50 cm in diameter, and is the mass equivalent to adding an entirely new tree of 10–20 cm in diameter to the forest each year. Our findings further indicate that the extraordinary growth recently reported in an intensive study of large *Eucalyptus regnans* and *Sequoia sempervirens*⁷, which included some of the world's most massive individual trees, is not a phenomenon limited to a few unusual species. Rather, rapid growth in giant trees is the global norm, and can exceed 600 kg per year in the largest individuals (Fig. 3).

Our data set included many natural and unmanaged forests in which the growth of smaller trees was probably reduced by asymmetric competition with larger trees. To explore the effects of competition, we calculated mass growth rates for 41 North American and European species that had published equations for diameter growth rate in the absence of competition. We found that, even in the absence of competition, 85% of the species had mass growth rates that increased continuously with tree size (Extended Data Fig. 3), with growth curves closely resembling those in Fig. 2. Thus, our finding of increasing growth not only has broad generality across species, continents and forest biomes (tropical, subtropical and temperate), it appears to hold regardless of competitive environment.

Importantly, our finding of continuously increasing growth is compatible with the two classes of observations most often cited as evidence of declining, rather than increasing, individual tree growth: with increasing tree size and age, productivity usually declines at the scales of both tree organs (leaves) and tree populations (even-aged forest stands).

First, although growth efficiency (tree mass growth per unit leaf area or leaf mass) often declines with increasing tree size^{8–10}, empirical observations and metabolic scaling theory both indicate that, on average, total tree leaf mass increases as the square of trunk diameter^{17,18}. A typical tree that experiences a tenfold increase in diameter will therefore undergo a roughly 100-fold increase in total leaf mass and a 50–100-fold

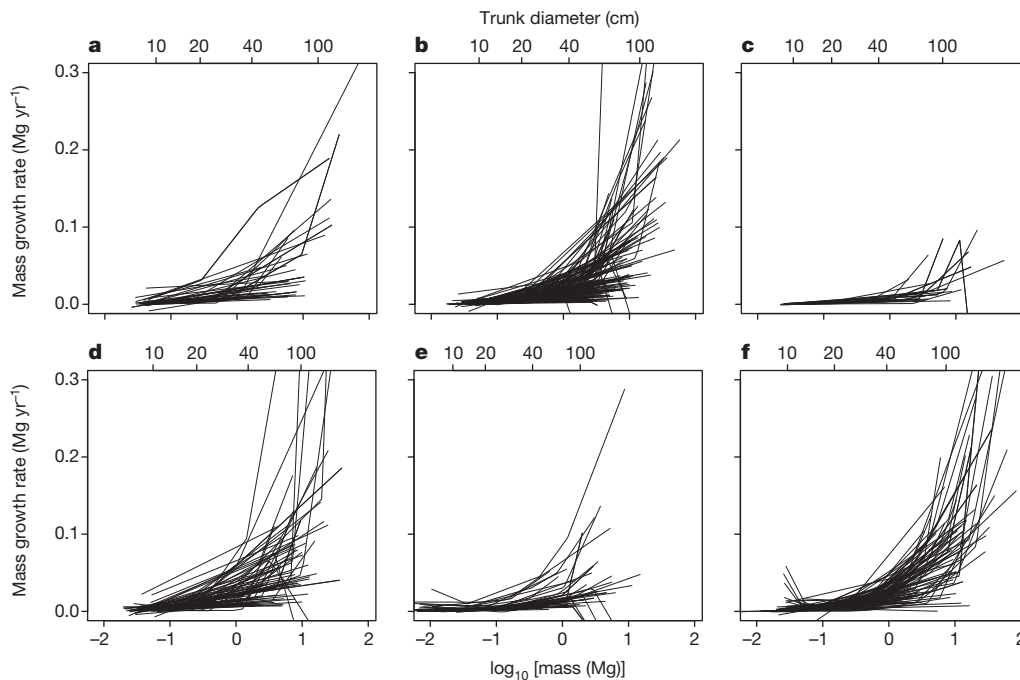


Figure 2 | Aboveground mass growth rates for the 403 tree species, by continent. a, Africa (Cameroon, Democratic Republic of the Congo); b, Asia (China, Malaysia, Taiwan, Thailand); c, Australasia (New Zealand); d, Central and South America (Argentina, Colombia, Panama); e, Europe (Spain); and

f, North America (USA). Numbers of trees, numbers of species and percentages with increasing growth are given in Table 1. Trunk diameters are approximate values for reference, based on the average diameters of trees of a given mass.

Table 1 | Sample sizes and tree growth trends by continent

Continent	Number of trees	Number of species	Percentage of species with increasing mass growth rate in the largest trees (percentage significant at $P \leq 0.05$)
Africa	15,366	37	100.0 (86.5)
Asia	43,690	136	96.3 (89.0)
Australasia	45,418	22	95.5 (95.5)
Central and South America	18,530	77	97.4 (92.2)
Europe	439,889	42	90.5 (78.6)
North America	110,153	89	98.9 (94.4)
Total	673,046	403	96.8 (89.8)

The largest trees are those in the last bin fitted by the model. Countries are listed in the legend for Fig. 2.

increase in total leaf area (depending on size-related increases in leaf mass per unit leaf area^{19,20}). Parallel changes in growth efficiency can range from a modest increase (such as in stands where small trees are suppressed by large trees)²¹ to as much as a tenfold decline²², with most changes falling in between^{8,9,19,22}. At one extreme, the net effect of a low (50-fold) increase in leaf area combined with a large (tenfold) decline in growth efficiency would still yield a fivefold increase in individual tree mass growth rate; the opposite extreme would yield roughly a 100-fold increase. Our calculated 52-fold greater average mass growth rate of trees 100 cm in diameter compared to those 10 cm in diameter falls within this range. Thus, although growth efficiency often declines with increasing tree size, increases in a tree's total leaf area are sufficient to overcome this decline and cause whole-tree carbon accumulation rate to increase.

Second, our findings are similarly compatible with the well-known age-related decline in productivity at the scale of even-aged forest stands. Although a review of mechanisms is beyond the scope of this paper^{10,23}, several factors (including the interplay of changing growth efficiency and tree dominance hierarchies²⁴) can contribute to declining productivity at the stand scale. We highlight the fact that increasing individual tree growth rate does not automatically result in increasing stand productivity because tree mortality can drive orders-of-magnitude reductions in population density^{25,26}. That is, even though the large trees in older, even-aged stands may be growing more rapidly, such stands have fewer trees. Tree population dynamics, especially mortality, can thus be a significant contributor to declining productivity at the scale of the forest stand²³.

For a large majority of species, our findings support metabolic scaling theory's qualitative prediction of continuously increasing growth

at the scale of individual trees⁶, with several implications. For example, life-history theory often assumes that tradeoffs between plant growth and reproduction are substantial¹¹. Contrary to some expectations^{11,16}, our results indicate that for most tree species size-related changes in reproductive allocation are insufficient to drive long-term declines in growth rates⁶. Additionally, declining growth is sometimes considered to be a defining feature of plant senescence¹². Our findings are thus relevant to understanding the nature and prevalence of senescence in the life history of perennial plants²⁷.

Finally, our results are relevant to understanding and predicting forest feedbacks to the terrestrial carbon cycle and global climate system^{1–3}. These feedbacks will be influenced by the effects of climatic, land-use and other environmental changes on the size-specific growth rates and size structure of tree populations—effects that are already being observed in forests^{28,29}. The rapid growth of large trees indicates that, relative to their numbers, they could play a disproportionately important role in these feedbacks³⁰. For example, in our western USA old-growth forest plots, trees >100 cm in diameter comprised 6% of trees, yet contributed 33% of the annual forest mass growth. Mechanistic models of the forest carbon cycle will depend on accurate representation of productivity across several scales of biological organization, including calibration and validation against continuously increasing carbon accumulation rates at the scale of individual trees.

METHODS SUMMARY

We estimated aboveground dry mass growth rates from consecutive diameter measurements of tree trunks—typically measured every five to ten years—from long-term monitoring plots. Analyses were restricted to trees with trunk diameter ≥ 10 cm, and to species having ≥ 40 trees in total and ≥ 15 trees with trunk diameter ≥ 30 cm. Maximum trunk diameters ranged from 38 cm to 270 cm among species, averaging 92 cm. We converted each diameter measurement (plus an accompanying height measurement for 16% of species) to aboveground dry mass, M , using published allometric equations. We estimated tree growth rate as $G = \Delta M / \Delta t$ and modelled G as a function of $\log(M)$ for each species using piecewise regression. The independent variable $\log(M)$ was divided into bins and a separate line segment was fitted to G versus $\log(M)$ in each bin so that the line segments met at the bin divisions. Bin divisions were not assigned a priori, but were fitted by the model separately for each species. We fitted models with 1, 2, 3 and 4 bins, and selected the model receiving the most support by Akaike's Information Criterion for each species. Our approach thus makes no assumptions about the shape of the relationship between G and $\log(M)$, and can accommodate increasing, decreasing or hump-shaped relationships. Parameters were fitted with a Gibbs sampler based on Metropolis updates, producing credible intervals for model parameters and growth rates at any diameter; uninformative priors were used for all parameters. We tested extensively for bias, and found no evidence that our results were influenced by model fits failing to detect a final growth decline in the largest trees, possible biases introduced by the 47% of species for which we combined data from several plots, or possible biases introduced by allometric equations (Extended Data Figs 4 and 5).

Online Content Any additional Methods, Extended Data display items and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

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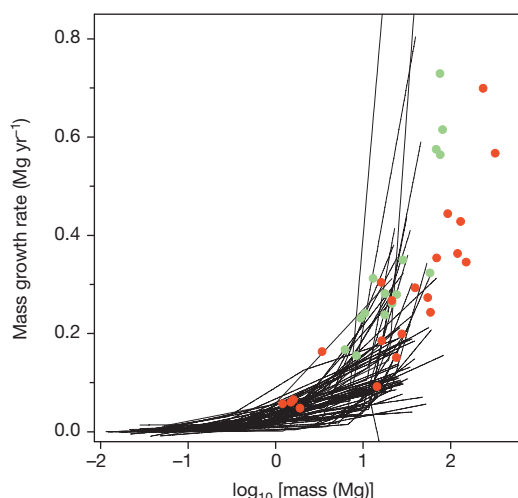


Figure 3 | Aboveground mass growth rates of species in our data set compared with *E. regnans* and *S. sempervirens*. For clarity, only the 58 species in our data set having at least one tree exceeding 20 Mg are shown (lines). Data for *E. regnans* (green dots, 15 trees) and *S. sempervirens* (red dots, 21 trees) are from an intensive study that included some of the most massive individual trees on Earth⁷. Both axes are expanded relative to those of Fig. 2.

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Supplementary Information is available in the online version of the paper.

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Author Contributions N.L.S. and A.J.D. conceived the study with feedback from R.C. and D.A.C., N.L.S., A.J.D., R.C. and S.E.R. wrote the manuscript. R.C. devised the main analytical approach and wrote the computer code. N.L.S., A.J.D., R.C., S.E.R., P.J.B., N.G.B., D.A.C., E.R.L., W.K.M. and N.R. performed analyses. N.L.S., A.J.D., R.C., S.E.R., P.J.B., D.A.C., E.R.L., W.K.M., E.A., C.B., S.B., G.C., S.J.D., A.D., C.N.E., O.F., J.F.F., H.R.G., Z.H., M.E.H., S.P.H., D.K., Y.L., J.-R.M., A.M., L.R.M., R.J.P., N.P., S.-H.S., I.-F.S., S.T., D.T., P.J.v.M., X.W., S.K.W. and M.A.Z. supplied data and sources of allometric equations appropriate to their data.

Author Information Fitted model parameters for each species have been deposited in USGS’s ScienceBase at <http://dx.doi.org/10.5066/F7JS9NFM>. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to N.L.S. (nstephenson@usgs.gov).

METHODS

Data. We required that forest monitoring plots provided unbiased samples of all living trees within the plot boundaries, and that the trees had undergone two trunk diameter measurements separated by at least one year. Some plots sampled minimally disturbed old (all-aged) forest, whereas others, particularly those associated with national inventories, sampled forest stands regardless of past management history. Plots are described in the references cited in Supplementary Table 1.

Our raw data were consecutive measurements of trunk diameter, D , with most measurements taken 5 to 10 years apart (range, 1–29 years). D was measured at a standard height on the trunk (usually 1.3–1.4 m above ground level), consistent across measurements for a tree. Allometric equations for 16% of species required, in addition to consecutive measurements of D , consecutive measurements of tree height.

We excluded trees exhibiting extreme diameter growth, defined as trunks where D increased by $\geq 40 \text{ mm yr}^{-1}$ or that shrank by $\geq 12\text{s}$, where s is the standard deviation of the D measurement error, $s = 0.9036 + 0.006214D$ (refs 31, 32); outliers of these magnitudes were almost certainly due to error. By being so liberal in allowing negative growth anomalies, we erred on the side of reducing our ability to detect increases in tree mass growth rate. Using other exclusion values yielded similar results, as did a second approach to handling error in which we reanalysed a subset of our models using a Bayesian method that estimates growth rates after accounting for error, based on independent plot-specific data quantifying measurement error³³.

To standardize minimum D among data sets, we analysed only trees with $D \geq 10 \text{ cm}$ at the first census. To ensure adequate samples of trees spanning a broad range of sizes, we restricted analyses to species having both ≥ 40 trees in total and also ≥ 15 trees with $D \geq 30 \text{ cm}$ at the first census. This left us with 673,046 trees belonging to 403 tropical and temperate species in 76 families, spanning twelve countries and all forested continents (Supplementary Table 1). Maximum trunk diameters ranged from 38 cm to 270 cm among species, and averaged 92 cm.

Estimating tree mass. To estimate each tree's aboveground dry mass, M , we used published allometric equations relating M to D (or for 16% of species, relating M to D and tree height). Some equations were species-specific and others were specific to higher taxonomic levels or forest types, described in the references in Supplementary Table 1. The single tropical moist forest equation of ref. 34 was applied to most tropical species, whereas most temperate species had unique species-specific equations. Most allometric equations are broadly similar, relating $\log(M)$ to $\log(D)$ linearly, or nearly linearly—a familiar relationship in allometric scaling of both animals and plants³⁵. Equations can show a variety of differences in detail, however, with some adding $\log(D)$ squared and cubed terms. All equations make use of the wood density of individual species, but when wood density was not available for a given species we used mean wood density for a genus or family³⁶.

Using a single, average allometry for most tropical species, and mean wood density for a genus or family for several species, limits the accuracy of our estimates of M . However, because we treat each species separately, it makes no difference whether our absolute M estimates are more accurate in some species than in others, only that they are consistent within a species and therefore accurately reveal whether mass growth rates increase or decrease with tree size.

For two regions—Spain and the western USA—allometric equations estimated mass only for a tree's main stem rather than all aboveground parts, including branches and leaves. But because leaf and stem masses are positively correlated and their growth rates are expected to scale isometrically both within and among species^{18,37,38}, results from these two regions should not alter our qualitative conclusions. Confirming this, the percentage of species with increasing stem mass growth rate in the last bin for Spain and the western USA (93.4% of 61 species) was similar to that from the remainder of regions (97.4% of 342 species) ($P = 0.12$, Fisher's exact test).

Modelling mass growth rate. We sought a modelling approach that made no assumptions about the shape of the relationship between aboveground dry mass growth rate, G , and aboveground dry mass, M , and that could accommodate monotonically increasing, monotonically decreasing, or hump-shaped relationships. We therefore chose to model G as a function of $\log(M)$ using piecewise linear regression. The range of the x axis, $X = \log(M)$, is divided into a series of bins, and within each bin G is fitted as a function of X by linear regression. The position of the bins is adaptive: it is fitted along with the regression terms. Regression lines are required to meet at the boundary between bins. For a single model-fitting run the number of bins, B , is fixed. For example, if $B = 2$, there are four parameters to be fitted for a single species: the location of the boundary between bins, X_1 ; the slope of the regression in the first bin, S_1 ; the slope in the second bin, S_2 ; and an intercept term. Those four parameters completely define the model. In general, there are $2B$ parameters for B bins.

Growth rates, while approximately normally distributed, were heteroskedastic, with the variance increasing with mass (Fig. 1), so an additional model was needed for the standard deviation of G , σ_G , as a function of $\log(M)$. The increase of σ_G

with $\log(M)$ was clearly not linear, so we used a three-parameter model:

$$\sigma_G = k \quad (\text{for } \log(M) < d)$$

$$\sigma_G = a + b \log(M) \quad (\text{for } \log(M) \geq d)$$

where the intercept a is determined by the values of k , d and b . Thus σ_G was constant for smaller values of $\log(M)$ (below the cutoff d), then increased linearly for larger $\log(M)$ (Fig. 1). The parameters k , d and b were estimated along with the parameters of the growth model.

Parameters of both the growth and standard deviation models were estimated in a Bayesian framework using the likelihood of observing growth rates given model predictions and the estimated standard deviation of the Gaussian error function. A Markov chain Monte Carlo chain of parameter estimates was created using a Gibbs sampler with a Metropolis update^{39,40} written in the programming language R (ref. 41) (a tutorial and the computer code are available through <http://ctfs.arnarb.harvard.edu/Public/CTFSRPackage/files/tutorials/growthfitAnalysis>). The sampler works by updating each of the parameters in sequence, holding other parameters fixed while the relevant likelihood function is used to locate the target parameter's next value. The step size used in the updates was adjusted adaptively through the runs, allowing more rapid convergence⁴⁰. The final Markov chain Monte Carlo chain describes the posterior distribution for each model parameter, the error, and was then used to estimate the posterior distribution of growth rates as estimated from the model. Priors on model parameters were uniform over an unlimited range, whereas the parameters describing the standard deviation were restricted to >0 . Bin boundaries, X_b , were constrained as follows: (1) boundaries could only fall within the range of X , (2) each bin contained at least five trees, and (3) no bin spanned less than 10% of the range of X . The last two restrictions prevented the bins from collapsing to very narrow ranges of X in which the fitted slope might take absurd extremes.

We chose piecewise regression over other alternatives for modelling G as a function of M for two main reasons. First, the linear regression slopes within each bin provide precise statistical tests of whether G increases or decreases with X , based on credible intervals of the slope parameters. Second, with adaptive bin positions, the function is completely flexible in allowing changes in slope at any point in the X range, with no influence of any one bin on the others. In contrast, in parametric models where a single function defines the relationship across all X , the shape of the curve at low X can (and indeed must) influence the shape at high X , hindering statistical inference about changes in tree growth at large size.

We used $\log(M)$ as our predictor because within a species M has a highly non-Gaussian distribution, with many small trees and only a few very large trees, including some large outliers. In contrast, we did not log-transform our dependent variable G so that we could retain values of $G \leq 0$ that are often recorded in very slowly growing trees, for which diameter change over a short measurement interval can be on a par with diameter measurement error.

For each species, models with 1, 2, 3 and 4 bins were fitted. Of these four models, the model receiving the greatest weight of evidence by Akaike Information Criterion (AIC) was selected. AIC is defined as the log-likelihood of the best-fitting model, penalized by twice the number of parameters. Given that adding one more bin to a model meant two more parameters, the model with an extra bin had to improve the log-likelihood by 4 to be considered a better model⁴².

Assessing model fits. To determine whether our approach might have failed to reveal a final growth decline within the few largest trees of the various species, we calculated mass growth rate residuals for the single most massive individual tree of each species. For 52% of the 403 species, growth of the most massive tree was underestimated by our model fits (for example, Fig. 1a); for 48% it was overestimated (for example, Fig. 1b). These proportions were indistinguishable from 50% ($P = 0.55$, binomial test), as would be expected for unbiased model fits. Furthermore, the mean residual (observed minus predicted) mass growth rate of these most massive trees, $+0.006 \text{ Mg yr}^{-1}$, was statistically indistinguishable from zero ($P = 0.29$, two-tailed t -test). We conclude that our model fits accurately represent growth trends up through, and including, the most massive trees.

Effects of combined data. To achieve sample sizes adequate for analysis, for some species we combined data from several different forest plots, potentially introducing a source of bias: if the largest trees of a species disproportionately occur on productive sites, the increase in mass growth rate with tree size could be exaggerated. This might occur because trees on less-productive sites—presumably the sites having the slowest-growing trees within any given size class—could be under-represented in the largest size classes. We assessed this possibility in two ways.

First, our conclusions remained unchanged when we compared results for the 53% of species that came uniquely from single large plots with those of the 47% of species whose data were combined across several plots. Proportions of species with increasing mass growth rates in the last bin were indistinguishable between the two groups (97.6% and 95.8%, respectively; $P = 0.40$, Fisher's exact test). Additionally,

the shapes and magnitudes of the growth curves for Africa and Asia, where data for each species came uniquely from single large plots, were similar to those of Australasia, Europe and North America, where data for each species were combined across several plots (Table 1, Fig. 2 and Extended Data Fig. 2). (Data from Central and South America were from both single and combined plots, depending on species.)

Second, for a subset of combined-data species we compared two sets of model fits: (1) using all available plots (that is, the analyses we present in the main text), and (2) using only plots that contained massive trees—those in the top 5% of mass for a species. To maximize our ability to detect differences, we limited these analyses to species with large numbers of trees found in a large number of plots, dispersed widely across a broad geographic region. We therefore analysed the twelve Spanish species that each had more than 10,000 individual trees (Supplementary Table 1), found in 34,580 plots distributed across Spain. Massive trees occurred in 6,588 (19%) of the 34,580 plots. We found no substantial differences between the two analyses. When all 34,580 plots were analysed, ten of the twelve species showed increasing growth in the last bin, and seven showed increasing growth across all bins; when only the 6,588 plots containing the most massive trees were analysed, the corresponding numbers were eleven and nine. Model fits for the two groups were nearly indistinguishable in shape and magnitude across the range of tree masses. We thus found no evidence that the potential for growth differences among plots influenced our conclusions.

Effects of possible allometric biases. For some species, the maximum trunk diameter D in our data sets exceeded the maximum used to calibrate the species' allometric equation. In such cases our estimates of M extrapolate beyond the fitted allometry and could therefore be subject to bias. For 336 of our 403 species we were able to determine D of the largest tree that had been used in calibrating the associated allometric equations. Of those 336 species, 74% (dominated by tropical species) had no trees in our data set with D exceeding that used in calibrating the allometric equations, with the remaining 26% (dominated by temperate species) having at least one tree with D exceeding that used in calibration. The percentage of species with increasing G in the last bin for the first group (98.0%) was indistinguishable from that of the second group (96.6%) ($P = 0.44$, Fisher's exact test). Thus, our finding of increasing G with tree size is not affected by the minority of species that have at least one tree exceeding the maximum value of D used to calibrate their associated allometric equations.

A bias that could inflate the rate at which G increases with tree size could arise if allometric equations systematically underestimate M for small trees or overestimate M for large trees⁴³. For a subset of our study species we obtained the raw data—consisting of measured values of D and M for individual trees—needed to calibrate allometric equations, allowing us to determine whether the particular form of those species' allometric equations was prone to bias, and if so, the potential consequences of that bias.

To assess the potential for allometric bias for the majority (58%) of species in our data set—those that used the empirical moist tropical forest equation of ref. 34—we reanalysed the data provided by ref. 34. The data were from 1,504 harvested trees representing 60 families and 184 genera, with D ranging from 5 cm to 156 cm; the associated allometric equation relates $\log(M)$ to a third-order polynomial of $\log(D)$. Because the regression of M on D was fitted on a log–log scale, this and subsequent equations include a correction of $\exp[(\text{RSE})^2/2]$ for the error in back-transformation, where RSE is the residual standard error from the statistical model⁴⁴. Residuals of M for the equation revealed no evident biases (Extended Data Fig. 4a), suggesting that we should expect little (if any) systematic size-related biases in our estimates of G for the 58% of our species that used this equation.

Our simplest form of allometric equation—applied to 22% of our species—was $\log(M) = a + b \log(D)$, where a and b are taxon-specific constants. For nine of our species that used equations of this form (all from the temperate western USA: *Abies amabilis*, *A. concolor*, *A. procera*, *Pinus lambertiana*, *Pinus ponderosa*, *Picea sitchensis*, *Pseudotsuga menziesii*, *Tsuga heterophylla* and *T. mertensiana*) we had values of both D and M for a total of 1,358 individual trees, allowing us to fit species-specific allometric equations of the form $\log(M) = a + b \log(D)$ and then assess them for bias. Residual plots showed a tendency to overestimate M for the largest trees (Extended Data Fig. 4b), with the possible consequence of inflating estimates of G for the largest relative to the smallest trees of these species.

To determine whether this bias was likely to alter our qualitative conclusion that G increases with tree size, we created a new set of allometric relations between D and M —one for each of the nine species—using the same piecewise linear regression approach we used to model G as a function of M . However, because our goal was to eliminate bias rather than seek the most parsimonious model, we fixed the number of bins at four, with the locations of boundaries between the bins being fitted by the model. Our new allometry using piecewise regressions led to predictions of M with no apparent bias relative to D (Extended Data Fig. 4c). This new, unbiased allometry gave the same qualitative results as our original, simple allometry

regarding the relationship between G and M : for all nine species, G increased in the bin containing the largest trees, regardless of the allometry used (Extended Data Fig. 5). We conclude that any bias associated with the minority of our species that used the simple allometric equation form was unlikely to affect our broad conclusion that G increases with tree size in a majority of tree species.

As a final assessment, we compared our results to those of a recent study of *E. regnans* and *S. sempervirens*, in which M and G had been calculated from intensive measurements of aboveground portions of trees without the use of standard allometric equations⁷. Specifically, in two consecutive years 36 trees of different sizes and ages were climbed, trunk diameters were systematically measured at several heights, branch diameters and lengths were measured (with subsets of foliage and branches destructively sampled to determine mass relationships), wood densities were determined and ring widths from increment cores were used to supplement measured diameter growth increments. The authors used these measurements to calculate M for each of the trees in each of the two consecutive years, and G as the difference in M between the two years⁷. *E. regnans* and *S. sempervirens* are the world's tallest angiosperm and gymnosperm species, respectively, so the data set was dominated by exceptionally large trees; most had $M \geq 20$ Mg, and M of some individuals exceeded that of the most massive trees in our own data set (which lacked *E. regnans* and *S. sempervirens*). We therefore compared *E. regnans* and *S. sempervirens* to the 58 species in our data set that had at least one individual with $M \geq 20$ Mg. Sample sizes for *E. regnans* and *S. sempervirens*—15 and 21 trees, respectively—fell below our required ≥ 40 trees for fitting piecewise linear regressions, so we simply plotted data points for individual *E. regnans* and *S. sempervirens* along with the piecewise regressions that we had already fitted for our 58 comparison species (Fig. 3).

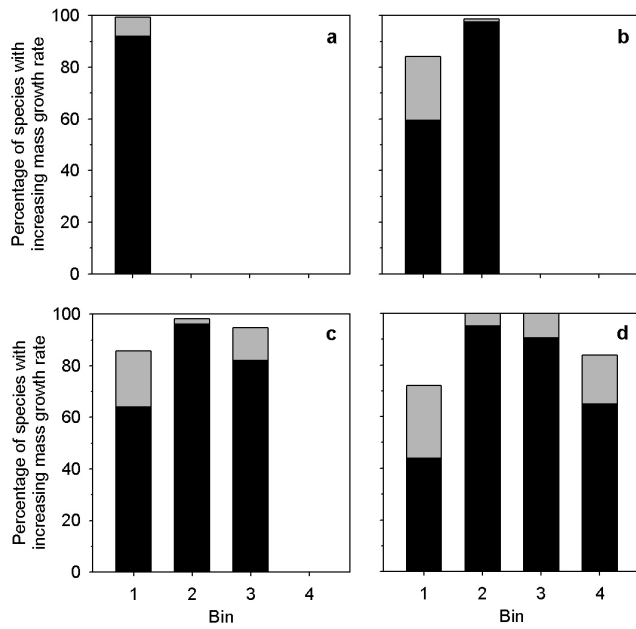
As reported by ref. 7, G increased with M for both *E. regnans* and *S. sempervirens*, up to and including some of the most massive individual trees on the Earth (Fig. 3). Within the zone of overlapping M between the two data sets, G values for individual *E. regnans* and *S. sempervirens* trees fell almost entirely within the ranges of the piecewise regressions we had fitted for our 58 comparison species. We take these observations as a further indication that our results, produced using standard allometric equations, accurately reflect broad relationships between M and G .

Fitting log–log models. To model $\log(G)$ as a function of $\log(M)$, we used the binning approach that we used in our primary analysis of mass growth rate (described earlier). However, in log-transforming growth we dropped trees with $G \leq 0$. Because negative growth rates become more extreme with increasing tree size, dropping them could introduce a bias towards increasing growth rates. Log-transformation additionally resulted in skewed growth rate residuals. Dropping trees with $G \leq 0$ caused several species to fall below our threshold sample size, reducing the total number of species analysed to 381 (Extended Data Fig. 2).

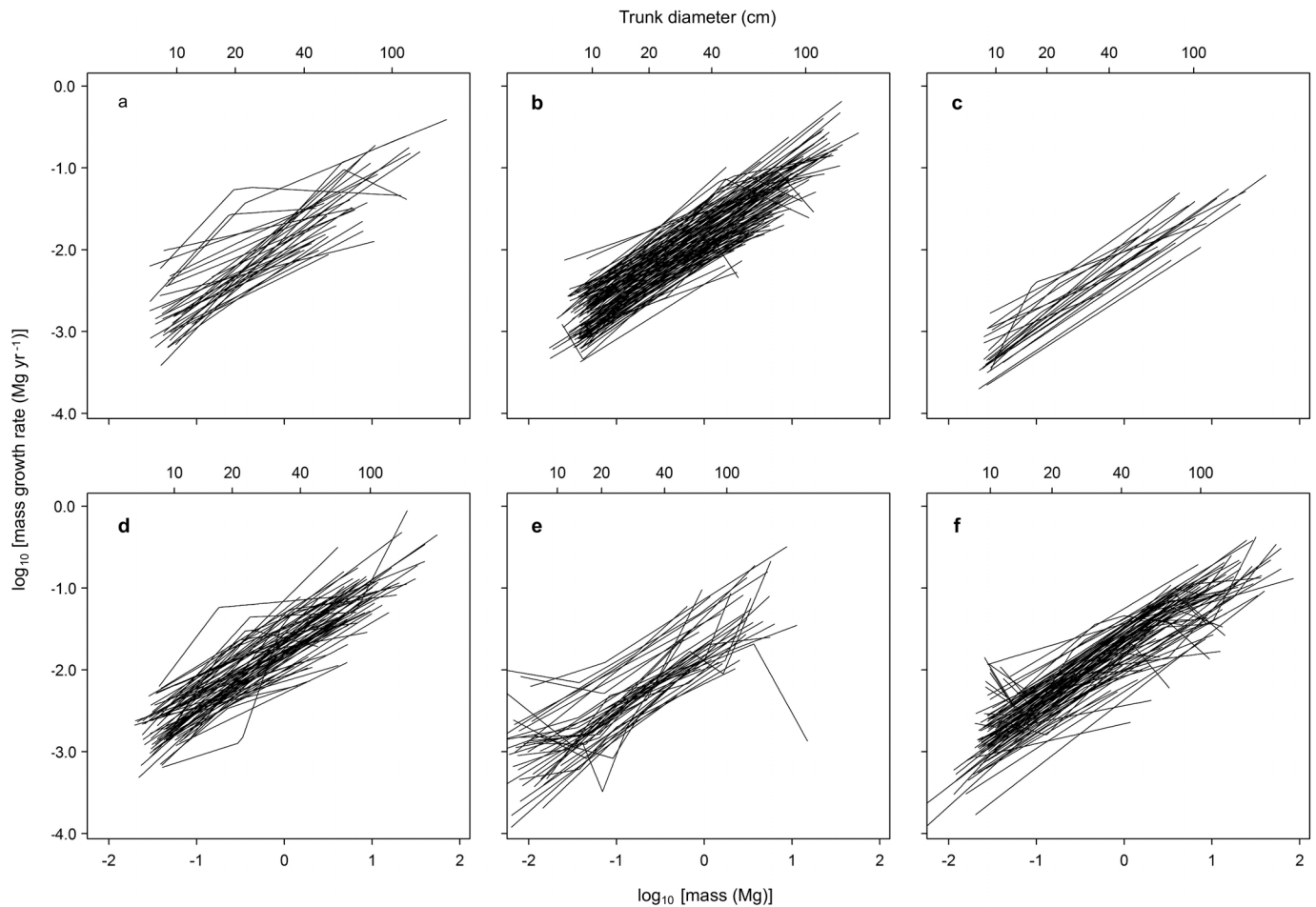
Growth in the absence of competition. We obtained published equations for 41 North American and European species, in 46 species-site combinations, relating species-specific tree diameter growth rates to trunk diameter D and to neighbourhood competition^{45–49}. Setting neighbourhood competition to zero gave us equations describing estimated annual D growth as a function of D in the absence of competition. Starting at $D_0 = 10$ cm, we sequentially (1) calculated annual D growth for a tree of size D_0 , (2) added this amount to D_0 to determine D_1 , (3) used an appropriate taxon-specific allometric equation to calculate the associated tree masses M_0 and M_1 , and (iv) calculated tree mass growth rate G_0 of a tree of mass M_0 in the absence of competition as $M_1 - M_0$. For each of the five species that had separate growth analyses available from two different sites, we required that mass growth rate increased continuously with tree size at both sites for the species to be considered to have a continuously increasing mass growth rate. North American and European allometries were taken from refs 17 and 50, respectively, with preference given to allometric equations based on power functions of tree diameter, large numbers of sampled trees, and trees spanning a broad range of diameters. For the 47% of European species for which ref. 50 had no equations meeting our criteria, we used the best-matched (by species or genus) equations from ref. 17.

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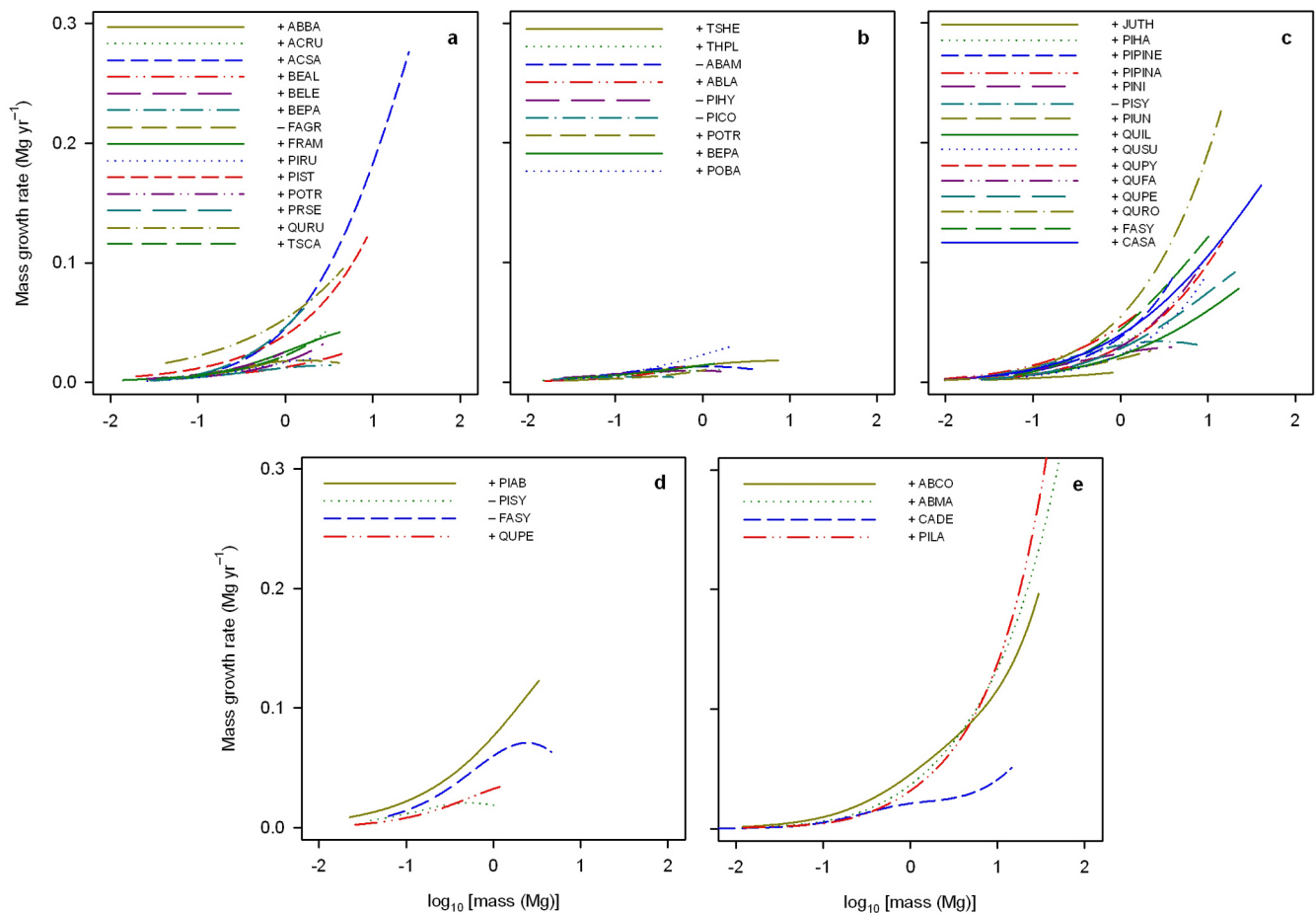


Extended Data Figure 1 | Summary of model fits for tree mass growth rates. Bars show the percentage of species with mass growth rates that increase with tree mass for each bin; black shading indicates percentage significant at $P \leq 0.05$. Tree masses increase with bin number. **a**, Species fitted with one bin (165 species); **b**, Species fitted with two bins (139 species); **c**, Species fitted with three bins (56 species); and **d**, Species fitted with four bins (43 species).



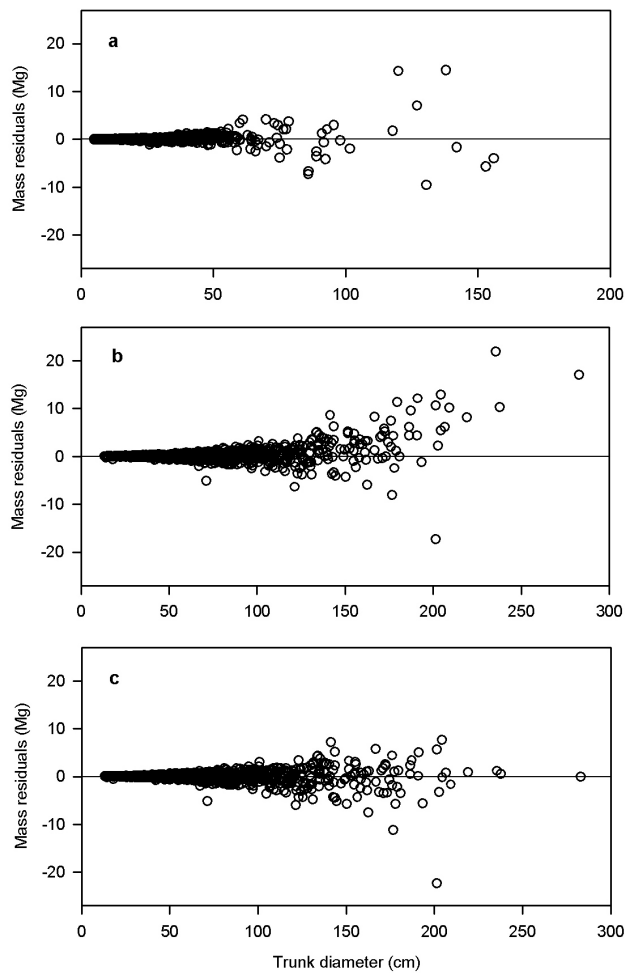
Extended Data Figure 2 | Log-log model fits of mass growth rates for 381 tree species, by continent. Trees with growth rates ≤ 0 were dropped from the analysis, reducing the number of species meeting our threshold sample size for analysis. **a**, Africa (33 species); **b**, Asia (123 species); **c**, Australasia

(22 species); **d**, Central and South America (73 species); **e**, Europe (41 species); and **f**, North America (89 species). Trunk diameters are approximate values for reference, based on the average diameters of trees of a given mass.



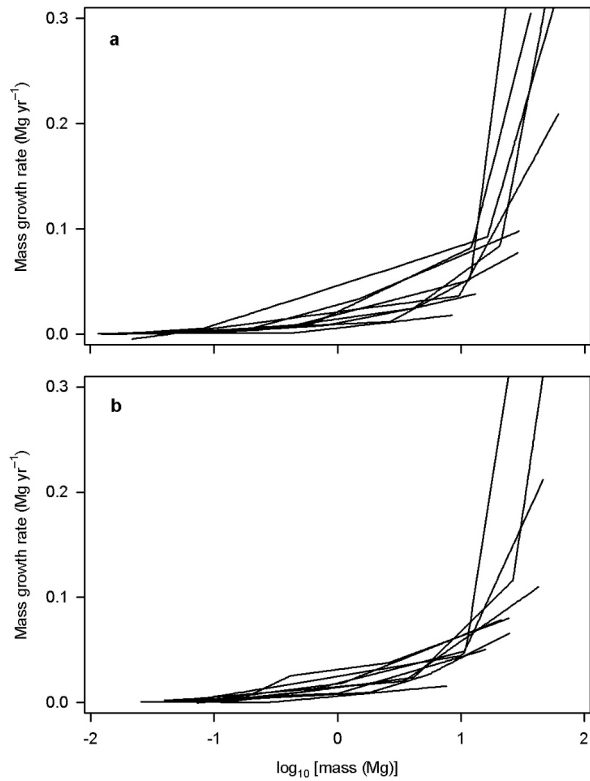
Extended Data Figure 3 | Aboveground mass growth rates for 41 tree species in the absence of competition. The '+' or '-' symbol preceding each species code indicates, respectively, species with mass growth rates that increased continuously with tree size or species with mass growth rates that declined in the largest trees. Sources of the diameter growth equations used to calculate mass growth were: **a**, ref. 45; **b**, ref. 46; **c**, ref. 48; **d**, ref. 47; and **e**, ref. 49. ABAM, *Abies amabilis*; ABBA, *Abies balsamea*; ABCO, *Abies concolor*; ABLA, *Abies lasiocarpa*; ABMA, *Abies magnifica*; ACRU, *Acer rubrum*; ACSA, *Acer saccharum*; BEAL, *Betula alleghaniensis*; BELE, *Betula lenta*; BEPA, *Betula papyrifera*; CADE, *Calocedrus decurrens*; CASA, *Castanea sativa*; FAGR, *Fagus grandifolia*; FASY, *Fagus sylvatica*; FRAM, *Fraxinus americana*; JUTH,

Juniperus thurifera; PIAB, *Picea abies*; PICO, *Pinus contorta*; PIHA, *Pinus halepensis*; PIHY, *Picea hybrid* (a complex of *Picea glauca*, *P. sitchensis* and *P. engelmannii*); PILA, *Pinus lambertiana*; PINI, *Pinus nigra*; PIPINA, *Pinus pinaster*; PIPINE, *Pinus pinea*; PIRU, *Picea rubens*; PIST, *Pinus strobus*; PISY, *Pinus sylvestris*; PIUN, *Pinus uncinata*; POBA, *Populus balsamifera* ssp. *trichocarpa*; POTR, *Populus tremuloides*; PRSE, *Prunus serotina*; QUFA, *Quercus faginea*; QUIL, *Quercus ilex*; QUPE, *Quercus petraea*; QUPY, *Quercus pyrenaica*; QURO, *Quercus robur*; QURU, *Quercus rubra*; QUSU, *Quercus suber*; THPL, *Thuja plicata*; TSQA, *Tsuga canadensis*; and TSHE, *Tsuga heterophylla*.



Extended Data Figure 4 | Residuals of predicted minus observed tree mass.

a. The allometric equation for moist tropical forests³⁴—used for the majority of tree species—shows no evident systematic bias in predicted aboveground dry mass, M , relative to trunk diameter ($n = 1,504$ trees). **b.** In contrast, our simplest form of allometric equation—used for 22% of our species and here applied to nine temperate species—shows an apparent bias towards overestimating M for large trees ($n = 1,358$ trees). **c.** New allometries that we created for the nine temperate species removed the apparent bias in predicted M .



Extended Data Figure 5 | Estimated mass growth rates of the nine temperate species of Extended Data Fig. 4. Growth was estimated using the simplest form of allometric model [$\log(M) = a + b\log(D)$] (a) and our allometric models fitted with piecewise linear regression (b). Regardless of the allometric model form, all nine species show increasing G in the largest trees.

Reburn severity in managed and unmanaged vegetation in a large wildfire

Jonathan R. Thompson^{*†}, Thomas A. Spies[‡], and Lisa M. Ganio^{*}

^{*}Department of Forest Science, Oregon State University, Corvallis, OR 97331; and [‡]Pacific Northwest Research Station, U.S. Department of Agriculture Forest Service, Corvallis, OR 97331

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Debate over the influence of postwildfire management on future fire severity is occurring in the absence of empirical studies. We used satellite data, government agency records, and aerial photography to examine a forest landscape in southwest Oregon that burned in 1987 and then was subject, in part, to salvage-logging and conifer planting before it reburned during the 2002 Biscuit Fire. Areas that burned severely in 1987 tended to reburn at high severity in 2002, after controlling for the influence of several topographical and biophysical covariates. Areas unaffected by the initial fire tended to burn at the lowest severities in 2002. Areas that were salvage-logged and planted after the initial fire burned more severely than comparable unmanaged areas, suggesting that fuel conditions in conifer plantations can increase fire severity despite removal of large woody fuels.

public land management | salvage-logging | Biscuit Fire | Landsat | landscape ecology

Large wildfires are increasingly common in western North America (1). Changing climate patterns and the legacy of fire suppression within fire-prone forests suggest that this trend will continue. Postfire management is, therefore, a growing concern for public land managers. Although it has been customary to salvage-log fire-killed trees and plant seedlings after large wildfires, there is a mounting debate regarding the practice (2–4). There are several reasons one might choose this management system, including recouping economic losses through timber sales and ensuring the reestablishment of desirable tree species. Another common justification for this approach has been a perceived reduction in future fire risk associated with the removal of dead wood (2, 5–7). The threat of severe reburns is real but not well understood (4). For example, Oregon's Tillamook burns of the 1930s, 1940s, and 1950s consisted of one large fire followed by three reburns 6, 12, and 18 years later. In sum, these fires burned more than 135,000 hectares. The threat of reburns motivates public land managers to construct fuel-breaks and to salvage-log to hedge against the risks of future fire (6). Recent studies have found, however, that salvage-logging can increase surface fuels available to fires above prelogging levels by transferring unmerchantable material to the forest floor, suggesting that this postfire management practice might actually increase fire risk for a time (3, 8). Until now, no study has quantified how recent fire history and postfire management actually affects the severity of a large wildfire (4).

The 2002 Biscuit Fire was among the largest forest fires in modern United States history, encompassing >200,000 hectares primarily within the Rogue-Siskiyou National Forest (RSNF) in southwest Oregon. In the years following, the Biscuit Fire has been a catalyst for national debate regarding forest management in the aftermath of wildfires on public land. This debate is taking place in the absence of empirical research on how future wildfire severity is associated with past wildfires and how postfire forest management alters future fire severity (4). We analyzed burn severity patterns within 18,000 hectares of the Biscuit Fire that burned 15 years earlier during the 1987 Silver Fire. Both fires burned heterogeneously, creating mosaics of live and dead trees

in variably sized patches. In the 3 years following the Silver Fire, >800 hectares were salvage-logged and planted with conifers. The arrangement of these disturbances presented a unique opportunity to address two important research questions. First, was severity in the Biscuit Fire associated with severity in the Silver Fire in unmanaged areas? Second, did areas that were salvage-logged and planted with conifers after the Silver Fire burn more or less severely in the Biscuit Fire than comparable unmanaged areas?

With regard to the first question, hereafter referred to as “the reburn question,” a negative correlation between Biscuit and Silver Fire severity is plausible if the forests that burned severely in 1987 had less remaining fuel to support the Biscuit Fire in 2002, or if regenerating young forests did not effectively carry fire. This relationship has been observed in lodgepole pine ecosystems (9–11). An alternate hypothesis is that Biscuit Fire severity would be positively correlated with Silver Fire severity. This would occur if areas of higher Silver Fire severity had greater accumulations of fire-killed trees and vegetative growth available as fuel to the Biscuit Fire. This scenario is assumed to have influenced forest dynamics in more mesic forests of the Pacific Northwest (12). Finally, there may be no discernible association between the severity patterns of the two fires. Many independent factors influence fire severity, including weather, topography, fuel, landscape structure, and fire suppression. Any of these could overwhelm the signal from the legacy of the Silver Fire.

The second question, hereafter referred to as “the salvage-plant question,” also has several plausible outcomes. The hypothesis that salvage-logging followed by planting conifers can reduce future fire severity is widely held and rests on the assumption that removing dead trees reduces fuel loads, and planting conifers and controlling competing vegetation hastens the return of fire-resistant forests (2, 5–7). An alternative hypothesis is that salvage-logging plus plantation creation exacerbates future fire severity. No studies have measured fire severity following salvage-logging, but it is known that it can increase available fine and coarse fuel loads if no fuel treatments are conducted (3, 8). In addition, several studies have documented high-severity fire within young conifer plantations, where surface fuels can be fine, homogeneous, and continuous (13–15).

Our study area is within the Siskiyou Mountains in southwest Oregon's mixed-conifer and mixed-evergreen hardwood zones

Author contributions: J.R.T., T.A.S., and L.M.G. designed research; J.R.T. performed research; J.R.T. and L.M.G. analyzed data; and J.R.T. and T.A.S. wrote the paper.

The authors declare no conflict of interest.

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Abbreviations: RSNF, Rogue-Siskiyou National Forest; dNBR, differenced normalized burn ratio; TM, Thematic Mapper; PAG, plant association group.

[†]To whom correspondence should be addressed. E-mail: jonathan.thompson@oregonstate.edu.

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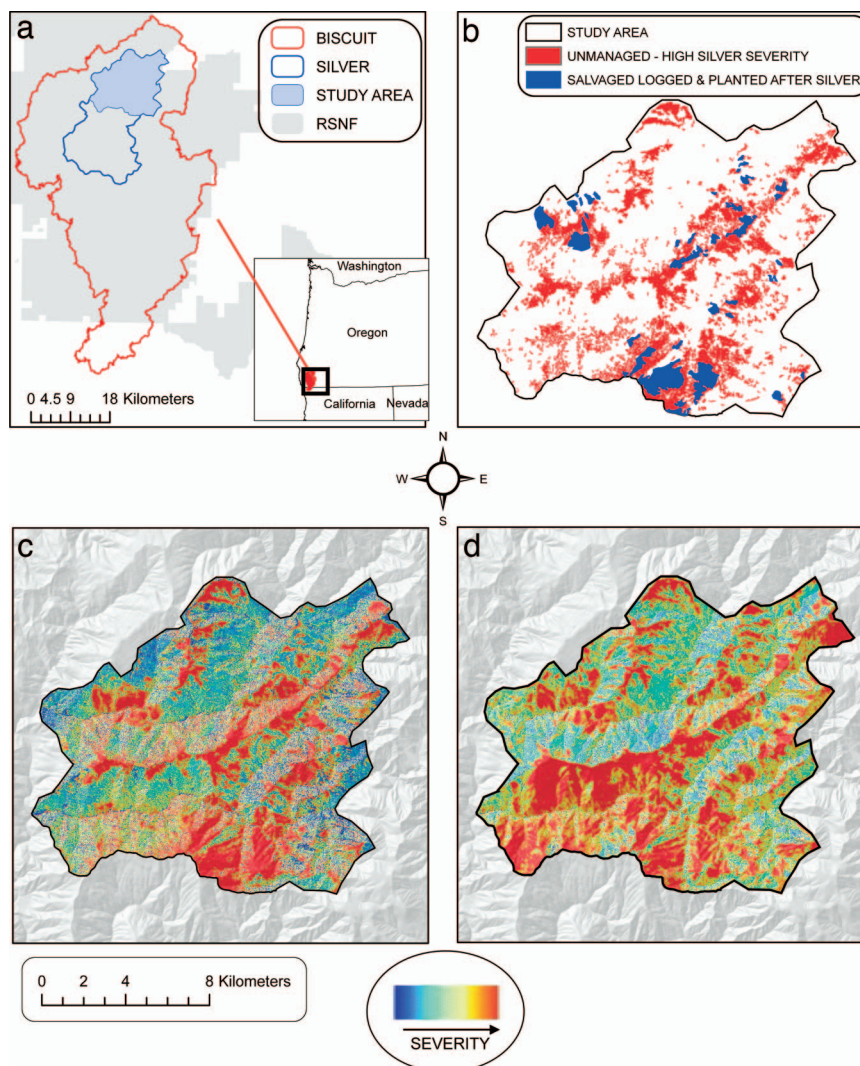


Table 2. Variables included and retained during regression model selection for the reburn and salvage-plant questions

Variables	Reburn	Salvage-plant	Definition
Disturbance history			
Silver severity	◆	†	Differenced NBR from the Silver Fire, calculated from pre- and postfire Landsat TM
Managed site		◆	Salvage-logged in 1988, 1989, or 1990, planted with conifers, then later certified as a "successful" plantation
Topography			
Elevation	†	†	In meters from a 10-m DEM
Aspect			Aspect folded around south facing slopes (folded aspect = $ 180 - \text{aspect} - 180 $), from 10-m DEM
Slope	†	†	In percent, from 10-m DEM
Topographic position (fine)	†	†	Difference between sample elevation and mean elevation of an annulus spanning 150–300 m from the sample
Topographic position (intermediate)			Difference between sample elevation and mean elevation of an annulus spanning 850–1,000 m from the sample
Topographic position (coarse)			Difference between sample elevation and mean elevation of an annulus spanning 1,850–2,000 m from the sample
Biophysical			
PAG	†	†	Potential vegetation in the absence of disturbance, based on climatic, biogeographical and physiographic factors; obtained from RSNF
1986 brightness			Brightness axis from tasseled cap transformation of 1986 Landsat data (15)
1986 wetness			Wetness axis from tasseled cap transformation of 1986 Landsat data (15)
1986 greenness	†	†	Greenness axis from tasseled cap transformation of 1986 Landsat TM data (15)
Soil			Soil data from Curry and Josephine counties (four soil types)
Weather and other temporal change			
Burn index			Daily fire behavior index measured using current and past weather data, heavily influenced by wind speed, Calculated by the ODF using data from the Quail Prairie, Oregon RAWs
Energy release component			Daily fuel moisture index that reflects the contribution of live and dead fuels to potential fire intensity, Calculated by the ODF using data from the Quail Prairie, Oregon RAWs
Day	†	†	The day on which the Biscuit Fire flaming front passed (a count from the first to the last day); obtained from RSNF

t, retained in full covariate regression model after AIC model selection; ♦, the variable being tested after fitting the best covariate regression model. NBR, normalized burn ratio; DEM, digital elevation model; ODF, Oregon Department of Forestry; RAWs, remote automated weather station.

after controlling for the covariates (95% confidence interval = 69–99 dNBR points). We confirmed that this relationship holds even for the low-to-moderate range of Silver Fire severity by

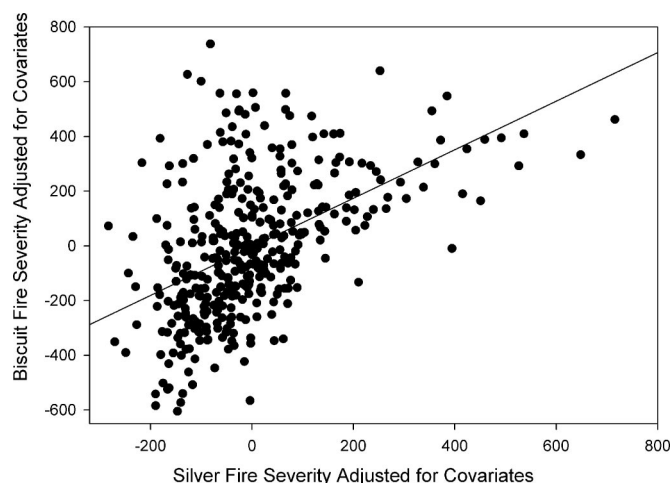


Fig. 2. Added variable plot displaying the relationship between Silver and Biscuit Fire severity as estimated through a Landsat-derived burn metric, dNBR. The effect of elevation, slope, PAG, day-of-burn, 1986 greenness, and topographic position on Biscuit Fire severity has been removed to illustrate the association between fire severities from both fires. See Table 2 for descriptions of the covariates.

reanalyzing the data after excluding the samples that burned at high Silver Fire severity. Overall, unburned areas or those that burned at lower severities in the Silver Fire tended to burn at lower severities in the Biscuit Fire, whereas areas that burned at higher severities in Silver Fire tended to reburn at higher severities in the Biscuit Fire.

To address the salvage-plant question (i.e., did logged and planted areas burn more or less severely than comparable unmanaged areas?), we restricted our second random sampling to areas that burned in the upper 20% of the Silver Fire severity range and to the logged-then-planted areas. In addition, we only sampled within those plant associations that contained managed stands. These constraints ensured that we were comparing the logged and planted sites only to similar areas that also experienced a stand-replacing disturbance. Again, there were two best covariate models. One included Silver Fire severity, elevation, slope, PAG, day-of-burn, and 1986 greenness. The other included all of these covariates plus a measure of topographic position; and again we chose the model that included topographic position (Table 2). When added to this model, the indicator for the salvage-logged and planted sites was associated with a 182.3-point increase in Biscuit Fire dNBR (Fig. 3; $P < 0.0001$, 95% confidence interval = 120.32–243.68, $df = 282$). Biscuit Fire severity in the logged and planted areas was 16–61% higher than comparable unmanaged areas depending on the values of the covariates. The particular ecological effects of this difference are unknown; nonetheless, the hypothesis that salvage-logging followed by planting reduces reburn severity is not supported by these data.

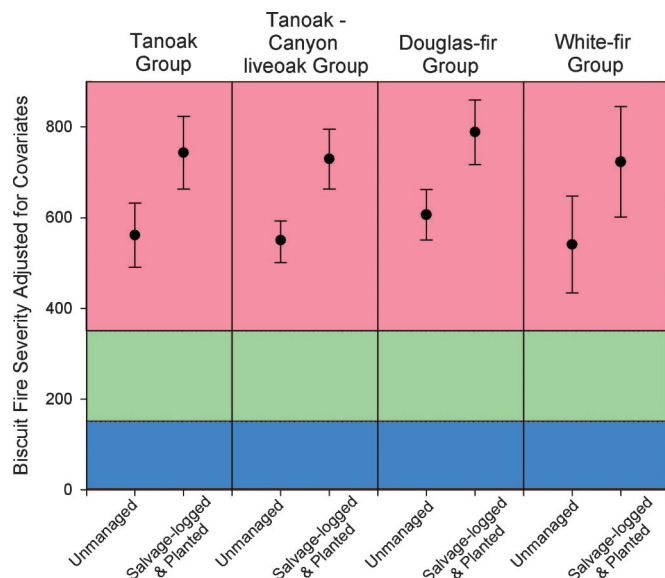


Fig. 3. Ninety-five percent confidence intervals for Biscuit Fire dNBR, a Landsat-derived burn severity metric. Estimates and confidence intervals compare regions burned at high severity in the 1987 Silver Fire that were unmanaged to areas that were salvage-logged and planted after the Silver Fire. Means were calculated at the multivariate centroid of the covariates: slope, elevation, topographic position, Silver Fire severity, day-of-burn, and 1986 greenness (see Table 2). Means were similar across the four PAGs. In this landscape, the Tanoak group is found on wetter sites in the western portion of the study area, whereas the Tanoak-Canyon live oak group is found on dryer, inland sites; the Douglas-fir group is found on relatively dry sites; and the White-fir group is found at somewhat higher elevation wetter sites (20). Colors correspond to Biscuit Fire severity calibrated through comparison with aerial photography: blue, <10% canopy scorch; green, 10–50% canopy scorch; red, >50% canopy scorch.

Discussion and Conclusion

No previous study has compared fire severity in plantations and naturally regenerated vegetation of similar ages. Our findings are consistent with studies that show that site history influences fire severity (15, 24, 25), and with studies that have found an association of high-severity fire with conifer plantations (13–15). Our limited knowledge of the fuel characteristics at the time of the Biscuit Fire prevents us from separating the effects of logging and planting. The relative influence of these management actions on burn severity would vary over time: the influence of dead fuels and harvest debris would diminish as they decayed (3) and the influence of live vegetation would increase as it developed. The patterns we observed apply to the particular conditions and history of post-Silver Fire management; they could change with shorter or longer intervals between fires.

The Biscuit Fire tended to burn at relatively high severity in young naturally regenerated stands and even more severely in young conifer plantations of comparable age and fire history. This suggests that young forests, whether naturally or artificially regenerated, may be vulnerable to positive feedback cycles of high severity fire, creating more early-successional vegetation and delaying or precluding the return of historical mature-forest composition and structure. Although patches of high-severity fire and reburns are a normal part of the mixed-severity fire regime within this forest type (12, 26), increasing occurrence of wildfire driven by climate warming in this region (1) may lead to increases in the prevalence of sclerophyllous species, which are adapted to frequent severe fires (12, 16, 20).

Our findings are inconsistent with the hypothesis that this particular postfire management system reduces the risk of high-severity fire in a reburn occurring 15 years after the original

fire. The logging component of this system is often considered a fuel-reduction treatment (2, 5–7). However, the large-diameter fuels removed during harvest do not readily carry wildland fire (12, 27). Thus, logging may not reduce available fuels. In fact, harvesting fire-killed trees may increase available surface fuels by transferring unmerchantable material, such as tops, branches, and broken boles to the ground immediately after harvest (3, 8). This effect may be mitigated as logging slash decays, or through fuel reduction methods, such as broadcast-burning (15). Records of site preparation and their effectiveness in reducing fuels in the plantations are incomplete; however, at least 17 of the 44 plantations are reported as “broadcast-burned.” In a separate analysis, we found that these 17 plantations also burned with higher severities than comparable unmanaged stands. The planting component of the system is intended to promote long-term regrowth of conifer trees, but it also creates dense or continuous fuels that are at elevated risk of high severity fire (14). It should be noted, however, that many of the plantations examined in this analysis had lower conifer densities and a larger component of shrubs and hardwoods than would be found in typical intensively managed plantations of the same age (11–14 years). Our analysis could not measure any details regarding differences in preburn structure and composition between the natural and artificially regenerated stands. Nonetheless, the naturally regenerated areas received no site preparation or planting; therefore, they likely contained a more diverse arrangement of young vegetation and open gaps (20, 28). Although these naturally regenerated areas also supported relatively high-severity fire, abrupt changes in fuel profiles, which can slow fire spread (12), may have reduced the average burn severity.

We currently lack general conceptual models or simulation models that can help us understand the effects of salvage-logging on fire severity over large landscapes and long time frames. As our work indicates, research needs to consider all of the components of postfire management systems, individually and together. Thus far, the few studies that have examined reburn potential in salvage-logged sites have emphasized the dead woody fuel transferred to the surface during harvest. But logging slash is only part of the fire risk story, and it may not be the most important after a few years. On public land, salvage-logging is almost always followed by conifer planting, even when the objective is ecological recovery, such as expediting the return of old-growth forests. We are currently unable to examine the short- and long-term tradeoffs associated with different postfire management systems. For example, we do not know how the apparent difference in fire hazard between plantations and natural stands that we observed at 15 years varies over time and whether this short-term risk is balanced in any way by longer term benefits in terms of stand development and reduced fire risk. However, the available evidence suggests that the combined influence from a pulse input of surface fuels resulting from salvage-logging (3, 8) followed by the establishment of uniform young plantations may increase susceptibility to severe reburns in the early stages of forest development.

Managers may have few options to reduce the risk of high-severity fire within areas that have recently burned severely. Typical fuel treatments, such as thinning, do not have much effect on fire risk in young forests (14). Reducing connectivity of surface fuels at landscape scales is likely the only way to decrease the size and severity of reburns until vertical diversification and fire resistance is achieved (29). The decision to salvage-log and plant, or not, after fire depends on a number of management considerations including risk of future high-severity fire, reducing hazards to fire fighters, timber revenue, and conservation of biodiversity. Further research, especially controlled experiments, is clearly needed to help managers understand tradeoffs. Given the difficulty of conducting experiments with large wild-

fires, it is important that good records of management actions are kept so that more can be learned from future wildfires.

Materials and Methods

Study Area. We limited our samples to the northern half of the Silver Fire, outside of the Kalmiopsis Wilderness Area, where an aerial photo record exists to gauge the accuracy of our characterization of fire severity and Landsat data were of sufficient atmospheric quality to map fire severity. The study area is 18,050 hectares centered at 123°89'W latitude, 42°49'N longitude. The vegetation is characterized by mixed-conifer and mixed-evergreen hardwoods (16), dominated by *Pseudotsuga menziesii*, *Lithocarpus densiflorus*, *Pinus lambertiana*, *Abies concolor*, *Chrysolepis chrysophylla*, *Ceanothus velutinus*, and *Quercus chrysolepis*. The region has steep climatic, edaphic, and topographical gradients and is renowned for floristic diversity (30). Much of the landscape has high forest productivity compared with other fire-prone ecosystems in the western United States (31). Topography is steep and complex; elevations range from 600 to >1,500 m. Soil parent materials include igneous, metasedimentary, and metamorphic types. The climate is Mediterranean, with dry, warm summers and wet, mild winters. Mean January temperature is 6°C. Mean July temperature is 16°C. Mean annual precipitation is 210 cm. Approximately 80% of the area falls within relatively dry Douglas-fir and tanoak PAGs, which historically burned at 10- to 50-year intervals at low and mixed severities (6). Most of the remaining 20% falls within moist tanoak PAGs, where the fire regime is characterized as mixed-severity with 50- to 100-year return intervals. Effective fire suppression began in 1940, and the dry PAGs are thought to have missed one or more fire cycles. The Silver Fire was ignited by lightning on August 30, 1987, and burned generally from the northeast to the southwest (32). The Biscuit Fire reburned the region of the Silver Fire beginning July 17, 2002 and continuing through August 18, 2002, burning generally from east to west (6).

Image Processing. Our procedures for image rectification and atmospheric correction and normalization were as follows. A Landsat TM scene acquired immediately after the Biscuit Fire (Table 1) was rectified to a 2003 United States Geological Survey Digital Orthoquad by using >150 tie-points, and a first-order polynomial transformation, which produced a 14.0-m root mean squared error. Three corresponding TM scenes, one acquired 1 year before the Biscuit Fire, one acquired immediately after the Silver Fire, and one acquired 1 year before the Silver Fire (Table 1), were then all coregistered to the 2002 Landsat image by using the Landsat Orthorectification tool in ERDAS Imagine version 8.7. Each rectification used a 10-m digital elevation model and >1,200 tie-points, which were located by using an automated tie-point finder (33); root mean squared errors were less than one-half pixel in all cases. Our Landsat images have a 29-m resolution and were registered in 1927 North American Datum, UTM Zone 10. The two prefire images were then converted to reflectance and atmospherically corrected by using the COST method (34). We then used an automated ordination algorithm called “multivariate alteration detection” (35, 36) that statistically located pseudoinvariant pixels, which were subsequently used in a reduced major axis regression to radiometrically normalize postfire to prefire images. We selected October imagery, despite the low sun angle in autumn, because we wanted to pair our imagery to the dates of historical aerial photos to aid an assessment of accuracy and because we wanted to capture the fire’s effects without the confounding influence of spring green-up that may have occurred had we used imagery from the following summer. Moreover, the use of near-anniversary dates within a change-detection of normalized vegetation indices greatly minimizes any negative effects of late-season imagery.

Burn Severity and Initial Vegetation Condition. Our measure of fire severity was the dNBR (17). It is a measure of pre- to postfire change in the ratio band (B) of near-infrared (B4, 0.76–0.90 μm) to shortwave infrared (B7, 2.08–2.35 μm) spectral reflectance. B4 is associated with foliage on green trees and understory, whereas B7 is associated with dry and blackened soil (17). dNBR compares well to ground data (18, 19) and has outperformed other satellite-derived measures of burn severity (18). Using the processed images described above, we calculated dNBR as described in ref. 17. Normalization of pre- and postfire imagery centers the unchanged (i.e., unburned) pixels within each fire to a dNBR value of zero. A comparison of dNBR values to aerial photography suggests that dNBR values are roughly equivalent in terms of their correspondence to vegetation damage; however, the severity maps were constructed independently to maximize the accuracy for each fire. Because our images were acquired immediately after the fire, our estimate of severity does not capture any vegetation that may have experienced delayed mortality or regreening in the years subsequent to the fire.

We excluded areas with ultramafic soils from this analysis because they had an anomalous spectral response and are ecologically distinct from the rest of the landscape (<4% percent of the study area). The fire weather indices Burn Index and Energy Release Component were calculated from Quail Prairie remote weather station data (≈ 25 km south of the study area) by the Oregon Department of Forestry. A digital map of PAGs was provided by the RSNF and included in the model selection procedure to control for differences in biophysical characteristics (i.e., productivity and plant composition). In addition, tasseled cap wetness, greenness, and brightness indexes (22) were derived from the processed 1986 Landsat TM data and were used during model selection to control for differences in pre-Silver Fire in vegetation condition. Tasseled cap indexes are closely related to forest composition and structure in Pacific Northwest forests (21).

We used the continuous dNBR data for all statistical analysis. We also constructed categorical burn severity maps to assess the accuracy of the satellite data in relation to characterizations of tree crown damage from high-resolution aerial photos. The categorical Silver Fire severity map was also used, in part, to define the sampling universe for the salvage-plant question. Three levels of severity were classified: (i) Unburned/Low Severity, where <10% of the crown was scorched or consumed by the fire; (ii) Moderate Severity, where 10–50% of the crown was scorched or consumed; and (iii) High Severity, where >50% of the crown was scorched or consumed. Using a set of 109 randomly placed high-resolution digital aerial photo plots, we developed thresholds in dNBR values that best classified the data for each fire. An independent sample of 141 aerial photo plots was used in an accuracy assessment which resulted in an overall estimate of accuracy of 83% for unburned/low-severity pixels, 75% for moderate-severity pixels, and 85% for high-severity pixels.

Forest Management Data. We identified 44 management units (≈ 850 hectares; Fig. 1) that were logged in the 3 years following the Silver Fire, then planted with conifers (primarily Douglas-fir), and later certified as “successful plantations.” The salvage-logging guidelines set by the Forest Service required that, within harvest units, 12–18 standing snags >60 cm diameter and >12 m tall, along with 2.8 m³ of down wood be retained per hectare (32). Plantations were deemed successful if, 3–5 years after planting, conifers exceeded 370 stems per hectare and were considered healthy enough to survive competition with shrubs and hardwood trees. Although post-Silver Fire records from the RSNF are not complete, they indicate that some certified plantations had undergone mechanical treatment to suppress competing vegetation and that conifer stocking typically ranged

from 600 to 1,100 trees per hectare. In addition to the logged and planted areas used in the analysis, we distinguished ≈ 250 hectares that were harvested in part or in full after the Silver Fire but were either not planted or the planted conifers were not certified “free to grow.” We excluded these later areas from all our analyses because their history was too uncertain and variable to accurately characterize. All management polygons were provided by the RSNF and were edited in a geographic information system (GIS) by using a 1-m Digital Orthoquad acquired in 1994 to better fit the perimeters of harvest units. Areas logged and planted before the Silver Fire were excluded from all analyses. The bulk of the remaining 17,000 hectares in the northern Silver Fire perimeter were not harvested. However, some small unknown proportion was selectively logged but not planted; no records describing management actions are known to exist and we could not see evidence of them in careful analysis of the Digital Orthoquads. It is likely that only the largest most valuable trees were extracted from these sites via helicopter. The unrecorded, lightly salvaged sites make up no more than 10% of the study area and are included in the population of unmanaged sites.

Sampling, Variable Selection, Model Fitting, and Hypothesis Testing.

All sampling and data extraction was done in a geographic information system in which all of the variables were converted to 29-m raster maps. The sample universe for the reburn question was the region within the northern Silver Fire but outside any management areas. All known management units dating back >50 years were excluded from reburn analysis. Sample locations were determined by randomly selecting locations for 381 points with the constraint that they be separated by at least 300 m to reduce spatial dependence. Sample values were calculated as the mean value of the closest nine contiguous pixels to the sample location (sample unit area, ≈ 0.75 hectares). When sampling for the salvage-plant question, we constrained the sample universe to the areas within the northern Silver Fire perimeter, areas within PAGs that contained

management units and either burned at high severity in 1987 and received no or minimal postfire management, or areas that burned at high severity and were clearcut during 1988, 1989, or 1990, and then planted in the years following and certified by the RSNF as an established conifer plantation. All other management units were excluded. We sampled 292 random locations (225 unmanaged and 67 managed) separated from each other by at least 300 m. Any plantation that did not include at least one sample during the initial sample selection had a sample randomly located within it. Data were extracted from all of the raster maps as described above.

Statistical analysis was completed in the computing software R (37). Empirical variogram models indicated spatial autocorrelation of Biscuit dNBR data; a spherical theoretical variogram model best described the autocorrelation. This spatial dependence precluded the use of ordinary least squares regression. Instead, for model selection and hypothesis testing, we used generalized least squares regression to fit linear models of predictor variables to Biscuit dNBR data. Generalized least squares models allow residuals to have a nonstandard covariance structure (38); we used a spherical spatial correlation structure. The modeled variogram from the reburn data had a range of 2,314 m, and the nugget:sill was 0.387. The modeled variogram from the salvage-plant data had a range of 1,096 m, and the nugget:sill was 0.399. Akaike information criteria were used for model selection (39, 40). For both questions, we evaluated Akaike information criteria scores from ≈ 100 *a priori* candidate covariate models, including global models containing all non-correlated predictor variables and null models that contained none. All candidate models contained plausible combinations of predictor variables based on what is known about fire behavior and from previous studies of burn severity patterns on other fires [supporting information (SI) Table 1].

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Canopy damage to conifer plantations within a large mixed-severity wildfire varies with stand age

Jonathan R. Thompson^{a,*}, Thomas A. Spies^{b,1}, Keith A. Olsen^{c,2}

^aSmithsonian Institution, Smithsonian Conservation Biology Institute, 1500 Remount Road, Front Royal, VA 22630, USA

^bUSDA Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331, USA

^cDept. of Forest Science, Oregon State University, Corvallis, OR 97331, USA

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ABSTRACT

The 2002 Biscuit Fire burned at mixed-severities encompassing over 200,000 ha of publicly owned forest-land, including more than 8300 ha of conifer plantations. We used pre- and post-fire digital aerial photography to examine how the level of canopy damage varied within these plantations in relation to topography, weather, vegetation-cover, and management history, with an emphasis on the age of the plantation. We examined 198 plantations that varied widely in age (5–47 years), size (1.25–47 ha), and landscape context. The average level of canopy damage within the plantations was 77%. Based on Random Forest variable importance values, plantation age was the best predictor of canopy damage. Average annual precipitation, elevation and topographic position were ranked second, third, and fourth, respectively. A model selection procedure, using geo-statistical regression models and Akaike's information criterion, corroborated the importance of plantation age relative to the other predictors tested and also suggested that the influence of age varied over time. The top ranked regression model indicated that the level of canopy damage reached its maximum around age 15 and stayed relatively high until age 25 before declining.

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1. Introduction

The legacy of past forest management can influence the mosaic of burn damage left in the aftermath of a large wildfire. Several studies have documented the persistent influence of partial harvests and fuel treatments on wildfire effects, (e.g. Finney et al., 2005; Pollet and Omi, 2002; Prichard et al., 2010; Raymond and Peterson, 2005). Equally important, though somewhat less represented in the literature, are studies that quantify the influence of even-aged silvicultural treatments on wildfire effects. Even-age plantations are a common feature of forested landscapes worldwide and there are more than 17 million hectares of conifer plantations in the US alone (FAO, 2005). The available evidence suggests that plantations experience higher levels of canopy damage than surrounding unmanaged forests (Odion et al., 2004; Thompson et al., 2007; Weatherspoon and Skinner, 1995). This is likely attributable to higher stem densities and continuous canopies, which are characteristic features of plantations and can increase vulnerability to crown fire (Kobziar et al., 2009; Stephens

and Moghaddas, 2005; Graham et al., 2004). However, as trees within plantations mature, self-pruning results in higher crown base heights, self-thinning can reduce tree density, and the thickness of tree bark can increase, all of which may decrease the risk of fire damage in some forest types (Agee, 1993; Hanus et al., 2000). This pattern suggests that the increased risk of canopy damage within plantations could be reduced with the passage of time, but an extensive search of the literature produced no empirical data regarding how fire damage varies with plantation age or structure.

The 2002 Biscuit Fire burned at mixed-severities across >200,000 ha of mixed conifer and evergreen hardwood forests in southwest Oregon and northwest California. The fuel complex encountered by the Biscuit Fire was strongly affected by a legacy of forest management, including silviculture treatments of various ages, sizes, and techniques. This included >8300 ha of even-aged conifer plantations, which were established following clearcut harvesting and planted primarily with Douglas-fir (*Pseudotsuga menziesii*) and to a much lesser degree ponderosa pine (*Pinus ponderosa*) and sugar pine (*Pinus lambertiana*). The region has a long history of using even-aged silvicultural practices to achieve timber production goals, which were a dominant management objective from the 1950s until the early 1990s, when federal logging was curtailed with the adoption of the Northwest Forest Plan (Walstad, 1992). Accordingly, most plantations encountered by the Biscuit Fire

* Corresponding author. Tel.: +1 540 635 6580; fax: +1 540 635 6506.

E-mail addresses: thompsonjr@si.edu (J.R. Thompson), tspies@fs.fed.us (T.A. Spies), keith.olsen@oregonstate.edu (K.A. Olsen).

¹ Tel.: +1 541 750 7354; fax: +1 541 750 7329.

² Tel.: +1 541 750 7279; fax: +1 541 750 7329.

range in age from approximately 10 to 50 years old. We are aware of no previous empirical studies to explicitly consider the relationship between plantation age and wildfire damage, however, Graham (2003) did note that plantations younger than 12 years experienced higher levels of burn severity (as determined from Landsat-derived burn mapping) than did older plantations during the 2002 Hayman Fire in Colorado. Similarly, Thompson et al. (2007) found high levels of canopy damage within 12- to 15-year-old management units that were salvage-logged and planted after the 1987 Silver Fire then burned again in the Biscuit Fire. Fire modeling also suggests that plantations are more vulnerable than unmanaged stands from the time they are young saplings (<5 years) at least until they reach >50 cm diameter at breast height (Stephens and Moghaddas, 2005).

Our overall objective was to develop a better understanding the factors that were associated with burn damage within the intensively managed portion of the Biscuit Fire. We used pre- and post-fire digital aerial photography to examine how the level of Biscuit Fire canopy damage varied within 198 plantations in relation to their age, topographical setting, the weather conditions on the day of burn, climate (productivity) and vegetation-cover. Ideally, fire effects should be quantified through pre-fire field measurements of fuel conditions coupled to post-fire measures of fire-effects on above- and below-ground resources. Unfortunately, the expense of field sampling and the inability to forecast wildfire locations and measure them in advance of wildfire occurrence limits the use of this approach. Instead, we interpreted vegetation conditions within pre- and post-fire digital aerial photos. By interpreting vegetation condition using digital aerial photography, we are able to attain some of the ecological resolution of ground plots but with the data collection facility of remote sensing.

Based on our previous work quantifying fire damage within the unmanaged portion of the Biscuit Fire, which showed the highest levels of canopy damage in very young and shrubby vegetation (Thompson and Spies, 2009), we hypothesized that plantation age would be negatively correlated with the level of canopy damage but that the effect of plantation age would decrease over time. Further, we hypothesized that daily fire weather conditions would also be an important predictor of canopy damage, with extreme fire weather conditions overriding all other structural or other environmental variables.

2. Methods

2.1. Study area

The study was conducted within the perimeter of the 2002 Biscuit Fire, which encompassed approximately 200,000 ha of the Klamath Mountains in southwest Oregon and northwest California. The area is primarily managed by the Rogue–Siskiyou National Forest (RSNF) and is within the mixed evergreen vegetation zone (Franklin and Dyrness, 1988). While the Biscuit region does include areas of low-productivity, ultramafic soils, those regions were excluded from this study. The plantations we examined are underlain by igneous, meta-sedimentary, and metamorphic soil parent materials. Unmanaged forests on these soils are dominated by conifer species such as Douglas-fir, sugar pine, and white fir (*Abies concolor*). Dominant evergreen hardwoods include tanoak (*Lithocarpus densiflora*), Pacific madrone (*Arbutus menziesii*), and canyon live-oak (*Quercus chrysolepis*). Manzanita (*Arctostaphylos* sp.), and Saddle oak (*Quercus sadleriana*) are common shrubs. Topography within the Biscuit Fire is steep and complex; elevations range from 100 to 1500 m. Mean January temperature is 6 °C. Mean July temperature is 16 °C. Mean annual precipitation is 270 cm, with greater than 90% occurring as a mixture of snow and rain during winter

and spring (Daly et al., 2002). A detailed account of the Biscuit Fire's effect on vegetation cover within unmanaged areas can be found in Thompson and Spies (2009).

2.2. Management data

Our analysis focused on 200 even-aged plantations randomly selected from a RSNF spatial database that described the location of all significant historical logging and planting, which included a total of 652 conifer plantations (8300 ha) within the fire's perimeter. To be eligible for inclusion in this study, each unit must have been clearcut between 1960 and 1996 and have a record of successful conifer planting. Of the 200 selected units, 35 were salvage-harvests completed between 1988 and 1991 following the 1987 Silver Fire (to determine if the salvage units had a unique influence on canopy damage we analyzed our data with and without these plantations.). Two units were later removed because their positions were inaccurate within the spatial database. Records were incomplete regarding species composition and volume removed, site preparation, and planting density. However, discussions with RSNF employees indicated that some live trees were left after harvests and that planting was overwhelmingly Douglas-fir with a much lesser component of ponderosa and sugar-pine. Multiple planting dates, all clustered within 1–3 years of harvest, were often associated with individual management units. We therefore used the date of harvest as a surrogate for the plantation's establishment date, unless there was evidence that original planting had failed and the site had been reforested at a later date. Harvest date information was considered reliable by RSNF personnel (pers. comm. J. Hawkins, Gold Beach Ranger District, RSNF).

2.3. Aerial photo plots

Photo-plots were a grid of 50-by-50 meter cells overlain onto the variably-shaped harvest unit polygons supplied by the RSNF. On large harvest units (>6.25 ha), we randomly selected 25 cells to use as the plot. For management units <6.25 ha but >1.25 ha, we used all cells as the photo-plot. Management units <1.25 ha were excluded from this study. The best available pre-Biscuit Fire photos were digital orthoquads taken as part of the USDA National Agriculture Imagery Program in August 2000; they were panchromatic with a 1 m grain size. The post-Biscuit Fire photos were taken on September 24, 2002, were true color, and had a 25 cm grain size. We spatially co-registered the pre- to post-fire photo plots using approximately 15 ground control points per plot and used a first-order polynomial transformation for geo-rectification. Starting with the pre-fire photos, a single researcher (Thompson) estimated the percent cover of live vegetation and bare ground/grass cover (which were indistinguishable) in each cell in every plot. Then, using the post-fire photos, the same researcher measured the percent of the vegetation cover that was scorched or consumed (i.e. canopy damage) by the Biscuit Fire. Cell-level estimates were then averaged to obtain plot-level values. Our original intent was to separate canopy consumption from canopy scorch to infer differences in fire behavior (i.e. surface fire versus torching). Unfortunately, however, the vertical and horizontal continuum between scotch and consumption we witnessed in the photos and in field assessments revealed that any attempts to make inferences in this regard would be unreliable. Therefore, we treated scorch and consumption collectively as “canopy damage.”

At the onset of the research, we developed a catalog of paired oblique-to-aerial photos for use as a training manual and later informally ground-truthed a subset of photo-plots, which revealed excellent correspondence between post-fire field conditions and photo measurements. Indeed, the 25 cm resolution of the post-fire photography permitted an unambiguous interpretation of the fire's

effects on tree canopies. Nonetheless, it is important to note that canopy damage measured from a planer view of the landscape (i.e. from an aerial photo) is not strictly equivalent to the proportion of the crown volume damaged as measured in the field.

2.4. Topographic and weather variables

We used a 10-m digital elevation model to calculate the average elevation, percent slope, Beers' transformed aspect (Beers et al., 1966), and topographic position for each photo-plot. To capture local and broad scale variation in topography, we calculated topographic position at two scales: "TP-Fine" is the difference between the mean plot elevation and the mean elevation in an annulus 150–300 m from the plot, while "TP-Coarse" uses an annulus 850–1000 m from the plot. The topographic index values are in units of meters, but their usefulness is chiefly in a relative sense (c.f. Jones et al., 2000). For example, within the TP-Fine index, a value of, say 30 m, reflects the fact that most of the area immediately around the focal site (within 150–300 m) is at a higher elevation. The RSNF provided a map that depicted the daily progression of the Biscuit Fire, which we used to assign weather data to each photo-plot based on the day it burned. We assigned the average temperature, relative humidity, wind speed, and cosine transformed wind direction between 10:00 and 19:00 for each day as calculated from the Quail Prairie Remote Automated Weather Station, located within the fire perimeter. To capture regional gradients in productivity associated with moisture availability, we assigned each photo plot the average local annual precipitation for the climatological period spanning 1971–2000 to each plot based on the PRISM model (Daly et al., 2002).

2.5. Data analysis

To rank the predictor variables in terms of the strength of their relationship to the response, we calculated variable importance values using the Random Forest (RF) algorithm (Liaw and Wiener, 2002) within the R statistical environment (R Development Core Team, 2006). While RF is relatively new to forestry and ecological research, its use is growing and, in simulation and comparative analyses, it has consistently out-performed other methods for prediction accuracy and ranking variable importance (Cutler et al., 2007; Lawler et al., 2006; Prasad et al., 2006). The RF algorithm (as applied to these data) selects 1500 bootstrap samples, each containing two-thirds of the photo plots. For each sample, it creates an un-pruned regression tree with modification that, at each node, it randomly selects only one-third of the predictor variables and chooses the best partition from among those variables. To assess the predictive power of the model, RF calculates an ensemble average of all the regression trees, which is used to predict the level of canopy damage for the plots not included in the bootstrap sample. The RF model is then used to calculate importance values for each of the predictor variables by calculating the percent increase in the mean squared error (MSE) in the predicted data when the values for that predictor are permuted and the others are left intact.

To further assess potential relationship between canopy damage and the predictor variables (including potential interactions) we compared a series of regression models using Akaike's information criterion, (AIC; Burnham and Anderson, 2002). We compared 11 different regression models that included the top-ranking predictors from the RF analysis (i.e. those predictors uses inclusion the model reduces the MSE by >10%) in addition to a null model that contained no predictor variables. Due to the relative importance of plantation age in the RF model and our hypothesis that the influence of age would vary over time, we also assessed whether the relationship between age and canopy damage varied

over time by adding a polynomial term. Semivariograms of model residuals from an ordinary least squares (OLS) regression displayed strong positive spatial autocorrelation to distances >5 km (not shown). Due to the lack of independence of the residuals and the shape of the semivariogram we chose to fit a generalized least squares (GLS) regression models that included a spherical spatial correlation structure using the 'nlme' package (Pinheiro et al., 2009) within the R statistical environment (R Development Core Team, 2006). GLS regression relies on the distance between sample locations and the form of the correlation structure to derive a variance–covariance matrix, which is, in turn, used to solve a weighted OLS regression (Dormann et al., 2007).

3. Results

Sampled plantations ranged in age from 5 to 47 years (Fig. 1) and in size from 1.25 to 47 ha. Ninety-seven percent of the plantations (192 of 198) had >1% canopy damage. The average level of canopy damage within photo plots was 77% (SD = 20.1; Table 1). The RF model explained 34% of variability in canopy damage and identified plantation age as the most important predictor variable (Fig. 2), with older plantations experiencing lower levels of canopy damage. Average annual precipitation had a generally negative relationship with canopy damage and was ranked second by the RF model. Elevation and topographic position both had a positive relationship with canopy damage and were ranked third and fourth, respectively. No other predictor variable included within the RF model reduced the MSE by >10%.

Based on the RF results, we compared 11 different GLS regression models (Table 2). The top ranked model included plantation age and a polynomial term that allowed the effect of age on canopy damage to vary. This model was significant at $P < 0.0001$ and had a pseudo- R^2 of 0.30 (Fig. 3). Modeled percent canopy damage reached its maximum (91%) in plantations that were around age 15 and stayed relatively high (above 80%) within plantations that were between 15 and 25 years old before declining in older plantations. Based on conventions of the information theoretic approach (whereby models whose AIC statistics are within two units of the highest ranked model are considered equal (Burnham and Anderson, 2002)), no other model fit the data as well. However, it is important to note that, while modeled canopy damage does decline after plantations reach age 25, there is considerable variability in the data, and some plantations >25 years did experience high levels of damage. These results were not qualitatively different when we removed those plantations that were created after post-fire salvage logging from 1988 to 1990 then reran the analyses.

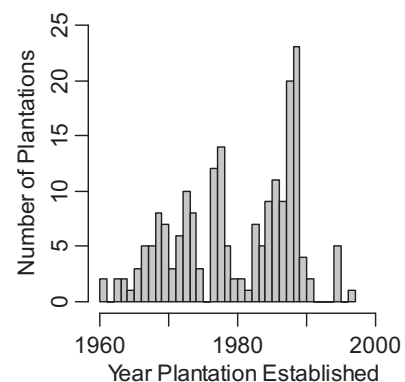


Fig. 1. The distribution of sampled plantation ages.

Table 1
Summary statistics for response and predictor variables used in the Random Forest analysis of crown damage within conifer plantations in the 2002 Biscuit Fire (DOB = day of burn).

Variables	Mean	Standard deviation	Minimum	Maximum
<i>Response variable</i>				
Percent crown damage	77.8	20.1	0	100
<i>Predictor variables</i>				
Age (years)	22	8.4	5	42
Harvest size (ha)	14.1	15.3	1.25	47
Vegetation cover (%)	89.8	10.7	47	100
Bare/grass cover (%)	10.3	10.0	0	53
Elevation (m)	885	227	265	1346
Topographic position (fine)	3.4	13.1	−25.7	49.4
Topographic position (coarse)	26.8	77.0	176.4	203.3
Slope (%)	40	13.6	12	79
Beer's aspect	−0.2	0.5	−0.97	0.99
Average annual precipitation (cm)	320	71	171	439
Temperature on DOB (°C)	26.6	4.9	16.6	35.8
Relative humidity on DOB (%)	31	15	10	65.5
Wind speed on DOB (km/h)	9	2.1	4.2	18.2
Wind direction on DOB (cosine transformed)	0.24	0.44	−0.3	0.75

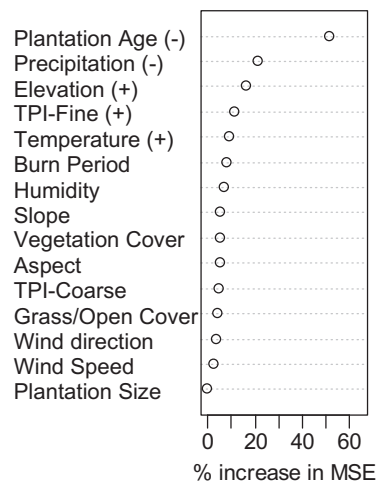


Fig. 2. Variable importance plots for predictor variables from a Random Forests model of canopy damage within conifer plantations. Predictor variables are along the y-axis and the average increase in the mean square error when data for that variable are permuted and all other are left unchanged is on the x-axis. The direction of the relationship is given in parentheses for predictor variables whose Pearson's correlation were significant at $p < 0.05$; however, we urge caution in this interpretation as Random Forest variable importance values are not based on linear relationships alone.

Table 2
Comparison of geo-statistical regression models based on Akaike information criteria (AIC; interaction terms implicitly include their associated additive term).

Rank	Model Form	AIC	Δ AIC	ω_i
1	AGE + AGE ²	1713.9	0	0.907
2	AGE + AGE ² + TPI	1719.3	5.4	0.061
3	AGE + AGE ² + ELEV	1721.3	7.4	0.022
4	AGE + AGE ² + PRECIP	1723.8	9.9	0.006
5	AGE + AGE ² + PRECIP + TPI	1726.7	12.8	0.002
6	AGE	1727.6	14.1	0.001
7	AGE + AGE ² + PRECIP + ELEV	1729.2	15.3	0.000
8	AGE * TPI	1738.5	24.6	0.000
9	AGE * ELEV	1748.8	34.9	0.000
10	AGE * PRECIP	1753.9	40.0	0.000
11	NULL MODEL	1760.2	46.3	0.000

4. Discussion

Given the absence of controlled experiments within large wildfires, long-term records of forest management type, location, and

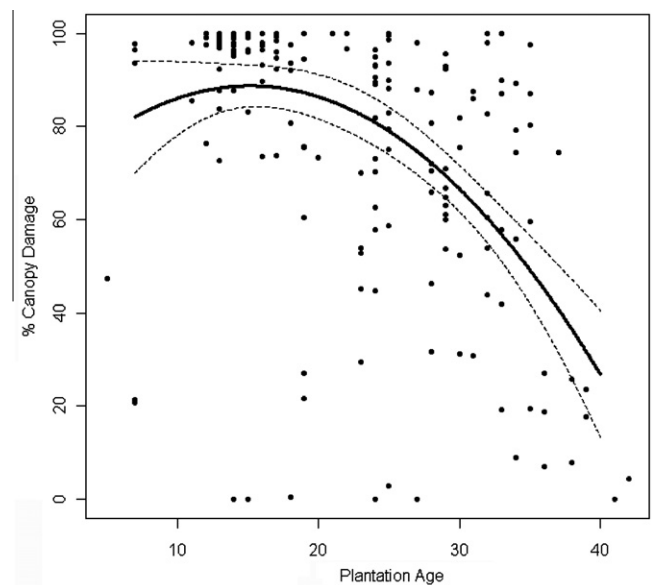


Fig. 3. Relationship between plantation age and percent canopy damage used to fit a generalized least squares regression model with a spatial spherical correlation structure to accommodate positive spatial autocorrelation. Dashed lines represent 95% confidence intervals.

intensity are important for retrospectively assessing wildfire effects. Unfortunately, with the exception of plantation age and its status as a “successful” reforestation effort, we had no reliable and consistent records documenting the plantations’ specific management history or composition at the time of the fire. The lack of site information is important limitation of this study. Indeed, site preparation has been shown to be an important predictor of plantation canopy damage, for example, where broadcast burned sites experienced significantly less damage than untreated or piled-and-burned sites (Weatherspoon and Skinner, 1995). Similarly, in a fortuitous experiment regarding fire effects after thinning in 90–120 year old unmanaged stands within the Biscuit Fire, tree mortality was lowest (5%) on sites that were thinned in 1996 then broadcast burned in 2001, just 1 year before the fire, intermediate in unmanaged sites (53–54%), and highest in sites that were thinned in 1996 but not broadcast burned (80–100%; Raymond and Peterson, 2005). Nonetheless, we were able to look back over 40 years of even-age forest management and document a relatively strong relationship between plantation age and the level of canopy

damage. To our knowledge, no similar empirical information documenting this relationship exists.

Of the 15 predictor variables we examined, we found that level of canopy damage in plantations was most strongly related to its age. Indeed, the variable describing the age of plantations reduced the error in the model by more than twice as much as any of the other predictors (Fig. 2). The shape of the best-fitting geo-statistical regression model suggested that the level of canopy damage reached its maximum around age 15 and stayed relatively high until age 25 before declining (Fig. 3). This pattern is consistent with what is known about the fire ecology of Douglas-fir forests, whether planted or naturally regenerated (Starker, 1934; Agee, 1993). The fire resistance of Douglas-fir increases with age due to a continually thickening layer of protective bark and due to increasing height-to-crown, which is associated with reduced likelihood of torching or crown fires (Scott and Reinhardt, 2001; Graham et al., 2004). In effect, as Douglas-fir matures it transitions from an “avoider” (a species that is vulnerable to low intensity fires) to a “resister” (a species that has adaptations that increase the probability of survival during low intensity fires; Agee, 1993, pp. 206 and 285). Empirical growth curves show that by the time a Douglas-fir plantation in southwest Oregon is 25 years old an average tree is typically between 8 and 16 m tall and have crown base heights >3 m off the ground, depending on site class and stem density (Hann and Scrivani, 1987; Hanus et al., 2000). The combination of bark thickness and a sufficiently high crown-base-height is the likely explanation for, on average, decreasing canopy damage in the older plantations. However, given the data available to us in this study it is impossible to know exactly which fire resistance strategy (or combination of strategies) was responsible for the pattern of decreasing canopy damage with plantation age.

Our previous research in the unmanaged portion of the Biscuit suggested that weather conditions on the day of the burn were an important correlate of canopy damage (Thompson and Spies, 2009). Therefore, it was surprising that the predictor variables describing daily weather conditions were comparatively unimportant (Fig. 2 and Table 2). There are at least two possible explanations for the difference. In the study of unmanaged forests, we did not have explicit information on the age or structure of the stands, but most were mature mixed-conifer >50 years old. It is possible that fire weather is a better predictor of canopy damage in older stands where extremes in wind and fuel moisture are necessary to transition from a surface fire to torching the canopy or running as a crown fire (Van Wagner, 1977). Another possible reason for the difference relates to differences in the sampling extent and intensity. The study of unmanaged forest had many more plots that encompassed a much larger area and burned over a longer period of time spanning a greater range of variability in weather conditions. Average annual precipitation was ranked as the second most important predictor of canopy damage within the plantation and had a generally negative correlation. In this landscape, precipitation is correlated with productivity (Coops and Waring, 2001). Given the much stronger relationship between canopy damage and plantation age, the weak negative relationship with precipitation may suggest that greater moisture and productivity accelerated stand development and, in turn, decreased the age at which fire resistance is reached.

Given the ubiquity of plantations within fire-prone landscapes, it is perhaps surprising that so little research has been done regarding fire behavior in even-aged conifer plantations. The existing empirical research suggests that when compared to more heterogeneous unmanaged forests, plantations are associated with elevated fire damage (Weatherspoon and Skinner, 1995; Odion et al., 2004). While the intent of this study was not to compare unmanaged stands to plantations, it is worth noting that, in a separate examination of Biscuit Fire effects (Thompson and Spies,

2009), the average level of canopy damage within unmanaged forest with variable stand histories was lower than it was within the plantations measured herein (65% in the previous study of unmanaged forests versus 78% in the present study). Given the relationship between plantation age and canopy damage, the difference in canopy damage between unmanaged and unmanaged stands may have more to do with the fact that most of the unmanaged stands were >50 years old, than with their origin as “unmanaged” (i.e. naturally regenerated).

With the clear proviso that our study was observational and only describes Douglas-fir plantations burned within the Biscuit Fire, for the sake of context it is also worth noting that fire modeling studies in other regions that have examined fire behavior and tree mortality within a range of silvicultural treatment types and ages have found a similar trends of decreasing fire damage with increasing age (e.g. Kobziar et al., 2009; Stephens and Moghaddas, 2005). For example, in Sierra Nevada ponderosa pine plantations, high rates of mortality were predicted for untreated conifer plantations (when compared to young growth reserves (80–100 years)) across all diameter classes up to 50 cm DBH, regardless of weather conditions (Stephens and Moghaddas, 2005). In the Biscuit Fire, young (<15 years) Douglas-fir stands tended experience high levels of canopy damage whether they were plantations or naturally regenerated stands. This was demonstrated through a separate examination of the areas that burned at high severity in the 1987 Silver Fire and were subsequently re-burned by the Biscuit Fire (Thompson and Spies, 2010).

5. Conclusion

In this paper, we utilized pre- and post-fire digital aerial photography to assess fire-related canopy damage within Douglas-fir plantations in southwest Oregon. We used parametric and non-parametric modeling approaches to examine the level of canopy damage in relation to several variables describing the vegetation-cover, topographic setting, weather conditions on the day a site burned, and the time since the plantations were established (i.e. the plantations' age). We found that age of a plantation was the best predictor of the level canopy damage and that the other variables were comparatively poor predictors. The best fitting geostatistical regression model indicated that the level of canopy damage reached its maximum around age 15 and stayed relatively high until age 25 before declining. Based on a previous analysis of unmanaged vegetation (Thompson and Spies, 2009), we had hypothesized that daily weather conditions would be important predictor variables within the models. However, the data did not support this hypothesis. Our findings, while observational and thus not generalizable, offer managers and forest scientists a rare empirical perspective on patterns fire damage within even-age conifer plantations, which are a common landscape feature throughout the western North America. At least in this case, the data suggest that young plantations were vulnerable to canopy damage regardless of their environmental setting.

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REVIEW

Impacts of salvage logging on biodiversity: A meta-analysis

Simon Thorn¹  | Claus Bässler² | Roland Brandl³ | Philip J. Burton⁴ | Rebecca Cahall⁵ | John L. Campbell⁵ | Jorge Castro⁶ | Chang-Yong Choi⁷ | Tyler Cobb⁸ | Daniel C. Donato⁹ | Ewa Durska¹⁰ | Joseph B. Fontaine¹¹ | Sylvie Gauthier¹² | Christian Hebert¹² | Torsten Hothorn¹³ | Richard L. Hutto¹⁴ | Eun-Jae Lee¹⁵ | Alexandro B. Leverkus¹⁶  | David B. Lindenmayer¹⁷  | Martin K. Obrist¹⁸ | Josep Rost^{19,20} | Sebastian Seibold^{2,21}  | Rupert Seidl²² | Dominik Thom²² | Kaysandra Waldron²³ | Beat Wermelinger²⁴ | Maria-Barbara Winter²⁵ | Michal Zmihorski²⁶ | Jörg Müller^{1,2} 

¹Field Station Fabriksschleichach, Department of Animal Ecology and Tropical Biology (Zoology III), Julius-Maximilians-University Würzburg, Rauhenbrach, Germany

²Bavarian Forest National Park, Grafenau, Germany

³Department of Ecology, Animal Ecology, Faculty of Biology, Philipps-Universität Marburg, Marburg, Germany

⁴University of Northern British Columbia, Terrace, BC, Canada

⁵Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA

⁶Department of Ecology, University of Granada, Granada, Spain

⁷Department of Forest Sciences, Seoul National University, Seoul, Korea

⁸Royal Alberta Museum, Edmonton, AB, Canada

⁹School of Environmental & Forest Sciences, University of Washington, Seattle, WA, USA

¹⁰Department of Ecology and Biodiversity, Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland

¹¹School of Veterinary and Life Sciences, Murdoch University, Murdoch, WA, Australia

¹²Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Quebec, QC, Canada

¹³Division of Biostatistics, University of Zürich, Zürich, Switzerland

¹⁴Division of Biological Sciences, University of Montana, Missoula, MT, USA

¹⁵Urban Planning Research Group, Daejeon Sejong Research Institute, Daejeon, Korea

¹⁶Ecology Unit, Department of Life Sciences, University of Alcalá, Alcalá de Henares, Madrid, Spain

¹⁷Fenner School of Environment and Society, The Australian National University, Canberra, ACT, Australia

¹⁸WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Biodiversity and Conservation Biology, Birmensdorf, Switzerland

¹⁹Department of Environmental Sciences and Food Industries, University of Vic-Central University of Catalonia, Catalonia, Vic., Spain

²⁰Department of Environmental Sciences, University of Girona, Girona, Spain

²¹Department of Ecology and Ecosystem Management, Chair for Terrestrial Ecology, Technische Universität München, Freising, Germany

²²Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences Vienna, Vienna, Austria

²³Department of Wood and Forest Sciences, Laval University, Québec, QC, Canada

²⁴WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Forest Dynamics – Forest Entomology, Birmensdorf, Switzerland

²⁵Forest Research Institute of Baden-Württemberg (FVA), Freiburg, Germany

²⁶Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence
Simon Thorn
Email: simon@thornonline.de

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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-saproxyllic 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. saproxyllic organisms) decreased more strongly than richness of non-saproxyllic 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 saproxyllic 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, saproxyllic 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 saproxyllic and non-saproxyllic 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,

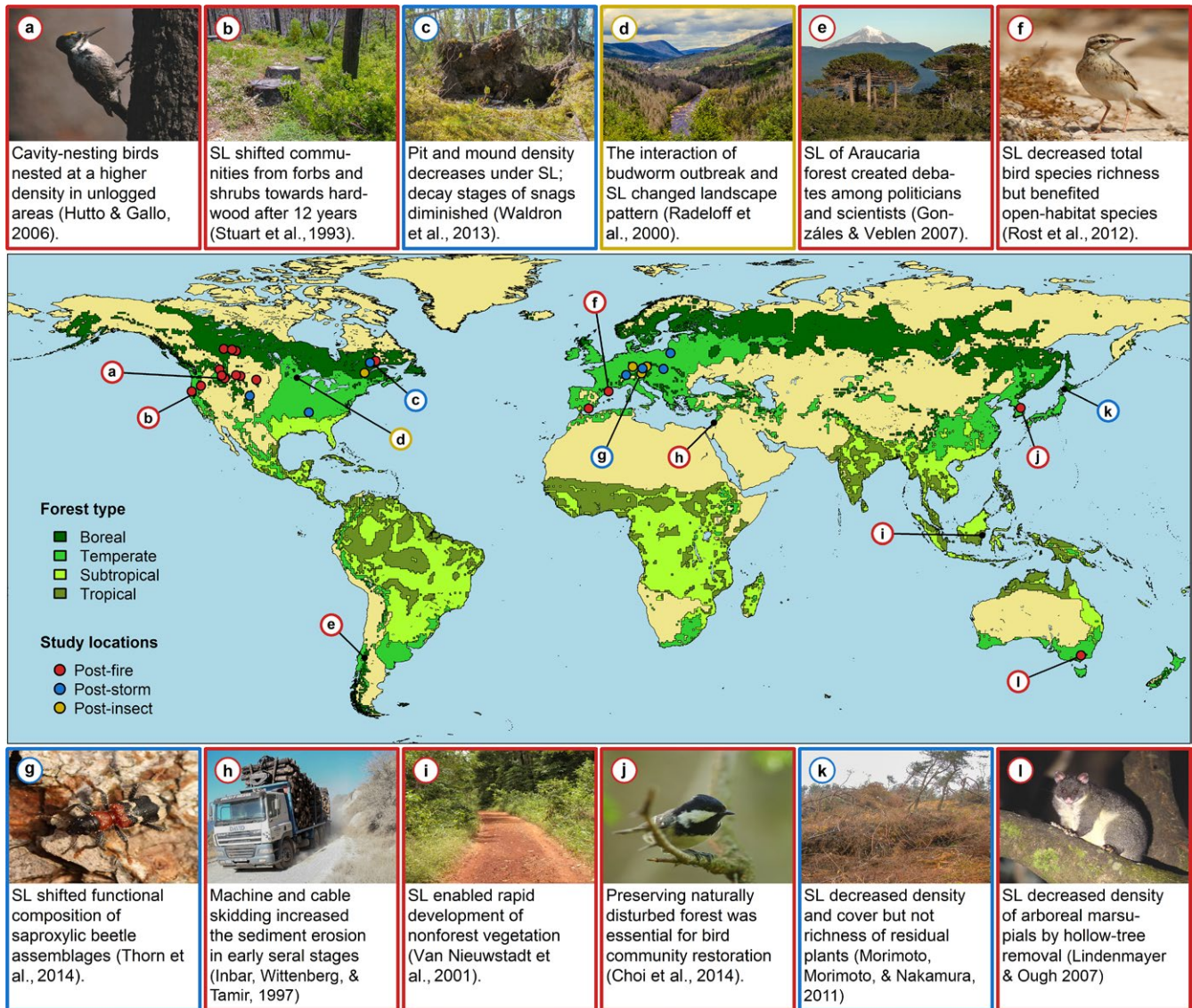


FIGURE 1 Salvage logging (SL) is commonly applied after wildfires, windstorms or insect outbreaks, and leads to changes in habitats and community compositions in various forest ecosystems around the world (as highlighted by the studies illustrated in panels (a–l). Study locations (coloured circles) represent 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, Hébert, & 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 were: 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).

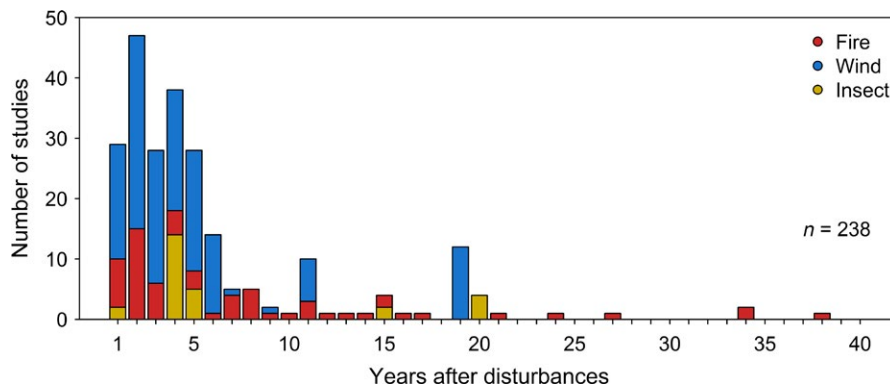


FIGURE 2 Distribution of studies investigating the effects of salvage logging on biodiversity after wildfire, windstorms and insect outbreaks according to the years after disturbance. [Colour figure can be viewed at wileyonlinelibrary.com]

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).

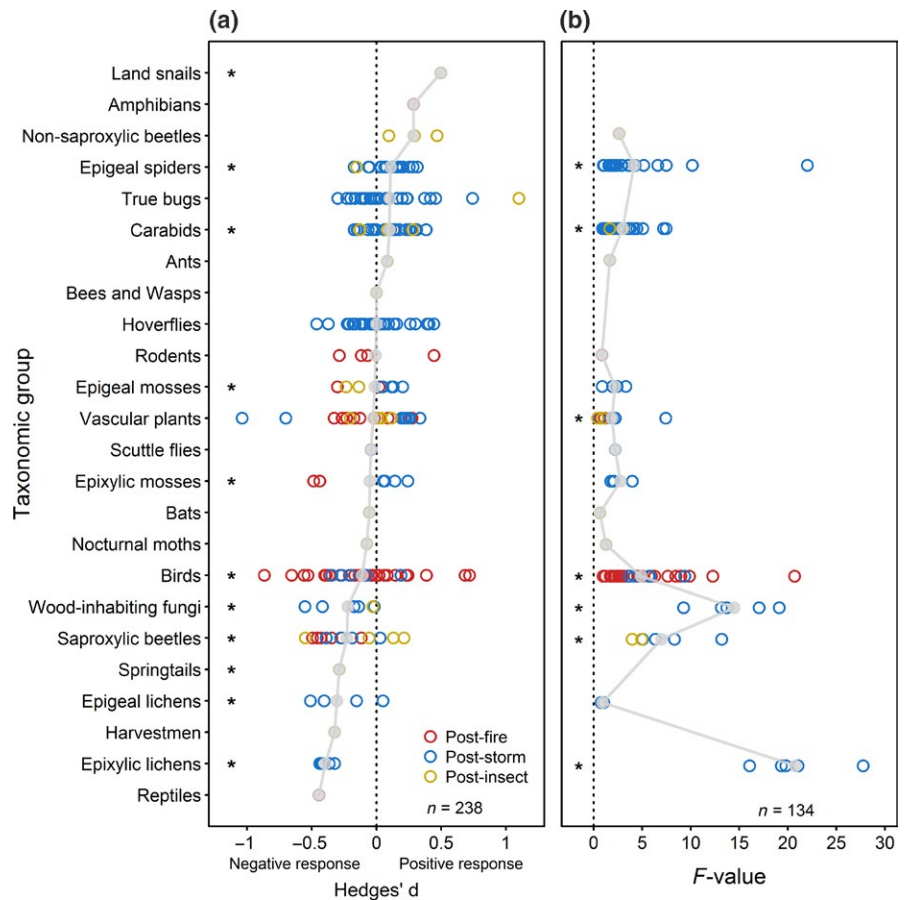
It is important to note that losses of saproxylic species can be present also within taxonomic groups that displayed no response in their overall species numbers (Figure 3a). For instance, birds (the most studied vertebrate group) were slightly negatively affected by salvage logging (Figure 3a), despite 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 wind-thrown 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

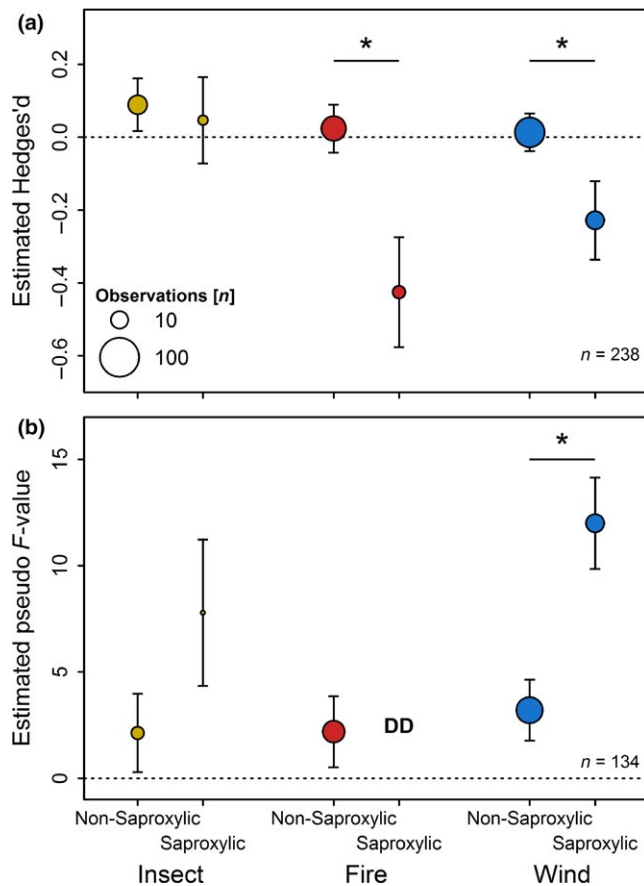


FIGURE 4 (a) Estimated response and corresponding standard error of saproxylic and non-saproxylic taxa to salvage logging based on 238 individual comparisons (based on Hedges' d) of numbers of species in burned, storm- and insect-affected forests. Negative estimates correspond to a decrease in numbers 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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Invader removal triggers competitive release in a threatened avian predator

J. David Wiens^{a,1}, Katie M. Dugger^b, J. Mark Higley^c, Damon B. Lesmeister^d, Alan B. Franklin^e, Keith A. Hamm^f, Gary C. White^g, Krista E. Dilione^a, David C. Simon^a, Robin R. Bown^h, Peter C. Carlson^g, Charles B. Yackulicⁱ, James D. Nichols^j, James E. Hines^j, Raymond J. Davis^d, David W. Lamphear^f, Christopher McCafferty^d, Trent L. McDonald^k, and Stan G. Sovern^l

^aUS Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, OR 97330; ^bUS Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331; ^cHoopa Tribal Forestry, Hoopa, CA 95546; ^dUS Department of Agriculture Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331; ^eUS Department of Agriculture Wildlife Services, National Wildlife Research Center, Fort Collins, CO 80521; ^fGreen Diamond Resource Company, Korb, CA 95550; ^gDepartment of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523; ^hUS Fish and Wildlife Service, Oregon State Office, Portland, OR 97266; ⁱUS Geological Survey, Southwest Biological Science Center, Flagstaff, AZ 86001; ^jUS Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708; ^kMcDonald Data Sciences, LLC, Laramie, WY 82070; and ^lDepartment of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331

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Changes in the distribution and abundance of invasive species can have far-reaching ecological consequences. Programs to control invaders are common but gauging the effectiveness of such programs using carefully controlled, large-scale field experiments is rare, especially at higher trophic levels. Experimental manipulations coupled with long-term demographic monitoring can reveal the mechanistic underpinnings of interspecific competition among apex predators and suggest mitigation options for invasive species. We used a large-scale before–after control–impact removal experiment to investigate the effects of an invasive competitor, the barred owl (*Strix varia*), on the population dynamics of an iconic old-forest native species, the northern spotted owl (*Strix occidentalis caurina*). Removal of barred owls had a strong, positive effect on survival of sympatric spotted owls and a weaker but positive effect on spotted owl dispersal and recruitment. After removals, the estimated mean annual rate of population change for spotted owls stabilized in areas with removals (0.2% decline per year), but continued to decline sharply in areas without removals (12.1% decline per year). The results demonstrated that the most substantial changes in population dynamics of northern spotted owls over the past two decades were associated with the invasion, population expansion, and subsequent removal of barred owls. Our study provides experimental evidence of the demographic consequences of competitive release, where a threatened avian predator was freed from restrictions imposed on its population dynamics with the removal of a competitively dominant invasive species.

invasive species | removal experiment | population dynamics | competition | *Strix* owls

Invasions by nonindigenous species are a pervasive cause of global biodiversity loss (1–3). The legacies of biological invasions, such as species extinctions, can permanently alter ecosystems and have long-term consequences for the management of natural resources. Removal of invasive species has become an increasingly common response in ecological restoration programs focused on maintaining native wildlife and biodiversity (4, 5). Removal efforts that reduce invader densities may have beneficial effects to natives, but whether such efforts can stabilize or reverse declining population trends of affected species remains largely untested, especially at higher trophic levels. A detailed understanding of how control measures affect populations of terrestrial predators, for example, requires field experiments conducted at large spatial scales under a range of environmental conditions. Experimental manipulation of terrestrial predators at broad spatial scales is logistically, financially, and ethically problematic. Consequently, studies that focus on competitive interactions at higher trophic levels are often limited to short-term, observational designs that

lack detailed demographic data, control populations, or sufficient spatial replication to capture species-level responses.

The conservation and management of northern spotted owls (*Strix occidentalis caurina*) is one of the largest and most visible wildlife conservation issues in United States history (6–8). The northern spotted owl, an old conifer forest obligate, was listed in 1990 as a federally threatened subspecies because of rapid declines in old-forest habitats (9). Despite over 30 y of protection under the Federal Endangered Species Act, populations have continued to decline and, in some cases, those declines have accelerated (10, 11). Long-term demographic monitoring of spotted owl populations across the species' range identified rapid increases in the occurrence of nonnative barred owls (*Strix varia*) as a primary reason for those declines, especially in recent years (10–12). As a species native to eastern North America, barred owls began expanding their populations westward in the early 1900s. The subsequent barred owl invasion into western North America has been well documented, and the newly extended range of this species now completely overlaps

Significance

Invasive species can cause extinctions of native species and widespread biodiversity loss. Invader removal is a common management response, but the use of long-term field experiments to characterize effectiveness of removals in benefitting impacted native species is rare. We used a large-scale removal experiment to investigate the demographic response of a threatened native species, the northern spotted owl, to removal of an invasive competitor species, the barred owl. Removal of barred owls had a strong, positive effect on survival of spotted owls, which arrested long-term population declines of spotted owls. The results demonstrate that the long-term persistence of spotted owls will depend heavily on reducing the negative impacts of barred owls while simultaneously addressing other threats, such as habitat loss.

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¹To whom correspondence may be addressed. Email: jwiens@usgs.gov.

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that of the northern spotted owl (13, 14) (Fig. 1C). While congeneric barred owls are morphologically (Fig. 1A and B) and ecologically similar to spotted owls, barred owls are larger, use smaller home ranges, and have a much broader (generalist) diet that includes many small mammal prey important to spotted owls (15, 16). Barred owls are also competitively dominant to spotted owls during territorial confrontations, and where the two species co-occur, they exhibit a high degree of overlap in patterns of habitat use (16). This combination of exploitation and interference competition, coupled with rapidly increasing numbers of barred owls in older forests throughout the Pacific Northwest, exacerbated spotted owl population declines historically triggered by habitat loss (7, 10, 17).

Mounting concerns about the threat of barred owls prompted consideration of several potential research and management options (15, 18). Among these, removal experiments were identified as having the greatest value in determining the role of barred owls in population declines of spotted owls, plus the experiments would provide a means of directly testing the effectiveness of removals as a possible management tool for spotted owl recovery (19, 20). A

review of possible study designs concluded that a paired before–after control–impact (BACI) experimental design could provide the strongest inference and greatest statistical power in addressing both research and federal regulatory agency needs (20, 21). As barred owl populations continued to expand throughout the spotted owl's range, a pilot removal experiment was initiated near the barred owl's invasion front into California (22, 23). The study concluded that removal of barred owls, when coupled with conservation of suitable forest conditions, can slow or even reverse population declines of spotted owls. Yet, this pilot study was conducted at a time and location where barred owl populations were relatively sparse compared to spotted owls (10). Meanwhile, in Oregon and Washington, populations of barred owls had grown so rapidly that they greatly outnumbered spotted owls in many areas and were having considerable impacts on spotted owl territory occupancy (10, 17, 24), resource use (16) and, ultimately, population trends (10, 12). It was unknown whether the positive results of barred owl removal documented previously in California could be achieved in areas with different forest conditions, greater densities of barred owls, and fewer remaining spotted owls.

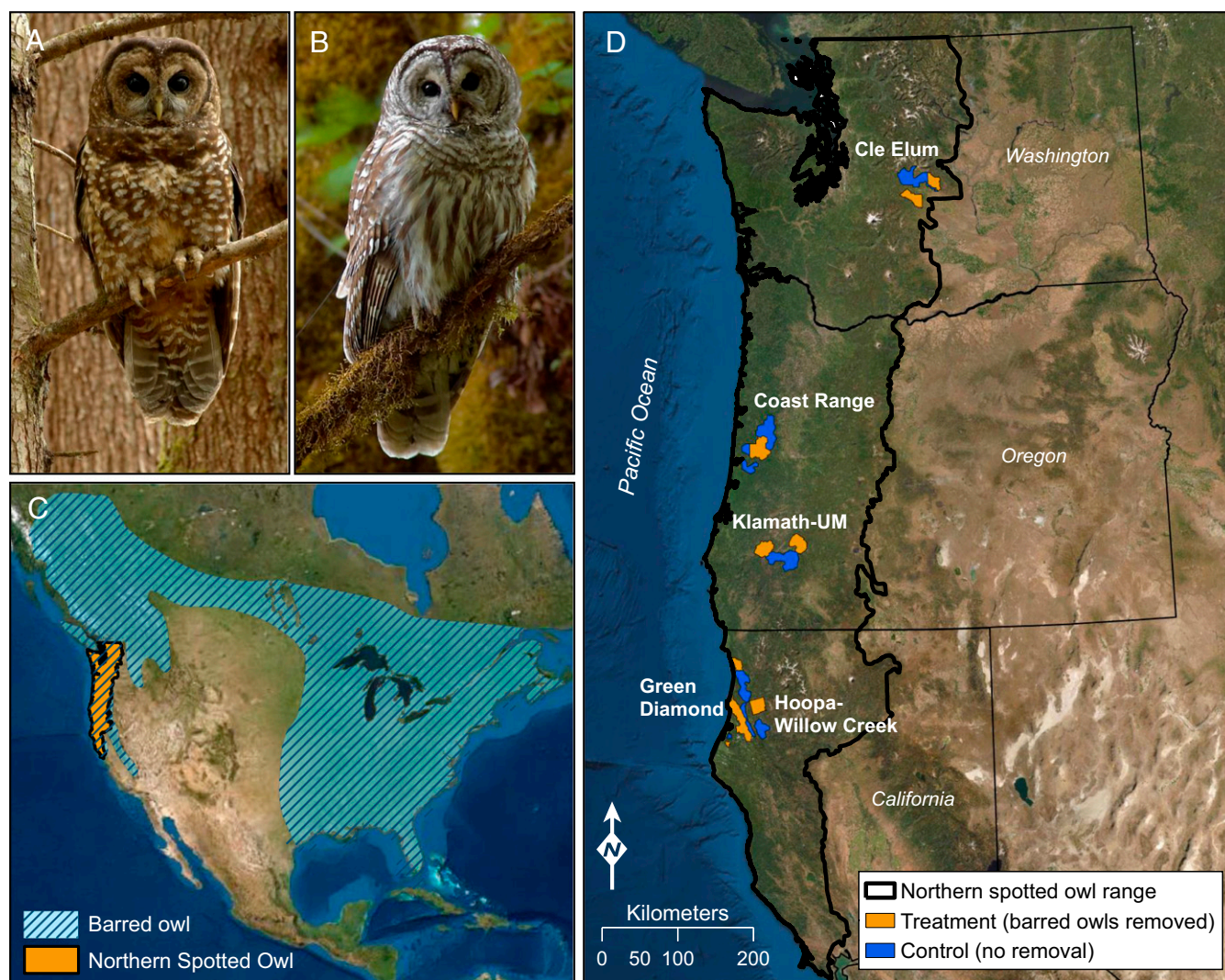


Fig. 1. Before–after control–impact experiment used to estimate the demographic response of threatened northern spotted owls to removal of invasive barred owls. (A) Adult northern spotted owl (*S. occidentalis caurina*) and (B) adult barred owl (*S. varia*). Owl images credit: Patrick Kolar (photographer). (C) Overlap between the geographic ranges of northern spotted owls (US range in orange) and barred owls (hatched-blue) in North America. Ranges were approximated from <https://birdsoftheworld.org/bow>. Barred owls were historically limited to eastern North America. (D) Locations of treatment (barred owls removed) and control (no barred owls removed) segments of five long-term experimental study areas within the range of the northern spotted owl in Washington, Oregon, and California.

We used a large-scale BACI removal experiment to investigate the impact of an invasive avian predator, the barred owl, on the population dynamics of an iconic old-forest native species, the northern spotted owl. Our goal was to test the research hypothesis that trends in vital rates (survival, dispersal, recruitment) and population rates of change (λ) of northern spotted owls would be positively influenced by barred owl removal. The removal experiment was spatially replicated across five study areas with long-term demographic data on northern spotted owls (Fig. 1D and Table 1), where ecological factors affecting populations, including the presence of barred owls, were well documented (10–12, 25). The removal experiment capitalized on this wealth of information, which allowed us to formally assess the impacts of an invasive avian predator on the population dynamics of a closely related native predator, as well as to suggest possible mitigation measures. Our approach to examining the effect of barred owl removal on spotted owl populations was twofold. We first used long-term mark-recapture data from each study area to examine the effect of barred owl removal on annual survival and dispersal of resident spotted owls in each study area separately. We then combined data from all five study areas in a single meta-analysis of apparent survival, recruitment, and annual rate of population change (*SI Appendix, Supplementary Text*). The meta-analysis treated each individual study area as a unit of replication, thereby providing the strongest possible inferences on the demographic consequences of competition.

Results

Barred Owl Removal. We used barred owl-specific surveys to locate and monitor barred owls (26, 27). We surveyed barred owls across treatment and control areas and throughout the removal period. Removals occurred on treatment areas for 3 to 6 y during 2009 to 2019, depending on the study area (Table 1 and *SI Appendix, Fig. S1*). Barred owls detected in treatment areas were removed using 12-gauge shotguns and well-established field protocols (20, 22, 23). A total of 2,485 barred owls were removed from treatment segments of five different study areas during the experiment (Table 1). The mean number of barred owls removed per year was highly variable among study areas, ranging from a low of 15.8 barred owls per year in Green Diamond (GDR), to a

high of 251.5 barred owls per year in the Oregon Coast Range (COA) (*SI Appendix, Fig. S1*).

Survival and Movement on Individual Study Areas. We used multi-state mark-recapture analysis (28–30) with 7,665 captures and recaptures of 1,721 nonjuvenile spotted owls to estimate the effect of barred owl removal on apparent annual survival and dispersal movements of spotted owls between areas with (treatment) and without (control) removal. We tested for an effect of barred owl removal on apparent survival of spotted owls by introducing a time (before–after) \times treatment (control–impact) interaction to the best mark-recapture models characterizing baseline variation in sex, time, and preremoval differences between treatment and control areas (*SI Appendix, Supplementary Text*). There were negligible differences between treatment and control areas in apparent survival before removals (Fig. 2A). After removals, we observed higher estimates of apparent survival on treatment areas relative to the control areas (Fig. 2A) and a positive mean effect size of removal (Fig. 2B) in all five study areas. All study areas included a positive effect of removals on apparent survival in the top model or in closely competing models (*SI Appendix, Tables S2 and S3*). The estimated mean increase in survival attributable to barred owl removal (mean effect size \pm SE) ranged from a low of 0.044 ± 0.031 in Hoopa-Willow Creek (HUP-WC) to a high of 0.172 ± 0.077 in Cle Elum (CLE) (Fig. 2B). Estimates of mean effect size in CLE, COA, and HUP-WC indicated similar increases in survival to that observed in Klamath-Union/Myrtle (KLA-UM), but with greater uncertainty as shown by larger 95% confidence intervals (CI) that marginally bounded zero. The estimated effect of removals was consistently positive in all five study areas, which provided additional evidence of treatment effects beyond that provided by model selection results and 95% confidence intervals alone.

Movement probability of resident spotted owls from historical territories on control areas to territories on treatment areas (ψ_{CT}) increased considerably in response to barred owl removal on two of the five study areas (CLE and COA) (Fig. 2C and *SI Appendix, Table S4*). In COA, estimates of ψ_{CT} increased from 0.012 ± 0.003 before removals to 0.094 ± 0.040 after removals (an 87% increase

Table 1. Study areas and samples of color-banded owls used to estimate the effect of barred owl removal on vital rates of northern spotted owls in Washington, Oregon, and California

Study area (study area acronym)	Area (km ²)	Total nonjuvenile spotted owls banded since 2002 (M, F)	Total barred owls removed*
Cle Elum, WA (CLE)			
Control	670	39 (22, 17)	
Treatment	604	42 (24, 18)	463
Coast Range, OR (COA)			
Control	1,015	148 (76, 72)	
Treatment	582	83 (43, 40)	1,006
Klamath-Union/Myrtle, OR (KLA-UM)			
Control	698	212 (115, 97)	
Treatment	783	198 (113, 85)	522
Hoopa-Willow Creek, CA (HUP-WC)			
Control	294	146 (70, 76)	
Treatment	348	156 (85, 71)	399
Green Diamond, CA (GDR)			
Control	727	120 (65, 55)	
Treatment	828	340 (178, 162)	95
All study areas combined			
Control	3,404	665 (348, 317)	
Treatment	3,145	819 (443, 376)	2,485

All study areas used 2002 as the start year for inclusion of demographic monitoring data.

*The period of barred owl removal for each study areas was: 2015 to 2019 (CLE), 2015 to 2019 (COA), 2016 to 2019 (KLA-UM), 2013 to 2019 (HUP-WC), and 2009 to 2014 (GDR).

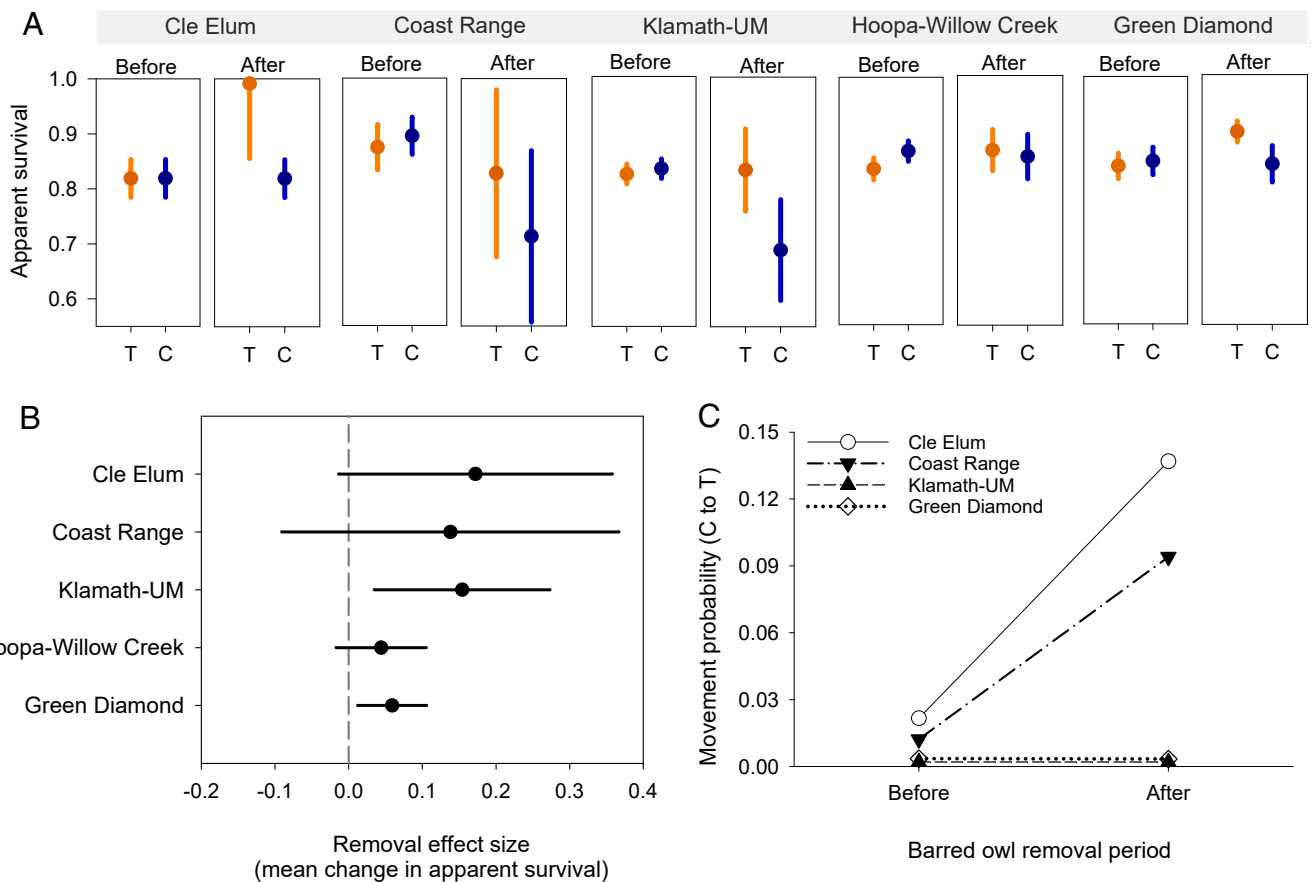


Fig. 2. Estimated effects of barred owl removal on survival and dispersal movements of northern spotted owls in each of five individual study areas in Washington, Oregon, and California. (A) Weighted mean estimates of apparent survival of northern spotted owls before and after barred owls were removed. Mean survival was estimated separately for treatment (T; orange) and control (C; blue) areas in each time period using the best multistate model that included an effect of barred owl removal; estimates were weighted by the inverse of the variance of annual estimates. (B) Mean change in apparent survival attributable to barred owl removal in each study area, calculated using Eq. 2 with estimates shown in A as the mean difference in survival between control and treatment areas before and after removals. Error bars in A and B are 95% CI. (C) Movement probability of resident northern spotted owls from territories in the control area to territories in the treatment (removal) area before versus after removals occurred. No movement was detected on the HUP-WC study area (i.e., movement probability = 0).

in movement; $\hat{\beta}_{CTpost-removal} = 2.00 \pm 0.56$, 95% CI: 0.89, 3.10). Elsewhere, movement probability ranged from a low of 0.002 ± 0.001 in KLA-UM to a high of 0.024 ± 0.008 in CLE (Fig. 2C). Movement models that allowed ψ_{CT} , ψ_{TC} to differ in CLE and GDR were competitive (SI Appendix, Table S4), but 95% CIs for estimated effect sizes overlapped zero in these study areas. We found weak evidence for sex-dependent effects on movement probabilities (SI Appendix, Table S4).

Meta-analysis of Survival, Recruitment, and Population Change. We used a reparameterized temporal symmetry mark-recapture model (31, 32) with 6,661 captures and recaptures of 1,484 nonjuvenile spotted owls across all five study areas in a meta-analysis of apparent survival, recruitment, and annual rate of population change of spotted owls (SI Appendix, Supplementary Text). The best base model prior to testing for an effect of barred owl removal included additive effects of study area, treatment area, and year for both survival (ϕ) and recruitment (f), with individual random effects (σ_p), year, and an interaction between study area and treatment area for capture probabilities (p). The addition of a BACI effect of barred owl removal to the best base model resulted in a new minimum Akaike's Information Criterion corrected for small sample size (AIC_c) model that contained 77% of the Akaike weight and was >22 times more likely (SI Appendix, Table S5). The top

model indicated that barred owl removal had a strong, positive effect on apparent survival, and a positive, but weaker, effect on recruitment across all study areas (Fig. 3 and SI Appendix, Table S6). After removals, mean estimates of apparent survival on treatment areas (\pm SE) increased by 0.08 ± 0.02 (GDR) to 0.12 ± 0.04 (KLA-UM) relative to estimates on control areas (Figs. 3 and 4A); the overall mean increase in survival across study areas was 10%.

The effect of removals on recruitment was positive in the top model, but there was uncertainty in the magnitude of the increase as shown by 95% CIs of BACI regression coefficients (SI Appendix, Table S6), and mean effect sizes that included zero (Fig. 4B). A second model that received less support ($\Delta AIC_c = 2.46$) included a strong, positive before–after effect of removal in treatment areas on both apparent survival ($\hat{\beta} = 0.61 \pm 0.14$, 95% CI: 0.34, 0.87) and recruitment ($\hat{\beta} = 0.55 \pm 0.13$, 95% CI: 0.29, 0.82). This second-ranked model received 3.4 times more support compared to the base model without removal effects, and together the top two models with removal effects contained 99.9% of the total AIC_c weight (SI Appendix, Table S5). Estimates of apparent survival were similar between these two models but estimates of recruitment from the top-ranked model indicated a concurrent increase on control areas during the removal period (Fig. 3) that was unaccounted for in the second-ranked model that lacked a before–after effect in control areas. Thus, we relied on estimates of survival

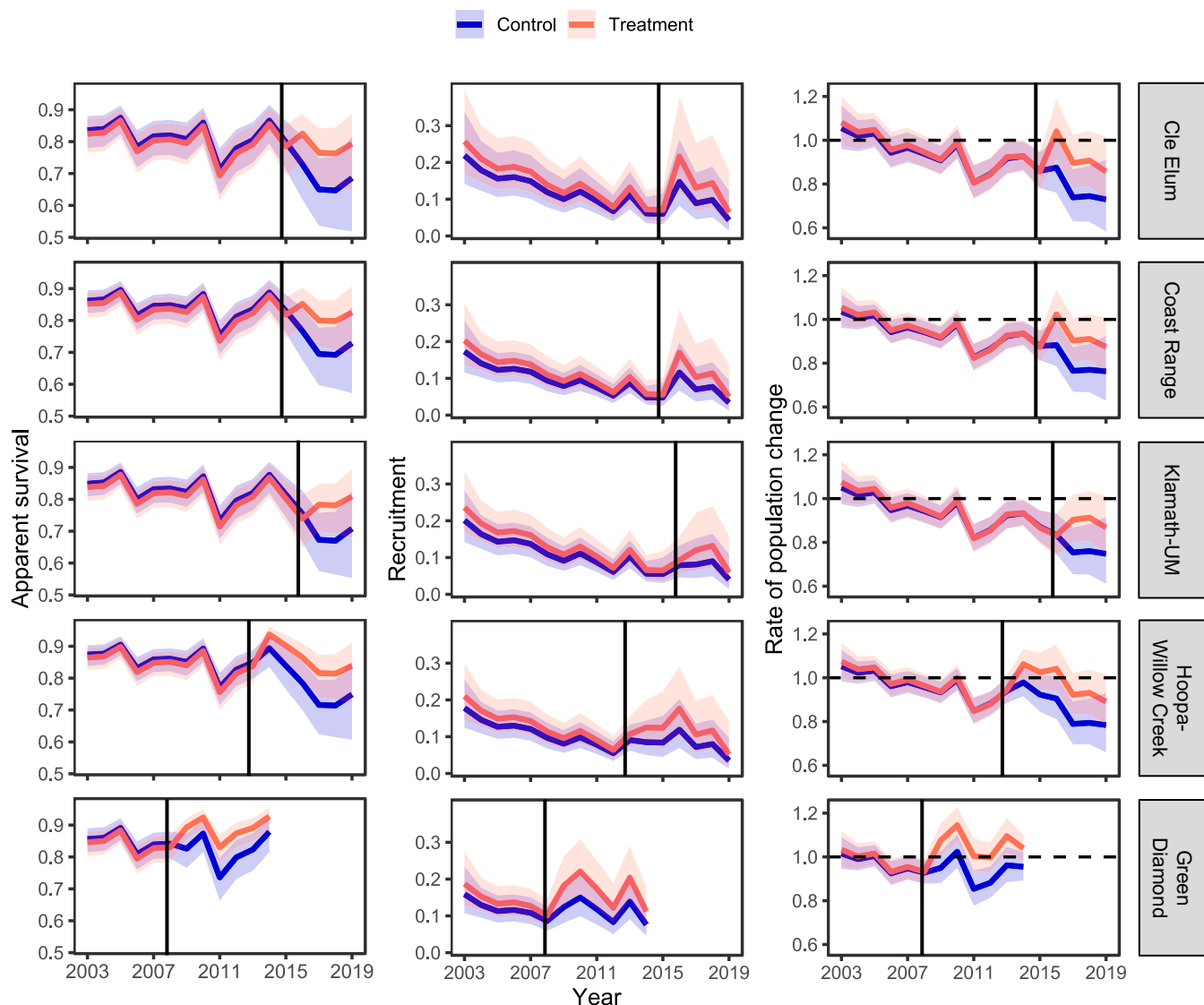


Fig. 3. Meta-analysis of estimated effects of barred owl removal on long-term population dynamics of northern spotted owls in five study areas in Washington, Oregon, and California. We show annual estimates of apparent survival, recruitment, and the rate of population change for treatment (barred owls removed) and control (no removal) areas. Estimates are from the best meta-analysis model with all study areas combined. Shaded regions represent 95% CIs; solid vertical lines indicate the start-date of barred owl removal on treatment areas.

and recruitment from the top-ranked model for final inferences and to derive estimates of the annual rate of population change (λ).

Before removing barred owls, mean estimates of annual population change ($\bar{\lambda}_t$) on both treatment 0.953 (95% CI: 0.914 to 0.993) and control areas 0.948 (95% CI: 0.913, 0.984) indicated a general decline across all study areas, with an increasing annual rate of decline prior to removals (Fig. 3). After removing barred owls, estimates of $\bar{\lambda}_t$ on treatment areas increased to 0.998 (95% CI: 0.899, 1.100), whereas estimates of $\bar{\lambda}_t$ on control areas decreased to 0.879 (95% CI: 0.776, 0.983). These estimates correspond to postremoval declines of 0.2% and 12.1% per year for treatment and control areas, respectively. The mean increase in λ_t attributable to barred owl removals was positive with 95% confidence limits that excluded zero in all study areas (Fig. 4C). The mean increase in λ_t in treatment areas relative to control areas across all study areas combined was 0.114 (95% CI: -0.039, 0.267). With the exception of GDR, point estimates of λ_t in treatment areas were <1 during the final 3 y of the study (2017 to 2019), but the magnitude

of annual declines was uncertain relative to that in control areas, as shown by upper 95% confidence limits that included 1.0 (stationary population) in areas with barred owl removal (Fig. 3).

Discussion

Our long-term removal experiment provided a clear demonstration of the demographic consequences of emergent competition, and competitive release, between two previously allopatric predators. Removal of invasive barred owls had a strong, positive effect on survival of native spotted owls, which in turn alleviated long-term population declines of this federally threatened species. Barred owl removal had a positive, but weaker, effect on recruitment of spotted owls. The weaker effect of removals on recruitment was likely a consequence of consistently depressed reproduction of spotted owls (and diminished availability of new recruits) during the later years of the study (10, 11, 27). Removal of competitors also influenced the dispersal dynamics of resident spotted owls in at least two study areas (COA, CLE), as shown by a marked increase in the

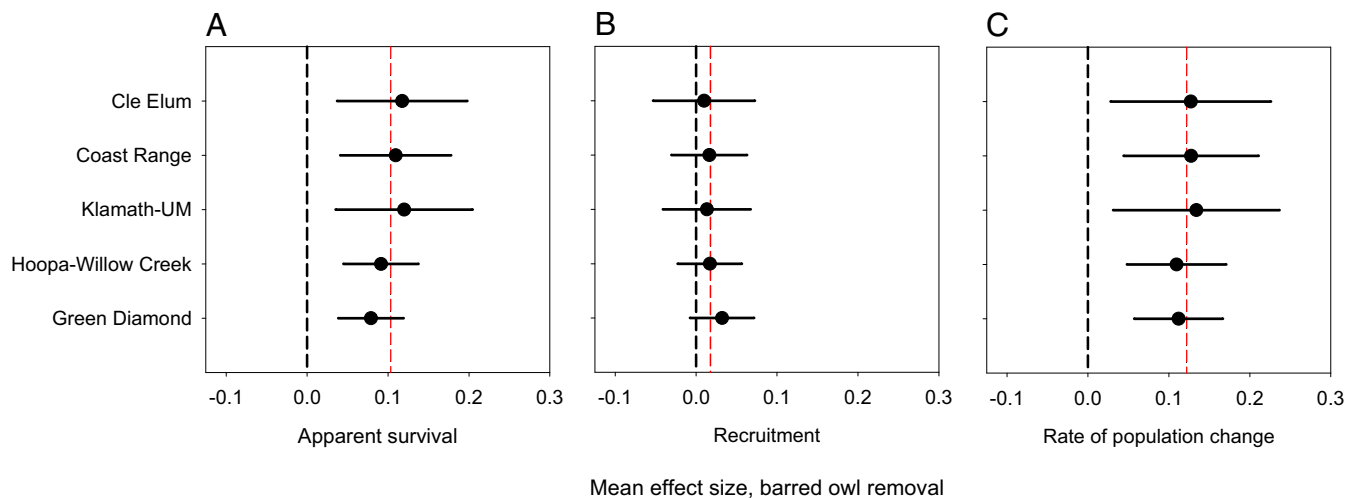


Fig. 4. Mean change in vital rates and population trends of northern spotted owls that was attributable to barred owl removal based on a meta-analysis of five experimental study areas in Washington, Oregon, and California. We show estimates of mean effect size for (A) apparent survival, (B) recruitment, and (C) rate of population change of northern spotted owls. Mean effect size was calculated using Eq. 2 and weighted geometric means of before–after, control–treatment estimates from the best meta-analysis model. Red-dashed vertical lines indicate mean effect sizes across the five study areas. Positive values with a 95% CI that did not overlap zero (black-dashed vertical line) indicate strong evidence that removals increased a given vital rate in the treatment (barred owl removal) area relative to the control area.

estimated probability of movement from territories in control areas to territories on treatment areas after barred owl occupants were removed.

The BACI design of the experiment was spatially replicated across much of the extent of the northern spotted owl's geographic range in the United States, thereby providing strong inference across a variety of environmental conditions in terms of forest types, prey availability, and densities of spotted owls and barred owls. There was unlikely to be any systematic, sustained bias in factors affecting the results because of the long duration of the study, the extent of spatial replication, and similarities in forest (and disturbance) conditions between paired treatment and control sites (SI Appendix, Fig. S2). The results establish that the most substantial changes in population dynamics of northern spotted owls during the study were associated with the invasion, population expansion, and subsequent experimental removal of barred owls. We conclude that barred owl removal can aid in sustaining populations of spotted owls, but that outcomes may vary depending on the size of remnant populations of spotted owls, densities of established populations of barred owls, and magnitude of change in other stressors affecting spotted owls (e.g., habitat loss, climate).

Demographic Consequences of Competitive Release. The availability and distribution of old forests promotes survival (16) and territory occupancy (10, 17, 24) of both spotted owls and barred owls. As such, a limited supply of old-forest resources underlies much of the competitive relationship between the two owl species. As barred owls invaded the geographic range of northern spotted owls, they displaced and subsequently excluded spotted owls from their breeding territories via interspecific territoriality (16). Barred owls also exhibit a high degree of ecological overlap with spotted owls in terms of space use, habitat selection, and diets (33). This combination of interference and exploitation competition led to decreased survival and recruitment of territorial spotted owls, thereby exacerbating historical population declines associated with habitat loss. Once barred owls were removed, spotted owl survival, rate of population change, and to a lesser extent, recruitment, increased. The mechanism by which vital rates increased was that of competitive release (34), which occurred as the realized niche of

spotted owls (compressed by competition from barred owls) (16, 35) approached the species' fundamental niche with reduced competition. With barred owls removed, the recently restricted ecological niche of spotted owls had expanded back into the niche space subjugated by the invasive competitor.

Our analyses of individual study areas provided strong evidence that barred owl removal increased survival of spotted owls in two study areas (KLA-UM, GDR) with weaker, but biologically relevant, evidence of increases in survival in the remaining three. The strong effect of removals on survival in KLA-UM was somewhat unexpected because this study area had the least amount of barred owl removal effort (3 y) relative to the other four study areas (4 to 6 y). Subtle differences in the response of spotted owls to barred owl removal among individual study areas may reflect regional differences in: 1) numbers of remaining spotted owls, 2) density of territorial pairs of barred owls in treatment areas prior to removals, and 3) postremoval recolonization rates of barred owls from landscapes surrounding treatment areas (23, 27). In the CLE and COA study areas, for example, we attributed a relatively weaker effect of removals to the sparse number of marked spotted owls remaining by the end of the study (10 to 20 individuals), which limited our ability to detect a statistically precise effect of removals in these areas. In HUP-WC, preremoval differences in apparent survival between control and treatment areas appeared to reduce the magnitude (and precision) of a full BACI effect in this paired study area despite an average 3% increase in mean apparent survival of spotted owls on the treatment area following removals. The size and precision of the estimated demographic response of spotted owls to barred owl removal may have varied among individual study areas, but the resulting trends in treated areas were a consistent improvement over alternative trends documented in control areas without removal.

The limitations we encountered in detecting a strong effect of barred owl removal for some individual study areas were overcome in the meta-analysis, which used the combined power of all study areas as experimental replicates to estimate treatment effects. This analysis provided robust evidence that removals increased apparent survival of spotted owls by ~10% across all study areas. The meta-analysis also indicated that the demographic impact of

barred owl removal on spotted owls was similar across study areas, despite differences among study areas in the occurrence and recolonization rate of barred owls after removals (23, 27). Constancy in removal effort among study areas, especially in the vicinity of sites occupied by spotted owls, may have contributed to a similar removal effect on spotted owls across areas. We also had high confidence that barred owl colonists were quickly detected and removed throughout the year, regardless of variation among study areas in the level of recolonization. Barred owl colonists in treatment areas had little time to establish and defend territories.

Previous studies suggest that barred owls may disproportionately impact apparent survival relative to other demographic traits of spotted owls, which could represent either increased mortality or permanent emigration beyond study area boundaries (10–12). Our study not only provided experimental evidence to support these findings, but also a deeper understanding of the mechanisms by which barred owls affected survival and dispersal movements of spotted owls. In our multistate analysis of survival and movement, for example, we showed that spotted owls in the COA and CLE study areas that had been displaced by barred owls from their territories on control areas before removals were able to detect and settle on new territory openings in treatment areas after barred owls were removed. These findings support the hypothesis that competitive release from barred owls increased apparent survival of spotted owls in some cases by allowing displaced, nonterritorial spotted owls to regain a territory after the barred owl occupants had been removed (16, 23, 36). Our findings further demonstrated that territorial interactions with barred owls are a primary cause of increased breeding dispersal movements observed in spotted owls over the past three decades (36).

In northern spotted owls, reproduction promotes future recruitment of new individuals into the territorial component of the population, while the additive effects of recruitment and apparent survival of territory holders define λ_t (11). Reproductive output by spotted owls was low and variable during the later years of our study (11, 27), which may in part explain the lack of a strong effect of barred owl removal on spotted owl recruitment. Low reproduction during the removal period indicated there were few younger, nonterritorial recruits available in landscapes to fill territory vacancies once barred owl occupants were removed. Following removals, a general pattern across study areas was the maintenance of survival (and estimates of λ_t) on treatment areas, with concurrent sharp decreases on control areas. This finding, coupled with low and variable recruitment, indicated that the immediate increase in λ_t on treatment areas relative to controls was a result of barred owl removal stabilizing apparent survival of resident spotted owls. With the exception of GDR, the estimated increase in survival (about 10%) was insufficient to result in positive population growth rates (i.e., $\lambda_t > 1$) near the end of the study period. Collectively, these results indicate that further increases in the annual rate of population change of spotted owls, or even maintaining stable rates of population change over time, will require increases in both reproductive rates and, subsequently, recruitment. Without additional recruitment, recovery and long-term persistence of spotted owls is unlikely.

Field experiments on the demographic consequences of competitive release between sympatric terrestrial predators are scarce. Notable exceptions include a field experiment on the impacts of reducing Eurasian badger (*Meles meles*) populations on densities of sympatric red foxes (*Vulpes vulpes*) (37). Results demonstrated that culling badgers, which are considered the dominant and more aggressive species, substantially increased fox densities through a combination of interference and exploitation competition. Elsewhere, coyote (*Canis latrans*) removals have triggered increases in the abundance of sympatric mesopredators, including badgers, bobcats (*Felis rufus*), and gray foxes (*Urocyon cinereoargenteus*)

(38). More recently, large-scale BACI experiments in southern British Columbia showed that reducing rapidly expanding populations of moose (*Alces alces*) stabilized declining population trends of Woodland caribou (*Rangifer tarandus caribou*) by reducing abundance of wolves (*Canis lupus*), a shared predator (39). Similar to the results of our experiment, the moose-removal experiment showed how a single management action (species removal) can effectively halt population declines of focal species, but that actions addressing multiple limiting factors (e.g., habitat, climate) are required to achieve population growth and long-term persistence.

Prospects for Management. The barred owl removal experiment represents a culmination of sequential studies implemented in the same system over time, where demographic monitoring was first used to accumulate knowledge on the complexity of factors affecting population dynamics of spotted owls. Those observations were then formally tested within a large-scale experimental framework. The natural next step would be adoption of this evolving information state into a management context (40). Experimental results indicate that barred owl control can achieve rapid results in benefitting the persistence of northern spotted owls, at least over the short term. This does not suggest that barred owl control alone is sufficient to achieve recovery of spotted owls, as the availability of older forests is a necessary condition for barred owl removal to succeed. The rate of decline of spotted owl populations in control areas by the end of the study was severe (~12% per year), indicating an increasingly high risk of these populations to local extirpations. A number of mechanisms that negatively affect small populations, including environmental stochasticity and Allee effects (11, 41), will make it increasingly difficult to recover spotted owl populations in some regions. Fast-moving development and implementation of management actions for barred owls based on experimental results, coupled with long-term management of suitable forest conditions, will be essential to the recovery and persistence of northern spotted owls.

The conservation and restoration of old forests, which has been a chief focus of recovery strategies for the northern spotted owl (19), is a major source of socio-economic controversy in the Pacific Northwest (42). The barred owl invasion has exacerbated this issue, placing an even higher ecological premium on remaining old conifer forests. Barred owls have become widespread and hyperabundant throughout much of the northern spotted owl's geographic range (27). Even if barred owls can be maintained at low levels in some areas, we believe it is inevitable that the species will continue to exert substantial ecological pressure on spotted owls and other native wildlife. Broad-scale management of barred owls, including lethal removal, would require a long-term resource commitment, as any lapse in management could allow barred owls to quickly recolonize and erode conservation gains. This prospect raises questions about how long removals could and should be perpetuated; public acceptance and values associated with such actions are an important consideration (43).

Culling overabundant invasive species to manage their ecological impacts on target species is widely practiced, but outcomes are often unpredictable (43). Our study represents a promising example of successful removal and suppression of an invasive and increasingly abundant competitor, with a positive demographic response from a threatened native species. While suppression of barred owls can be difficult, costly, and ethically challenging, improvements in vital rates and population trends of spotted owls, and perhaps other threatened wildlife, can be expected when densities of barred owls are reduced from current levels. Alien predators are considered to be more harmful to prey populations than native predators (44), and the dynamic interactions between invasive and native predators can lead to profound changes in ecosystems by precipitating trophic cascades, often with considerable conservation and economic impacts (45, 46). In this sense,

long-term management of barred owls may be critical not only to the preservation of spotted owls, but also to conservation of biodiversity in old-forest ecosystems of the Pacific Northwest.

Materials and Methods

Study Areas and Experimental Design. The barred owl removal experiment was spatially replicated on five study areas distributed across the geographic range of the northern spotted owl (Fig. 1D and Table 1). All study areas had long-term, mark-recapture demographic data on northern spotted owls (10–12) and represented a range of different forest conditions cooccupied by spotted owls and barred owls (20). We included data from the pilot removal study in California (GDR), which included 1 additional year of barred owl removals and spotted owl demographic data not previously analyzed (23) (Table 1). The five study areas varied in climate, vegetation composition, and topography, but all were dominated by conifer or mixed conifer-hardwood forests (10, 20). The fieldwork occurred on federal, private, tribal, and state lands so that results and inferences would not be limited to certain ownerships and forest conditions.

Ideally in ecological experiments, treatment and control plots should be randomly selected and alternated during the study period to avoid the potentially confounding effects of unknown plot differences on results (47, 48). This was not possible in our study due in part to scale and logistics, but also because of considerations such as availability of pretreatment demographic data on spotted owls, land ownership restrictions, and the need to remove barred owls in the same areas over several years to limit compensatory immigration from surrounding landscapes (23, 27). Therefore, we divided each study area into two or more similar treatment (barred owls removed) and control (barred owls not removed) areas with respect to number of historical spotted owl territories, forest structural conditions within owl sites, and forest disturbance (e.g., wildfire, timber harvesting) (SI Appendix, Supplementary Text). This process resulted in five paired before–after treatment and control areas totaling 3,145 km² and 3,404 km², respectively (Fig. 1D and Table 1).

Demographic Monitoring and Barred Owl Removal. The removal experiment was conducted within the framework used to assess range-wide population status and trends of the northern spotted owl (10–12, 25, 49). As such, we integrated our experimental design and analysis into existing protocols used by these previous studies. Although demographic monitoring of spotted owls generally began in 1985 to 1990, we used 2002 as a common start year for demographic analyses across all study areas. This narrowed the pretreatment timeline of the experiment to a period when barred owls had become well established and were having measurable impacts on spotted owls (10). Spotted owls were surveyed during the breeding season of each year (March to August) using standardized protocols to document occupancy status of territories, locate and confirm previously banded owls, band unmarked owls, and document reproduction (50, 51).

We used barred owl-specific surveys to locate and remove barred owls throughout the year (26, 27). Our protocol for removals prohibited collection of nesting barred owls with dependent young, so removals were completed primarily in the nonbreeding season (September to April), or limited to barred owls not provisioning young during the breeding season. Barred owls detected in treatment areas were removed using a 12-gauge shotgun (22, 27). We did regular follow-up visits to detect colonizing owls and conduct additional removals as needed throughout the year. Repeated surveys and removals of barred owls indicated frequent and regionally variable recolonization of treatment areas by barred owls (23, 27). The single-visit detection rate of barred owls during surveys was generally high (66 to 74%) (26, 27), so we were confident that newly colonizing barred owls in treatment areas were quickly detected and removed. This dynamic of seasonally intermittent and temporary use of treatment areas by colonizing barred owls, which was a consistent pattern across experimental study areas, was in stark contrast to control areas where the majority of historical spotted owl territories were occupied by well-established resident pairs of barred owls (27). Removal and scientific collection of barred owls was approved by the Institutional Animal Care and Use Committee at Oregon State University and completed under Federal Fish and Wildlife and State Scientific Collection Permitting.

BACI Analysis. We determined the influence of barred owl removal on population dynamics of spotted owls using a paired BACI experimental design with long-term mark-recapture data. This approach permitted the impact of removal to be reliably distinguished from background time effects or underlying pretreatment differences in spotted owl vital rates between treatment and control areas. We conducted two different BACI analyses, where the first examined the effect of removals on survival and dispersal of spotted owls

(i.e., movement between control and treatment sites) for each study area separately, and the second combined data from all five study areas in a meta-analysis of apparent survival, recruitment, and annual rate of population change (SI Appendix, Supplementary Text). For both analyses, we used program MARK to develop candidate models and estimate model parameters (52).

Previous studies of spotted owl population dynamics (10–12) and a pilot barred owl removal study (23) guided our analytical approach. We included all banded, territorial birds, and combined second-year and adult birds into a single age class (10, 11). For each analysis we began with a general fixed-effects model structure and then constrained model parameters in sequential sets (53), where capture probabilities (p) were modeled first, and the best structure was retained as we moved on to model focal demographic parameters. At each modeling stage, we used AIC_c and Akaike weights (w_i) to select between competing models, while retaining the nonfocal parameters in their most general form. We generally selected the model with the lowest AIC_c value and highest Akaike weight (w_i) as our best-supported model, but models within two AIC_c units ($\Delta\text{AIC}_c \leq 2.0$) were further evaluated as potentially competitive models (54).

Before testing for an effect of barred owl removal, we first investigated underlying variation in capture probabilities and vital rates of spotted owls with respect to: 1) treatment versus control areas, 2) time (categorical effects of year, and a continuous time trend [T]), 3) owl sex, and 4) study areas (meta-analysis only). For capture rates, we included models with an individual-specific random effect intercept term, $\sigma_p(\cdot)$, to account for potential unexplained heterogeneity in capture rates among marked individuals (55) (SI Appendix, Supplementary Text). We assumed minimal overdispersion of the data (i.e., $\hat{c} = 1$) because: 1) previous analyses of spotted owls detected little to no lack of independence of the data (12, 25), and 2) models with an individual random effect on capture probability are robust to overdispersion (55).

We tested for an effect of barred owl removal on vital rates of spotted owls by introducing a time (before–after) \times treatment (control–impact) interaction to the best models characterizing baseline variation in sex, time, and preremoval differences between treatment and control areas. We specified a basic fixed-effects BACI model as:

$$\theta_{ij} = \beta_0 + \beta_1(\text{period}_i) + \beta_2(\text{treated}_j) + \beta_3(\text{period}_i \times \text{treated}_j), \quad [1]$$

where θ_{ij} was a given vital rate between year i and $(i + 1)$ on area j , period_i was a before–after indicator (0 before removals began and 1 after removal began), and treated_j was an indicator for treatment sites with barred owl removal (0 for areas never treated and 1 for areas treated at some point during the study). This model structure embraced classic BACI concepts in that it provided a direct test of whether changes in vital rates from the preremoval to postremoval time periods were different in treatment compared to control areas (23, 56, 57). Specifically, if removal of barred owls on the treated area had no effect on a given vital rate, the BACI interaction term (β_3 in the example above) would be 0 because β_3 measures pre- and posttreatment differences between treated and control areas. Thus, if β_3 was >0 , we concluded that removal of barred owls had a positive effect. In other words, $\beta_3 > 0$ indicated that barred owl removal increased the vital rate above that expected by the pretreatment difference between controls and treatments. A positive β_3 term with a 95% CI that did not overlap 0 was the strongest evidence of an effect. Positive effects with $\leq 10\%$ of the 95% CI “slightly” overlapping 0 were regarded as weaker, but biologically relevant, evidence of an effect. We compared models with $(\text{period} \times \text{treated})$ to an additive model $(\text{period} + \text{treated})$ and used evidence ratios to characterize the weight of evidence for models with barred owl removal effects (54). We also included a model with a before–after covariate ($BA:\text{treat}$) that was specific to treated sites during the removal period (56). Similar to a full BACI model, a model with $BA:\text{treat}$ tested for a before–after change in vital rates on treated areas relative to control areas. A key difference between the two models was that the full BACI model allowed parameters to vary before and after removals on both treatment and control areas, whereas a model with $BA:\text{treat}$ (and two fewer parameters) allowed vital rates to vary before and after removals on treatment areas only (i.e., assumes no before–after change on control areas).

We estimated the mean amount of change in vital rates that could be attributed to barred owl removal (mean effect size) as:

$$\left(\hat{\theta}_{\text{treatment:after}} - \hat{\theta}_{\text{control:after}} \right) - \left(\hat{\theta}_{\text{treatment:before}} - \hat{\theta}_{\text{control:before}} \right), \quad [2]$$

where $\hat{\theta}$ was the weighted geometric mean of annual estimates for a given vital rate from the best BACI model. We used the reciprocal of variances and the variance-covariance matrix output from MARK to calculate weighted means, SEs, and 95% CIs. Positive values with a 95% CI that did not overlap zero provided evidence that removals increased a given vital rate on treated areas relative to controls.

Data Availability. Data included in the manuscript and supporting information are available to qualified researchers upon request from the corresponding author.

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Severe fire weather and intensive forest management increase fire severity in a multi-ownership landscape

HAROLD S. J. ZALD^{1,3} AND CHRISTOPHER J. DUNN²

¹Department of Forestry and Wildland Resources, Humboldt State University, 1 Harpst Street, Arcata, California 95521 USA

²Department of Forest Engineering, Resources, and Management, Oregon State University, 280 Peavy Hall, Corvallis, Oregon 97331 USA

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 \pm 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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³ E-mail: hsz16@humboldt.edu

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, pre-fire 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.

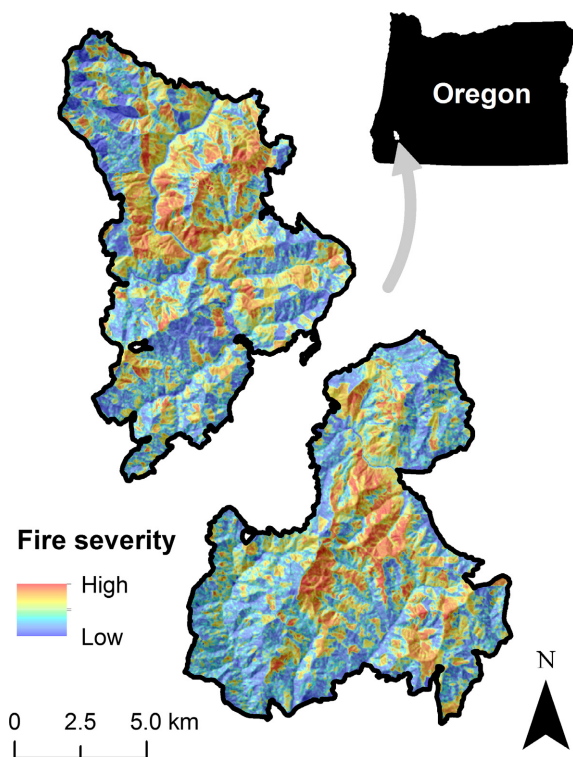


FIG. 1. Location of and fire severity within the Douglas Complex in Oregon, USA. Fire severity quantified using the Relative differenced Normalized Burn Ratio (RdNBR).

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 densiflorus*). 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 $NBR_{\text{post-fire}}$ from $NBR_{\text{pre-fire}}$ values, and RdNBR was then calculated following Miller et al. (2009), where:

$$RdNBR = \frac{dNBR}{\sqrt{\text{Absolute Value } (NBR_{\text{pre-fire}}/1,000)}}. \quad (1)$$

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 ($\text{MJ}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$). 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 a 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-needed

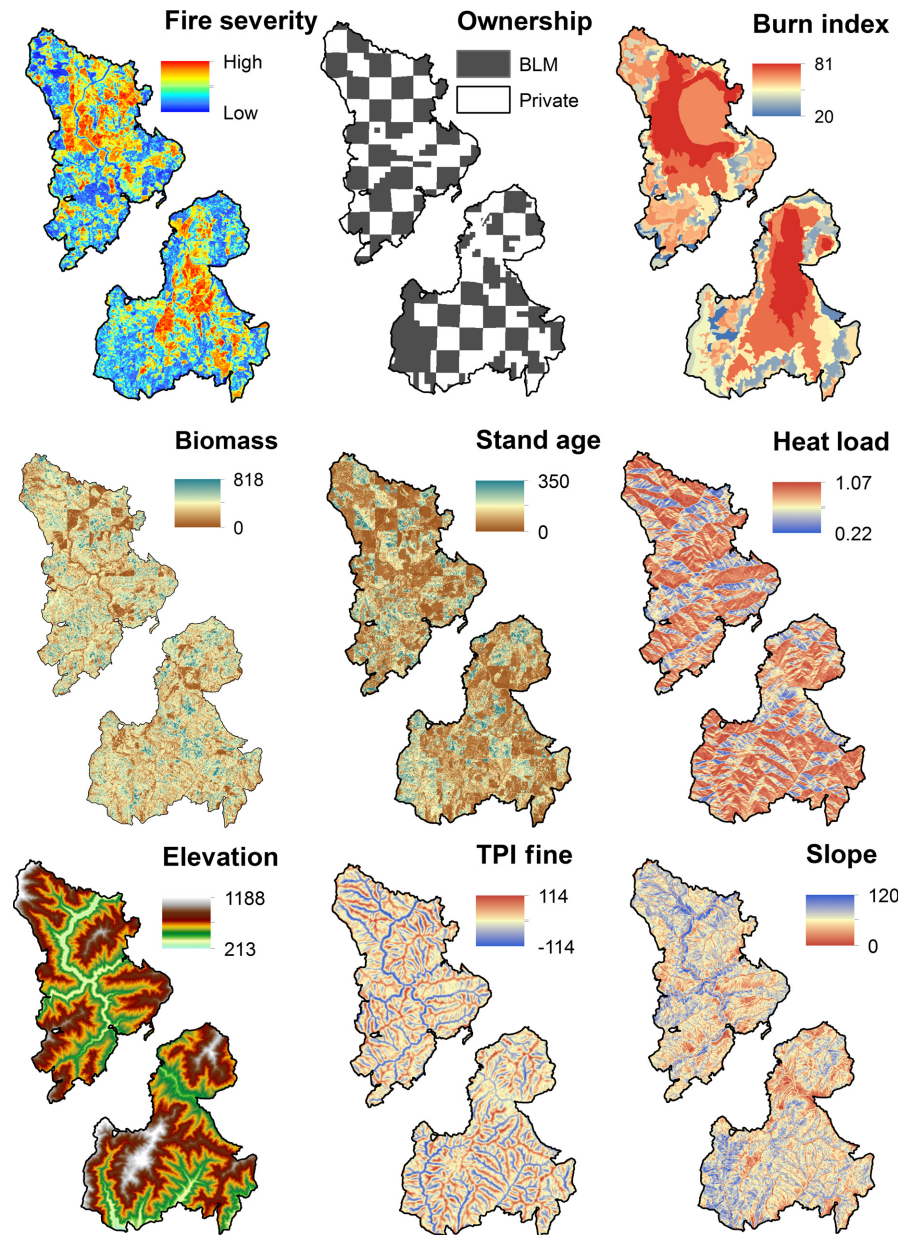


FIG. 2. Maps of response and predictor variables for Douglas Complex. TPI, topographic position index.

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 ($\Delta AIC = 3.3816$), 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.

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 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	$L(g_i x)$	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; $L(g_i|x)$, likelihood of a model given the data; w_i , Akaike weights; SC, spread component; BI, burn index; RH, relative humidity; ERC, energy release component.

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.

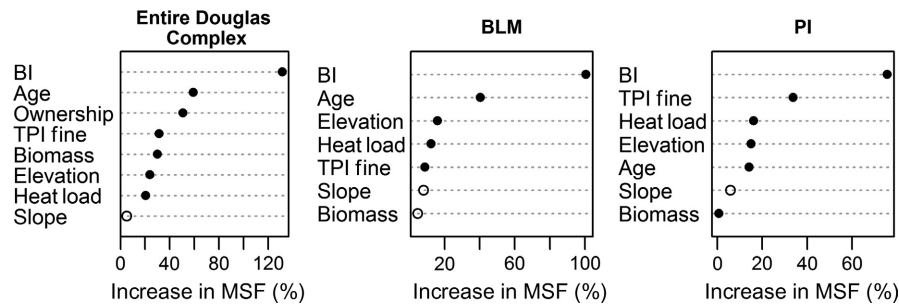


FIG. 3. Variable importance plots for predictor variables from Random Forest (RF) models of RdNBR for 1090 sample plots across the entire Douglas Complex (left panel), 571 plots on Bureau of Land Management (BLM) forests (middle), and 519 plots on private industrial (PI) forests (right). Solid circles 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.

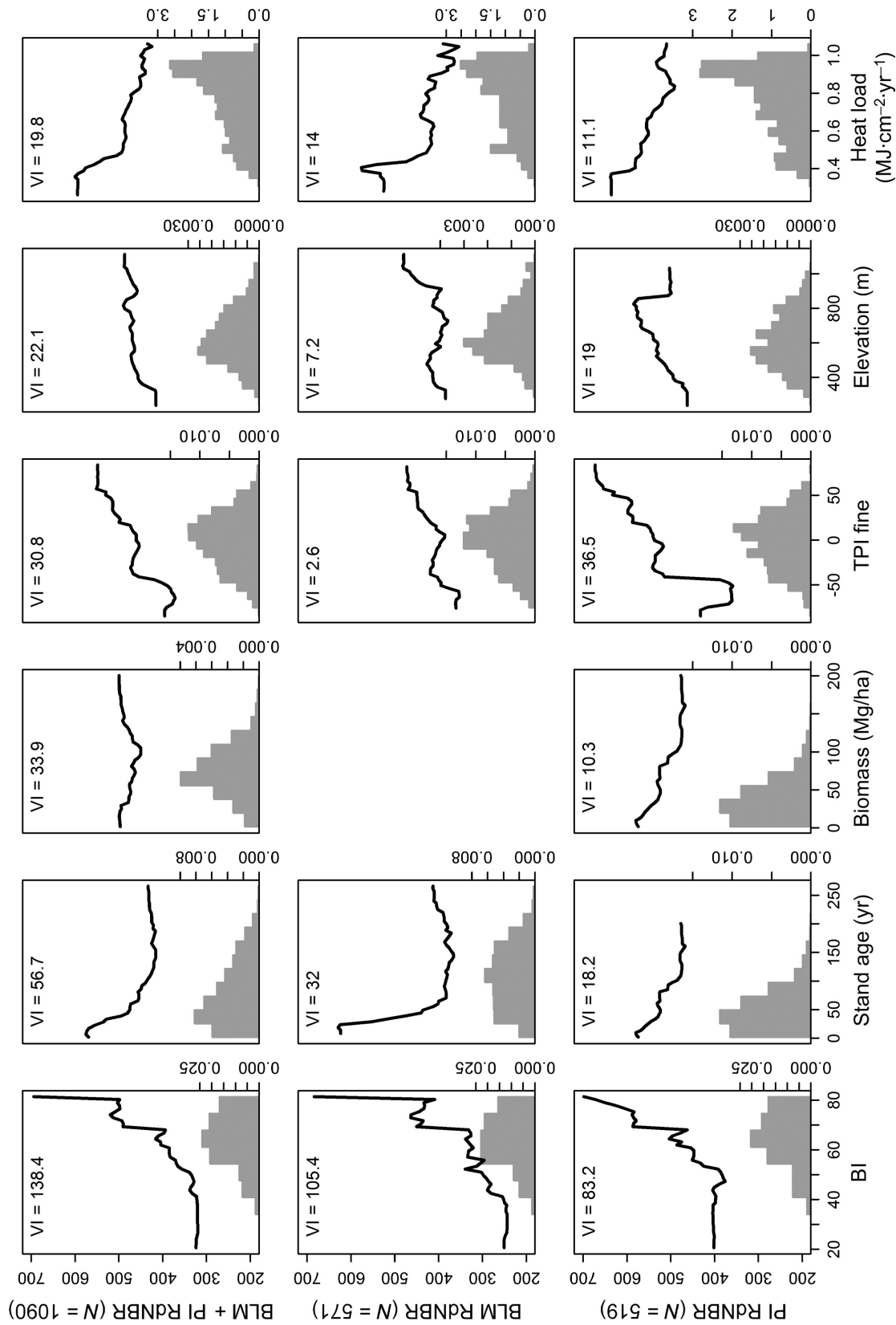


FIG. 4. Partial dependency plots showing relationships between each predictor variable and response variable for all forests (BLM and PI, top panels), forests on Bureau of Land Management (BLM, middle panels), and private industrial land (PI, bottom panels). Number within each panel shows variable importance (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 based on two-stage variable selection procedures.

TABLE 3. Coefficients of predictor variables in generalized least squares model of RdNBR.

Variable	Parameter estimate	SE	<i>t</i>	<i>P</i>
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 \pm 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 wild-fire 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>